Purely endogenous capture of attention by task-defining features proceeds independently from spatial attention

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ABSTRACT

Attention can be focused voluntarily and effectively on spatial locations in order to enhance the processing of task-relevant events. However, work on 'attentional capture' has demonstrated that spatial biases can be temporarily reset by transient and salient stimuli, especially if they share defining characteristics with the targets of a task goal. In the current study, we investigated whether the appearance of stimuli containing task-defining features at an unattended location was sufficient to capture attention, even when these were not perceptually salient. We used event-related-potential (ERP) markers to test whether the selection of task-defining features was modulated by top-down spatial attention, and to test whether the appearance of 'unattended targets' transiently disrupted the spatial bias. Surprisingly, the results revealed that ERP markers of selection of task-defining features were equivalent for stimuli appearing at spatially attended and unattended locations. In addition, the presentation of task-defining stimuli at the spatially unattended location induced a short-lived redistribution of the pre-established spatial attention bias toward the 'capture' side. These findings show that task-defining features of a stimulus are automatically processed independently from spatial attention, and suggest the co-existence of multiple sources of top-down biasing signals, which might in part sustain the capture mechanism.

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Introduction

It is clearly established that we are able to orient attention voluntarily to a spatial location to monitor for task-relevant events. Spatial orienting is an effective mechanism, which results in reliable facilitation of behavioural and neural responses to items appearing at attended vs. ignored locations (Posner, 1978, 1980; Hillyard and Anllo-Vento, 1998; Luck et al., 2000; Reynolds and Desimone, 2003). In vision, many of the modulatory actions of spatial attention have been charted, at both the cellular and system levels in the brain. Spatial attention biases neuronal firing rates and synchronisation, as well as receptive-field properties, toward the items appearing at the relevant, attended spatial location starting from very early levels of stimulus analysis (Desimone and Duncan, 1995; Luck et al., 1997; Fries et al., 2001; O'Connor et al., 2002; McAlonan et al., 2008).

Despite these strong biases, the spatial focus of attention does not completely shut-off the processing of items of possible behavioural relevance appearing at other locations. Early research using the dichotic listening paradigm (Cherry, 1953), showed that semantic information about items of particular significance to participants could occasionally break through into awareness (e.g., Treisman, 1964; Corteen and Wood, 1972). More recently, research on attentional capture has shown that transient or salient stimuli are able to disrupt the current focus of attention and re-direct it to their location (Yantis and Hillstrom, 1994; Ruz and Lupianez, 2002; Rauschenberger, 2003). Controversy remains as to whether attentional capture can be driven purely by bottom-up factors related to the saliency of the stimulus features (e.g., Theeuwes, 1991a, 2004; Hickey et al., 2006), or whether capture is necessarily contingent upon top-down factors related to the presence of task-defining features (Folk et al., 1992; Yantis, 1993; Folk and Remington, 1998; Folk et al., 2002).

Less controversial, but perhaps more intriguing, is the ability of task-defining features to influence the degree of capture (Folk et al., 2002; Leblanc et al., 2008). Such an observation suggests that the top-down set comprising the task-defining features is also capable of biasing ongoing neural processing, over and above any salient low-level feature of the stimuli. In turn, this would suggest the co-existence of multiple sources of top-down biasing signals (Serences et al., 2005; Serences and Yantis, 2007). In line with this interpretation, single-unit and brain-imaging studies have shown that the selection of a task-relevant feature, such as direction of motion or colour, can bias neural activity across spatial locations, including locations that are irrelevant

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to the task at hand (Treue and Martinez Trujillo, 1999; Saenz et al., 2002; Egner et al., 2008).

Whether and how these biases carried by voluntary monitoring of a spatial location and by the detection of task-relevant features interact is not well understood. We investigated this issue in the present experiment by recording event-related potentials (ERPs) while participants performed an adaptation of a task developed by Yantis et al. (2002) to study voluntary and stimulus-driven shifts of spatial attention. We tested whether non-salient stimuli matching the task set were detected outside the focus of spatial attention, whether selection of task-defining features was modulated by spatial attention, and whether the presence of task-defining features at unattended locations was sufficient to capture attention away from the monitored spatial location.

Following up on a previous report in which we charted neural activity related to voluntary shifts of spatial attention and subsequent perceptual modulation of visual processing by spatial attention in this same task (Brignani et al., 2009), here we analyse the neural activity related to the presentation of stimuli containing the task-defining features at the attended, relevant spatial location (targets) and at the unattended spatial location (capture events). In this task, participants viewed rapidly presented peripheral streams of visual letter stimuli covertly. They focused attention upon one stream at a time to detect pre-designated target stimuli (the letter 'X' or 'O').

We used the N2pc potential (Luck and Hillyard, 1994; Eimer, 1996) as a marker of the selection of the task-defining stimulus shapes in the spatially attended and unattended streams (Kiss et al., 2008b). To date, the N2pc potential has been measured mainly in the context of visual search tasks, where it has been shown to be elicited both by targets and by non-target stimuli that share task-relevant features or that are particularly salient (Luck and Hillyard, 1994; Girelli and Luck, 1997; Hickey et al., 2006; Jolicoeur et al., 2006; Eimer and Kiss, 2008; Kiss et al., 2008a; Leblanc et al., 2008). Recent publications have further indicated that the N2pc reflects some aspect of stimulus selection rather than the act of orienting spatial attention to a particular location or distractor suppression (Kiss et al., 2008b; Mazza et al., 2009).

Our initial hypothesis was the intuitive one: that spatial attention would facilitate the processing of targets at the attended side. We expected the N2pc elicited by spatially attended targets to be larger or to commence earlier than the N2pc elicited by spatially unattended stimuli sharing the task-defining features. However, since we started running our experiment, two recent papers showed minimal effects of spatial attention on the N2pc potential triggered by salient singleton or transient events appearing at unattended locations (Leblanc et al., 2008; Seiss et al., 2009). Both papers also showed that the size of the N2pc was correlated to the degree to which the capture item shared the relevant task-defining features. Our investigation builds on this foundation to test the counterintuitive possibility that task-defining features are sufficient to induce 'contingent capture' even in the absence of any salient low-level feature, and that the processing of these features proceeds unabated by top-down voluntary spatial attention.

We also investigated the consequences of capture by stimuli with task-defining features appearing at the task-irrelevant location upon subsequent perceptual events. One might expect that after capture, spatial attention would linger over at the incorrect (capture) side until it is efficiently re-allocated. We have previously shown that in our task, which uses bilateral peripheral arrays, the amplitude of the visual P1 over the posterior contralateral scalp correlates with the voluntary allocation of spatial attention to a particular side. If a stimulus with task-defining features were able to pull attention to its own side, the transient re-direction of spatial attention would lead to a transient enhancement of the P1 contralateral to the capture event and therefore a disruption of the previously established P1-amplitude asymmetry.

Materials and methods

Participants

Eighteen healthy volunteers participated in this experiment. Data from two participants were excluded from the analysis because of excessive noise in the recording in one and poor performance accuracy in the other one. The remaining 16 participants (10 females) had a mean age of 26.7 years (range of 19 to 47). All were right-handed according to the Edinburgh handedness inventory test (mean score: +92) (Oldfield, 1971) and had normal or corrected-to-normal visual acuity. The experimental methods were non-invasive and had the approval of the Ethics Committee of the University of Oxford. Informed consent was obtained from all participants.

Behavioural task

The task design combined features of tasks used previously by Yantis et al. (2002) and Rushworth et al. (2005). The display consisted of a central fixation box and a set of four rapid-serial-visual-presentation (RSVP) streams on each side (Fig. 1). All visual stimuli were presented in light grey on a black background. Subjects were instructed to maintain visual fixation on the central box and to focus attention upon one stream at a time in order to detect target stimuli. They were instructed to press the space bar whenever a target letter (i.e. 'X' or 'O') appeared on the instructed side (attended side), while ignoring their appearance on the other side (unattended side). Target letters appeared only within the two peripheral streams that were closest to fixation, centred at 4.2° to the left and right of the central fixation box along the horizontal meridian. The other streams surrounding the two central streams on three sides with an edge-to-edge separation of 1.05°, served as flanking distracters to increase perceptual selection demands.
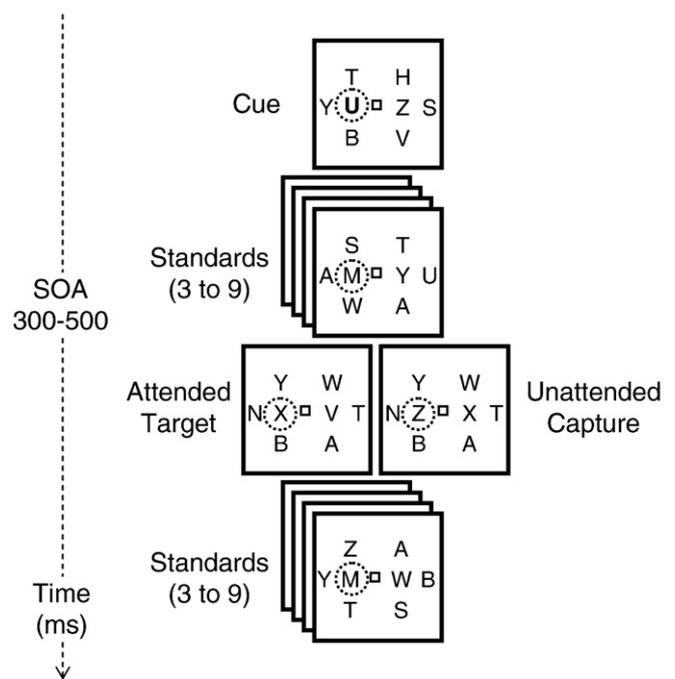
Fig. 1. Schematic illustration of the task. Participants were instructed to press the space bar whenever a target letter 'X' or 'O' appeared on the instructed side (attended targets), while ignoring their appearance on the other side (unattended captures). The attended side, represented here by dotted circles only for illustrative purposes, was indicated by coloured cue letters, which prompting participants either to maintain the spatial focus of attention or to shift the focus of attention to the other side. All visual stimuli were rendered in light grey on a black background. Cue letters are in bold here, but were presented in red and green during the experiment.

The streams were temporally synchronised. Their presentation lasted for 50 ms and they changed identity with a stimulus-onset asynchrony (SOA) randomised between 300 and 500 ms. The letters A – B – H – M – N – S – T – U – V – W – Y – Z were used as distracters and the letters X – O were used as targets, each one subtended approximately .56° horizontally and .7° vertically. There were no other task-defining features other than the shape of the letters and there were no pop-out features that could guide target identification. Target identification was difficult, and relied purely on shape discrimination. At the beginning of each experimental block, a small tick mark appeared to one side of the fixation box for 3 s, indicating the initial side that was relevant for target detection. Subsequently, coloured not-target letters (i.e., red and green) appearing within the RSVP stream served as spatial 'cues', instructing participants either to maintain the spatial focus of attention (hold cue) or to shift the focus of attention to the other side (shift cue). Shift and hold cues appeared with equal probability and in a randomised and unpredictable order. For half the participants, a green letter instructed them to maintain attention at the currently attended location, while a red letter instructed them to shift attention to the currently unattended side. For the other half of the participants the colour association was reversed. In total, there were 260 cues, 230–280 attended targets and 230–280 unattended captures. Overall, attended and unattended targets appeared equally often on the left and right sides. Targets and cues were embedded within streams of standard letter stimuli in a random order, with the constraint that they were separated by at least 3 and at most 9 standard items (1350–5450 ms). Consequently, each target and each cue was always followed by at least 3 standard arrays. A more detailed description of the experimental paradigm is provided in Brignani et al. (2009).

Participants had to maintain a high level of focused attention throughout the entire experimental block in order to detect the imperative target stimuli and the instructive cues. They performed 26 experimental blocks, each lasting about 90 s. Participants sat in a dimly illuminated room at 80-cm distance from a computer screen. A chin rest ensured that they were centred with respect to the monitor and keyboard. They were instructed to maintain visual fixation on the central box and to avoid making eye movements during the experimental blocks. Eye position was monitored with an ISCAN RK-464 eye-tracker (ISCAN Inc., Burlington, MA). Participants used their right and left hands alternately for half of the task. The starting hand was counterbalanced across participants.

Behavioural analyses

Separate corroborating behavioural evidence was collected to confirm the efficacy of the task in manipulating the focus of spatial attention (Brignani et al., 2009 Experiment 1). We compared the behavioural performance in a focused attention condition equivalent to that used in the present experiment with performance in a divided-attention condition, in which participants were instructed to detect targets in both peripheral streams simultaneously. Results revealed that participants were significantly more accurate in identifying peripheral targets under conditions of focused attention (87%) compared to divided attention (81%) [$F(1,14) = 5.39$, $p = .036$]. Performance to detect targets in the right visual field was also reliably better than that for detecting targets in the left visual field [$F(1,14) = 9.44$, $p = .008$].

In the present experiment we evaluated accuracy (i.e., % correct responses) and reaction times (RTs) by comparing targets appearing on the right and left sides through two separate paired *t*-tests. Only blocks in which participants maintained the correct focus of spatial attention as directed by the spatial cues were analysed. The loss of the correct relevant side for target detection was clearly indicated by a concomitant severe drop in accuracy and surge of false alarms (i.e., responses to X's and O's appearing at the unattended side). This

occurred in only one block across all participants, which was excluded from the analyses.

ERP recordings and data processing

The electroencephalogram (EEG) was recorded continuously with active electrodes mounted on an elastic cap (http://www.biosemi.com) from 128 standard locations according to the 10-5 electrode system (Oostenveld and Praamstra, 2001). Two additional electrodes placed on the right and left mastoids were used as off-line reference sites, and four other electrodes were used to record the eye movements (EOG) bipolarly. Horizontal EOG was measured by electrodes placed on the left and right of the external canthi. Vertical EOG electrodes were placed above and below the left eye. EEG and EOG signals were amplified with a band-pass filter of 0–417 Hz by BioSemi Active-Two amplifiers, and digitized at a sampling rate of 2048 Hz.

The continuous EEG recordings were segmented off-line. Epochs were constructed from 100 ms before to 500 ms after (1230 points) stimuli of interest: (a) attended targets and unattended capture events; (b) standard arrays appearing in the first, second and third position after attended targets and unattended capture events; (c) standard arrays appearing in the third position after the cue presentation. Data were re-referenced to the mean of both mastoid electrodes and re-filtered digitally with a low-pass of 40 Hz. All amplitude values were referred to the 100-ms pre-cue baseline. Epochs with excessive drift, eye movements, blinks, or muscle artefacts were excluded from analysis. Trials were automatically eliminated if the voltage exceeded ±50 μV at either the vertical or horizontal EOG channels or if it exceeded ±100 μV at any other channel. In addition, the EOG channels were inspected visually. Trials corresponding to incorrect behavioural performance were also eliminated from the analysis. Separate averages were computed for attended (targets) and unattended (capture events) stimuli with task-defining features, and for each type of standard array (first, second and third position after attended targets; first, second and third position after capture events; third position after the cues).

ERP analysis

Two sets of statistical analyses were conducted, in which we investigated (a) the effects of spatial attention on the N2pc elicited by attended targets and unattended capture events and (b) the consequence of contingent capture upon the visual P1 potentials elicited by subsequent standard stimuli.

Modulation of N2pc elicited by attended targets and unattended capture events

First, we analysed the N2pc elicited by X and O stimuli appearing within the attended versus unattended position. Because the spatial attention bias is well known to influence the amplitude of the contralateral visual potentials, direct comparisons between ERPs at electrode sites contralateral vs. ipsilateral to the target would also include attention-related differences in the earlier visual potentials (especially differences related to P1 enhancement contralateral to the direction of spatial attention) (see Brignani et al., 2009). In order to avoid contamination of the N2pc by other lateralised influences of attention, ERPs triggered by standard arrays appearing in the third position after cues were subtracted from ERPs elicited by attended or unattended target stimuli. Because of the well known property of ERPs to summate linearly (Vaughan et al., 1983; Allison et al., 1986), the resulting subtraction waveforms isolated processing related to the specific stimulus array, uncontaminated by the general influences of modulations related to pre-established biases in spatial attention. We used ERPs from standard arrays appearing in third position after cues because they provided a reliable signal without contamination from

processes related to response execution or to shifting spatial attention. All the analyses described in this section were performed on the subtraction waveforms even if not explicitly mentioned.

The N2pc was quantified by measuring mean amplitudes at lateral posterior electrodes contralateral and ipsilateral to the side of the stimulus containing the task-defining features (A10/B7, A11/B8, A12/B9, D31/B11 and D32/B10) (see Fig. 2) in the 200–300 ms time window. Mean amplitudes were analysed in a three-way repeated-measures ANOVA testing the factors stimulus type (target, capture), hemisphere (ipsilateral, contralateral to the eliciting stimulus) and electrode site (5 levels).

Additional ANOVAs tested the effects of spatial attention upon the mean-amplitude and the peak latency of the lateralised N2pc potential. The N2pc for target and capture events was isolated by calculating the difference between waveforms at electrodes contralateral versus ipsilateral to the stimulus. Mean-amplitude values were measured between 200 and 300 ms, as above. The latency range was increased to 200–330 ms for peak-latency measures, to ensure the peak could be reliably measured across participants. In both analyses, ANOVAs tested the factors stimulus type (target, capture) and electrode site (5 levels).

Modulation of visual responses to subsequent stimuli

One of the main aims of the experiment was to test whether and how the attentional capture by the appearance of task-defining features within the unattended visual stream influenced the processing of subsequent visual stimuli. In other words, we investigated whether the spatial biases enhancing perceptual processing over the scalp sites contralateral to the task-relevant location remained unchanged or were instead perturbed by contingent capture. To this end, we compared the amplitude of the P1 potential over contralateral vs. ipsilateral electrodes elicited by standard arrays appearing in the first, second and third position after either attended targets or unattended capture events.

The mean amplitude of the P1 was measured over four pairs of symmetrical electrodes placed over the lateral posterior region (A8/B5, D31/B11, D30/B12 and D29/B13) within a latency window centred on the peak latency of the P1 (90–140 ms). A repeated-measures ANOVA was performed with four factors: stimulus type preceding standard arrays (target and capture), standard position after the target (first, second and third), hemisphere (ipsilateral, contralateral to the task-relevant and attended side), and electrode site (4 levels).

The Greenhouse–Geisser epsilon correction factor was applied in all ERP analyses, where appropriate, to compensate for possible effects of non-sphericity in the measurements. Subsidiary analyses were used where necessary to clarify the pattern of significant interactions between experimental factors.

Results

Behavioural data

The behavioural data for this experiment have been reported previously (Brignani et al., 2009 Experiment 3). Participants were highly accurate (94%) and only one block in one participant was discarded due to the loss of the correct, attended side. The accuracy was unaffected by the target position. Reaction times showed a significant benefit for identifying targets appearing in the right visual field ($M = 584$ ms, $SD = 37$ ms compared to $M = 606$ ms, $SD = 49$ ms) [$t(15) = 3.36$, $p = .004$]. This pattern of results was equivalent to that observed in the focused spatial attention condition of behavioural Experiment 1 of our previous paper, where accuracy was significantly higher than in the divided-attention condition, indicating that participants performed the task effectively and under focused attention condition (Brignani et al., 2009).

The effective allocation of spatial attention to the cued side during task performance was also confirmed by the previous analysis of the early visual potential P1 elicited by the bilateral arrays containing only standard stimuli. The P1 was significantly larger at the posterior electrodes contralateral to the cued, attended side, by the second array after spatially directing cues (Brignani et al., 2009 Experiment 3).

Identification and selection of attended targets vs. unattended capture events

Waveforms elicited by both attended targets and unattended capture events showed a clear larger negativity over contralateral vs. ipsilateral posterior electrodes, starting around 200 ms (N2pc)
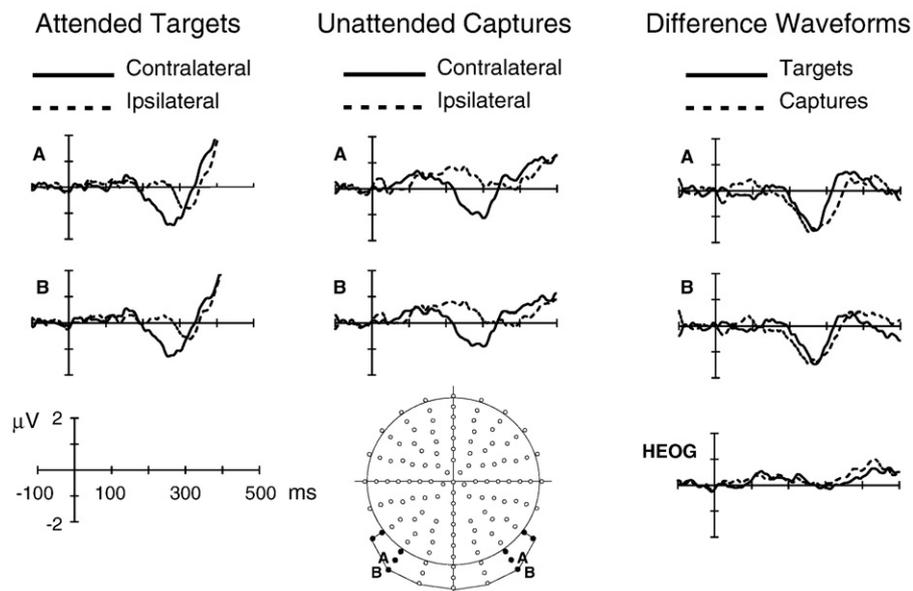
Fig. 2. N2pc effect. Grand-averaged waveforms elicited by attended targets and unattended capture at posterior electrode sites contralateral (solid lines) and ipsilateral (dashed lines) to the side of target/capture presentation. On the right, difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for targets (solid lines) and capture (dashed lines). The bottom panel shows the locations of the electrode sites used in the statistical analysis shaded black and horizontal eye movements for attended targets (solid lines) and unattended capture (dashed lines).

(Fig. 2). No earlier effects were observable, indicating that our approach of subtracting the ERP from the third array after the cues was effective at removing the contribution of spatial biases on earlier stages of visual processing of these stimuli. The analysis of mean amplitudes between 200 and 300 ms at contralateral and ipsilateral electrodes revealed a main effect of the factor hemisphere [$F(1, 15) =$ 21.89, $p < .001$], according to which contralateral electrodes showed a larger negativity in comparison to ipsilateral sites. Spatial attention had no effect upon the magnitude of the N2pc. The factor hemisphere showed no interaction with stimulus type [p's > .72], suggesting that an equivalent N2pc was present for both attended targets and unattended capture events. Follow-up analyses performed on the lateralised difference waveforms (contralateral minus ipsilateral) also showed no significant modulation involving the stimulus type factor for either N2pc amplitude or latency [p's > .37].

Modulatory consequences of contingent capture

Analysis of the visual P1 potential elicited by standard arrays after attended targets vs. unattended capture events showed an overall enhancement of visual processing at the task-relevant attended location, which was modulated by the type of stimulus preceding the standard stimuli (Fig. 3). A significant main effect hemisphere [$F(1, 15) = 35.08$, $p < .001$] indicated that, overall, the P1 was larger over the posterior electrodes that were contralateral to the designated task-relevant side for attentional monitoring. However, a significant three-way interaction also occurred, involving hemisphere, stimulus type and standard position [$F(2, 30) = 4.07$, $p = .05$]. Subsidiary analyses indicated that after attended targets, the visual P1 was consistently larger over contralateral electrodes for standard arrays in first, second and third position [$p < .001$]. This is consistent with the fact that spatial attention remained focused on the task-relevant location, without disruption of this effect by the identification of an attended target. In contrast, contingent capture by a stimulus with task-defining features temporarily disrupted the effect of spatial selective attention to the task-relevant side. The P1 elicited by the standard array immediately after contingent capture was enhanced over the side contralateral to the capture event, resulting in no reliable difference between P1 amplitude over the two hemispheres ($p = 1$). The effect of capture was short-lived, and the enhancement of the P1 contralateral to the task-relevant side returned to being significant for arrays at the second and third position (p's < .002) after the capture event.

Discussion

Our results demonstrated that non-salient stimuli whose features match the task-defining target attributes capture attention even when
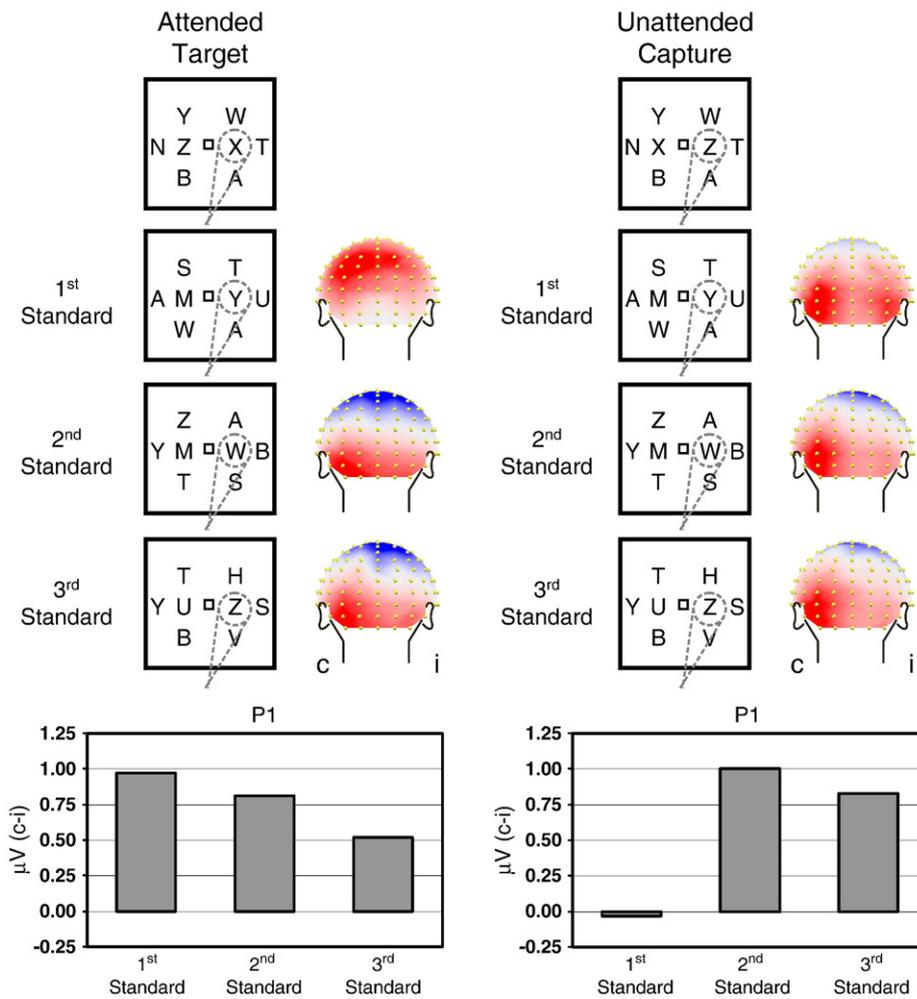
Fig. 3. Topographical maps representing brain activity in the temporal interval between 90 and 140 ms over the ipsi- (right hemisphere) and contralateral (left hemisphere) hemispheres to the task-relevant attended side for standard arrays appearing in the first, second and third position after attended targets (on the left) and unattended capture (on the right). An enhancement of the P1 component was observed over the posterior electrodes contralateral to the attended side for all standards after attended targets and only for standard arrays appearing in second and third position after unattended capture. The graphs at the bottom show the P1 difference between contralateral and ipsilateral hemispheres for standard arrays appearing in the first, second and third position after attended targets and unattended capture.

spatial attention is voluntarily and effectively oriented toward a competing stream of stimuli at a different location. The capture events occurring at the unattended spatial location elicited neural responses associated with stimulus selection (N2pc) that were indistinguishable from those elicited by attended targets, and triggered a short-lived redistribution of the pre-established voluntary spatial attention bias toward the 'capture' side.

Our results build on the previous attentional capture literature by demonstrating that attention can be drawn by stimuli with task-defining features, even if there are no other low-level physical features that make these stimuli pop-out in the display. This type of contingent capture appears to be very effective, operating even when there is a significantly reliable pre-established spatial focus at another location. These findings therefore emphasise the role of a top-down attentional set signalling the task-defining features as a strong determinant of the amount of attentional capture that a stimulus will trigger and the degree of processing it will receive. Whereas these findings cannot comment on the possibility that capture might occur in the absence of any task-defining features, purely on the basis of low-level salient perceptual features or transient appearance, they do clearly show the strength of task-set biases (Folk et al., 1992; Folk and Remington, 1998; Leblanc et al., 2008). Furthermore, unlike capture driven purely by low-level features (Yantis and Jonides, 1990; Theeuwes, 1991b), capture driven solely by task-defining features was not prevented by previous orienting of spatial attention.

Surprisingly, and counter to our initial hypothesis, the N2pc marker of stimulus selection was completely unaffected by spatial attention. However, similar findings were recently reported by Seiss et al. (2009), who investigated whether endogenously focusing attention on one side of a visual search array can prevent capture by salient singleton events appearing in the opposite, unattended side. They found that singletons appearing outside the focus of attention, at the un-cued side, also elicited an N2pc, and that the increasing demands on the target-nontarget discrimination had only a moderate effect on the N2pc amplitude. Leblanc et al. (2008) also measured significant N2pc potentials to irrelevant peripheral transients while participants focused attention voluntarily on a central rapid-serial-visual-presentation stream. We therefore extend these previous observations by showing that salient pop-out or transient features are not necessary to drive capture. Our task involved high levels of selection requirements throughout performance, in which participants had to detect target letters (X, O) embedded within distracter letters in one of two rapidly presented competing visual streams (Brignani et al., 2009). There were no low-level distinguishing features that separated the target-designated letters from distractor letters. The N2pc elicited by targets at the attended location and capture events at the unattended, task-irrelevant location had equivalent amplitude and time-courses.

In both of the previous studies, the amplitude of the N2pc varied with the degree of similarity between the singleton or transient stimulus and the task-defining target template (Leblanc et al., 2008; Seiss et al., 2009). In this context, our findings suggest that the extent of stimulus selection, as indexed by the N2pc, is primarily driven by the top-down set comprising the target features for the current task. It would be interesting to test this notion further, by manipulating systematically the degree of overlap or similarity between distractor events and target events, in the absence of low-level salient features. Unfortunately, we were not able to do this within the current task design.

Upon reflection, this remains a counterintuitive finding: though spatial attention exerts strong biases in retinotopically based processing from early stages of visual analysis, focusing attention at a spatial location seems to have little consequence to the identification of the task-relevant features of stimuli appearing outside the attended location. The counterintuitive nature of this finding may lead one to consider whether the manipulation of spatial attention in our task

was effective in the first place. If participants distributed their attention equally between both streams, task-relevant and irrelevant targets might have been attended in the same way. However, we know that this was not the case, since a separate behavioural investigation confirmed significant benefits for identifying peripheral targets under the focused attention condition compared to divided attention (Brignani et al., 2009 Experiment 1). In addition, we also demonstrated that the early visual P1 potential elicited by the bilateral arrays in the task was significantly enhanced contralaterally to the cued side, confirming the spatial biasing of visual processing according to focused attention (Brignani et al., 2009 Experiment 3). Of course, it is impossible to rule out occasional lapses in the spatial focus of attention throughout task performance. However, the reliable behavioural and electrophysiological markers of attention show that the spatial bias was effective overall. Similarly, other potentials reflecting neural processes subject to spatial attention would therefore have been expected to show spatial modulation. Indeed, the P1 potentials elicited by attended target and unattended capture stimuli in question did show significant modulation by spatial attention, clearly showing that spatial biases were in place when these stimuli were viewed. In order to isolate neural processes related to stimulus selection, however, these pre-established biases were subtracted out by normalising the target and capture waveforms by ERPs elicited by previous standard arrays occurring in the same spatial attention condition.

Having established that spatial biases were effective in our task, we can return to considering the implication of these counterintuitive findings. According to current theories of attentional selection (e.g., Desimone and Duncan, 1995), simultaneously presented stimuli compete for processing and their processing is biased to favour the current behavioural goals. In our case, the task goals were defined by visual features – the shape of the letters (X and O) – and spatial location — the cued side. Given the strong and early effects of spatial attention, one might expect focused spatial attention to enhance the selection of task-defining features at the attended location and/or to attenuate the processing of these same features at unattended locations, by modulating either the amount or timing of neural activity. However, neither the amplitude nor the latency variables of the N2pc marker of stimulus selection were affected. Therefore, the feature- or object-based bias for target letters appears to have operated across both visual fields, in parallel with the spatial bias for the task-relevant location. This suggests that the feature-based task set operated largely independently of spatial attention, at least at this stage of neural processing (see Kuo et al. (2009), for a similar interpretation). We cannot rule out the possibility that the present result depends on the specific experimental attributes used in this study, such as the kind of stimuli (i.e., letters) and the distance between non-attended stimuli and fixation. Thus, further investigations will be necessary to generalize these observations. However, evidence from single-unit recordings (Treue and Martinez Trujillo, 1999; McAdams and Maunsell, 2000; Martinez-Trujillo and Treue, 2004; Patzwahl and Treue, 2009) and fMRI experiments (Saenz et al., 2002; Serences and Yantis, 2007; Egner et al., 2008) also suggest some degree of independence between spatial and feature-based biases upon stimulus analysis. Spatial and non-spatial biases may be integrated at later stages to influence target selection, for instance by linking the task-relevant attributes and locations to response selection. The integration of spatial and non-spatial biases may be difficult to detect with ERPs, since neural markers of these processes may not give rise to lateralised potentials.

In the present study, we were also able to measure the consequences of contingent capture upon the perceptual processing of successive stimuli. Consistent with previous findings about the effects of spatial attention with bilateral arrays (Luck et al., 1990), cued spatial attention leads to an enhancement of the P1 potential contralaterally to the task-relevant location. The capture of attention

by stimuli with task-defining features at the unattended side temporarily disrupted this established spatial bias of attention, leading to an enhancement of the P1 contralaterally to the capture event. This effect developed rapidly and was very short-lived, being measurable only in the first array after the unattended targets. The spatial bias was promptly refocused over the task-relevant attended location. By the second array after unattended targets, the P1 was again significantly larger contralaterally to the instructed attended location. The timing of these effects is consistent with the findings reported by the only behavioural study that systematically manipulated the stimulus-onset-asynchrony between distracter and target in order to estimate the time-course of capture effect (Leblanc and Jolicoeur, 2005). Our results are also consistent with electrophysiological evidence of consequences to attentional capture by emotional stimuli (Fox et al., 2008; Pourtois et al., 2004; Santesso et al., 2008). These studies reported that fearful and angry faces capture attention and subsequent targets appearing at the same location showed an enhanced sensory processing at the P1 stage. In addition, Fox et al. (2008) showed a very rapid and short-lived time-course of this effect, present after a short cue-target interval (300 ms) but not a longer one (750 ms). To our knowledge, no other data about consequences of attentional capture have been reported.

The neural consequences of attentional capture in our task were similar to the effect of cued attention, inducing a spatial biasing of perceptual processing at the P1 stage of visual processing (Brignani et al., 2009). However, it is interesting to note that the time-course of the capture effect was quite different than what we observed when participants oriented their attention voluntarily in this task after instructive spatial cues (Brignani et al., 2009). After voluntary spatial orienting, the contralateral P1 effect took some time to develop, becoming significant only from the second array (i.e., 600–1000 ms) after 'shift' cues. The capture effect developed and decayed more rapidly, within the period of the first array presentation. This difference implies two distinct attentional mechanisms, one engaged reflexively and transiently by stimuli sharing target-defining features, the other one required for voluntary shifts of attention. This interpretation matches the findings from a recent study by Busse et al. (2008). They investigated how reflexive and voluntary shifts of attention interact, by acquiring activity of single neurons in the extrastriate area MT of two monkeys. Their results suggested two distinct mechanisms of orienting, with exogenous attention having a much faster time-course than endogenous attention.

Recently, Folk et al. (2009) showed that the engagement of attention on a transient stimulus within a central rapid-serial-visual-presentation stream can temporarily prevent attentional capture by peripheral stimuli that share its attributes, in a way that is similar to the attentional blink effect (Raymond et al., 1992; Chun and Potter, 1995). It will be interesting to test whether, unlike voluntary attentional monitoring, the temporary engagement of attention would be sufficient to prevent contingent capture by task-defining features. Electrophysiological markers will be especially informative, since it has been shown that stimuli occurring within the period of the attentional blink can nonetheless be processed through late stages of analysis, including those related to semantic integration, as indexed by the N400 potential (Luck et al., 1996; Vogel et al., 1998).

In conclusion, the present study provides electrophysiological evidence that task-defining attributes of a stimulus continue to be processed even when attention is focused somewhere else, and provides new evidence about the perceptual consequences of attentional capture.

Acknowledgments

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