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RESEARCH NOTE

Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses

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Abstract Lateralised ERP responses were measured over posterior visual brain regions in response to visual search arrays that contained one colour singleton. In the localisation task, responses were determined by the visual hemifield where this singleton was presented. In the discrimination task, they were determined by the singletons' shape. While an N2pc component was elicited in an identical fashion in both tasks, a subsequent sustained contralateral negativity was consistently present at posterior sites in the discrimination task only. This dissociation demonstrates that these two activations reflect distinct visual processing stages. We suggest that while the N2pc reflects the ability of the visual system both to identify and localise a relevant stimulus in the scene, the late sustained activity reflects the subsequent in-depth analysis and identification of these stimuli.

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Introduction

Visual attention selects relevant objects in the environment to enable their localisation and identification and to ensure that response selection is based on appropriate perceptual information. The idea that the attentional processing of visual stimuli consists of at least partially separable and sequential processes (such as spatial selection and stimulus identification) is central to many models of visual cognition (Treisman and Gelade 1980; Treisman 1996).

The aim of the present study is to investigate whether the process of localising and selecting relevant items in the scene, and further detailed analyses of the selected items can be reflected by distinct electrophysiological responses. We recorded event-related brain potentials (ERPs) in two visual search tasks that were identical with respect to physical stimulus parameters, and only differed in the level of visual processing required to determine the correct response. We presented circular arrays of 12-coloured diamond shapes that had a corner cut-off on the left or right side (see Fig. 1a; also see Bravo and Nakayama 1992). One of these items had a unique colour (colour singleton: red among green, or vice versa). In the localisation task, participants reported the visual hemifield where the singleton was presented. In the discrimination task, they reported which side of the colour singleton was trimmed.

Based on previous research (Theeuwes 1991; Luck et al. 1997; McPeek et al. 1999) we predicted that spatial attention would be allocated to the singleton in both tasks. However, compared to the task where the singleton has only to

be localised, further processing should be involved when a detailed analysis of its shape is required. This further analysis may involve the contribution of visual short-term memory (VSTM) to maintain the singleton representation active until a decision is made (Bravo and Nakayama 1992).

To identify ERP correlates of attentional target selection and subsequent target identification, respectively, we measured lateralised activity over posterior visual areas in response to the display onset. Specifically, we compared ERPs obtained at posterior electrodes contralateral and ipsilateral to the location of the colour singleton target in each display. ERP studies on visual search tasks have shown that targets usually evoke a specific brain response, named N2pc (Luck and Hillyard 1994; Eimer 1996; Wascher and Wauschkuhn 1996; Hickey et al. 2006). The N2pc is typically elicited at post-stimulus latencies of 200–300 ms at posterior electrodes contralateral to the side of the target. Previous studies have demonstrated that relevant colour singletons are efficient attractors of attention (Turatto and Galfano 2000). Thus, in terms of ERP measures we could predict that the N2pc was elicited contralateral to the singleton position. In addition, since the visual stimulation was physically identical in the localisation as well as in the discrimination task, we expected an N2pc of equivalent magnitude in both tasks.

A second more sustained contralateral posterior negativity has recently been reported at longer post-stimulus latencies in experiments investigating working memory in response to stimulus arrays that contained to-be memorized visual stimuli in the left versus right hemifield (Vogel and Machizawa 2004; Dell'Acqua et al. 2006). This lateralised and sustained activity is thought to reflect the maintaining of visual representations in VSTM for further cognitive operations. If this sustained lateralisation represents VSTM processes that are distinct from the initial attentional selection reflected by the N2pc, these two activities should be dissociable in the present study. Specifically, the late and sustained activity should be present in the discrimination task, where response selection was contingent upon a finer analysis of the shape of the colour singleton, but should be strongly attenuated (if not suppressed) in the localisation task, where no further processing of the singleton beyond its detection in the left versus right side was required.

Methods

Participants

Thirteen healthy paid volunteers with normal or corrected vision participated in the experiment, after providing informed consent. Three participants were excluded from analysis due to a large number of eye movement artefacts (see below). Thus, ten participants (7 females, 1 left-handed, aged 23–35 years, mean age 28.5 years) remained in the sample. The study was conducted following the guidelines laid down in the Helsinki declaration and was approved by the local ethics committee.

Stimuli and procedure

Stimuli consisted of 12 equiluminant red or green diamonds (8 cd/m^2) presented on a computer monitor and arranged in a circle at a constant eccentricity (5° of visual angle) from the fixation dot (0.1° × 0.1°). Each diamond (0.8° × 1°) had a 0.25° corner trimmed on the left or right side (Fig. 1a). On each trial, one diamond had a unique colour and could appear in one of the five positions to the left or right of fixation (Fig. 1a), with equal probability and in random order. Each visual display was presented for 150 ms, to prevent the occurrence of eye movements to the target location. Participants were instructed to maintain fixation on the central dot and to respond by pressing the keys 'B' and 'N' on a computer keyboard with the index or middle fingers of their right hand. In the localisation task, they had to report the side where the colour singleton occurred (left/right). In the discrimination task, they indicated the side of the cut (left/right) for the colour singleton. Speed and accuracy were emphasized equally. Maximum time for responding was 1,500 ms. The intertrial interval was 1,500 ms.

Three experimental blocks of 80 trials per block were successively delivered for each task. Two training blocks of 80 trials were delivered prior to the start of the first experimental block of each condition. The order in which the two tasks were delivered was counterbalanced across participants.

EEG recording and data analysis

EEG was recorded with a linked-earlobe reference from 23 scalp electrodes, including lateral occipital sites PO7 and PO8. Horizontal EOG (HEOG) was recorded bipolarly by means of two electrodes positioned on the outer canthii of both eyes. Impedance was kept below 5 KΩ for all electrodes. Amplifier bandpass was 0.1–40 Hz, and digitisation rate was 200 Hz. Trials with horizontal eye movements (HEOG exceeding ±20 μV) and other artefacts (any electrode exceeding ±80 μV) were excluded. For three participants, these criteria led to the rejection of more than 59% of trials in at least one condition, thus their data were excluded from the analyses. The average of trials retained for the remaining participants was 81.5% (range 58–99%).

Averages were computed relative to the 100 ms interval preceding the display onset, separately for the localisation and discrimination tasks. Statistical analyses were conducted on mean amplitude values obtained at PO7 and PO8 for two post-stimulus intervals (N2pc: 180–300 ms; late sustained contralateral negativity: 350–600 ms), for the factors contralaterality (electrode contralateral versus ipsilat-

eral to the visual hemifield where the target was presented), task (localisation versus identification), and target side (left versus right). Additional analyses were conducted separately for both task conditions.

Results

Behavioural performance

The ANOVAs on response times and percentage of correct responses (factors: target side, left versus right; task, localisation versus discrimination) showed that participants were faster to localise the target ($M = 451$ ms, SE $= 16.8$) than to discriminate its shape ($M = 643$ ms, SE $= 23.8$), as indicated by a significant effect of task, $F(1,9) = 247.0$, $p < 0.001$. Participants were also faster for right targets ($M = 540$ ms, SE $= 19.6$) than for left targets ($M = 555$ ms, SE $= 20.2$), $F(1,9) = 5.3$, $p < 0.05$, presumably due to the spatial compatibility between target side and the right hand used to respond. They were slightly better at localising ($M = 99\%$, SE $= .002$) than at discriminating the target ($M = 96\%$, SE $= 0.012$), $F(1,9) = 9.0$, $p = 0.015$, confirming that the discrimination task was more difficult.

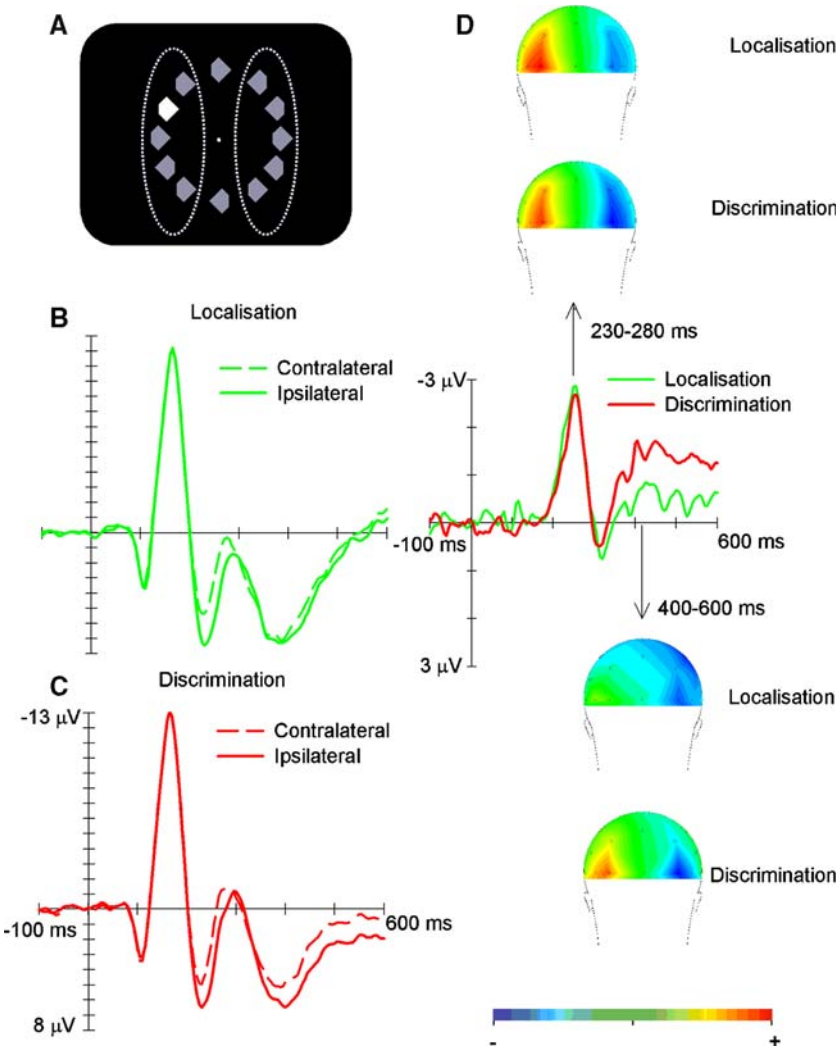

Fig. 1 **a** On each trial 11 non-target stimuli (here depicted in grey) were presented together with one colour singleton (target, here depicted in white), which could appear in one of the five positions to the left or right of fixation (as indicated by the dashed ovals not visible during the experiment). **b, c** Grand-averaged ERP waveforms in the 600 ms post-stimulus interval at posterior electrodes P07/P08 contralateral (dashed lines) and ipsilateral (solid lines) to the target location, separately for the localisation task (B) and the discrimination task (C). **d** Difference waveforms obtained by subtracting ipsilateral activity from contralateral activity, separately for the localisation task (green line) and the discrimination task (red line). Topographical ERP scalp distribution maps obtained from average voltages, computed by subtracting activity for right targets from activity for left targets, are shown separately for the N2pc component (230–280 ms post-stimulus, top panels) and the late sustained contralateral negativity (400–600 ms post-stimulus, bottom panels), for both tasks. Contralateral negativities are represented by symmetrical positive and negative activation patterns over left and right posterior hemispheres. The scale was optimised for each map (N2pc: ±2.3 µV for both tasks; late sustained contralateral negativity: ±1.1 µV for the localisation task; ±1.5 µV for the discrimination task)

ERP results

As can be seen from Fig. 1, an N2pc of almost identical amplitude and latency was elicited in both tasks. In contrast, the two tasks started to diverge at around 350 ms post-stimulus (Fig. 1d), where a contralateral negativity was clearly present in the discrimination task, but appeared strongly attenuated in the localisation task.

These observations were confirmed by statistical analyses. For the N2pc time window (180–300 ms post-stimulus), a main effect of contralaterality was present, $F(1,9) = 41.4$, $p < 0.001$, but no evidence of any contralaterality × task interaction was obtained, $F(1,9) = 1$, $p > .33$. Additional analyses conducted separately for both tasks revealed main effects of contralaterality for the localisation task, $F(1,9) = 42.4$, $p < 0.001$, as well as for the discrimination task, $F(1,9) = 32.7$, $p < 0.001$. A very different pattern was obtained for the subsequent sustained activity (350–600 ms post-stimulus). Here, a main effect of contralaterality, $F(1,9) = 12.7$, $p < 0.007$, was accompanied by a significant contralaterality × task interaction, $F(1,9) = 11.2$, $p < 0.009$, thus demonstrating that this sustained contralateral activity was substantially reduced in the localisation relative to the discrimination task. Follow-up analyses conducted separately for both tasks confirmed the presence of a sustained lateralised activity for the discrimination task (main effect of contralaterality: $F(1,9) = 16.75$, $p < 0.003$). In contrast, no significant effect of contralaterality was present in the localisation task, $F(1,9) = 4.2$, $p > 0.068$, indicating the absence of a reliable contralateral sustained activity in this task.

Discussion

The results were clear-cut. While an N2pc of equivalent magnitude was triggered in both tasks, the subsequent sustained contralateral activity was observed for the discrimination task, but was strongly reduced when participants only had to localise the colour singletons.

Before evaluating these results in terms of two dissociable ERP components linked to different cognitive operations in target processing, potential alternative interpretations need to be considered. In our experiment, observers performed a feature search task, in which a uniquely coloured item (the target) was presented together with 11 homogeneous distractors. Although all stimuli were equiluminant, the presence of a colour singleton implied that visual displays were not fully balanced in terms of sensory energy. Thus, some of the lateralised effects found in the present study could purely reflect the sensory differences between the two sides of the array. It is clearly important to balance arrays in terms of sensory energy when studying lateralised brain activities, yet this factor is unlikely to have affected our results for several reasons. First, previous studies (Luck and Hillyard 1994) have already shown that non-target colour singletons do not elicit a reliable N2pc component, suggesting that sensory asymmetries per se are not responsible for the N2pc effect found here. Second, the sensory imbalance cannot explain the difference found in the late sustained negativity between the two tasks, for the displays in both tasks were physically identical. Third, any effects of such a sensory imbalance on ERP waveforms should be most pronounced at short latencies, as sensory-perceptual differences will predominantly modulate early stages of stimulus processing. To examine this, we conducted a statistical analysis on the mean amplitudes recorded at posterior electrodes (PO7 and PO8) in the P1 range (80–130 ms post-stimulus). No significant effects of contralaterality were obtained from the ANOVAs in both tasks, all $F(1,9) < 1.9$, all $p > 0.19$, indicating that the sensory imbalance did not substantially affect the early lateralised ERP activity. Thus, we can reasonably rule out the possibility that the lateralised effects found here were primarily due to the physical asymmetry in the displays.

Another issue relates to the difficulty of determining whether two successively triggered patterns of ERP activation genuinely reflect two dissociable ERP components that can be linked to distinct cognitive processes. For example, one may argue that the late activation found in the discrimination task is just a prolonged N2pc for the more difficult task. Although we acknowledge the difficulty of unequivocally determining the existence of two functionally distinct and separable components, any interpretation of the late contralateral negativity observed in the present study as a late N2pc needs to account for the fact that the first contralateral activity returned to the baseline level before the appearance of the second sustained lateralisation (Fig. 1d), especially in the discrimination task. To substantiate this observation, we conducted an ANOVA in the 50 ms interval just after the N2pc (300–350 ms) but we did not find any significant effect of lateralisation ($F < 1$) or of task × lateralisation $F(1,9) = 1.08$, $p > 0.3$, demonstrating that the N2pc and the subsequent lateralised activity were clearly separated in time. Some previous studies have also uncovered successively triggered lateralised activities in visual arrays that contain several potentially relevant items (Woodman and Luck 1999; Hickey et al. 2006), and have interpreted these activities as the correlates of sequential attention shifts towards the different relevant locations in the visual scene. This interpretation, however, cannot be applied to our results, as there was no other salient or relevant location apart from that occupied by the target singleton. Further evidence for a functional distinction between the two activations comes from the study by Vogel and Machizawa (2004), which found that whereas the number of memory stimuli strongly affects the late contralateral negativity, it has no effect on the N2pc. Interestingly, McCollough et al. (2007) recently found that the late

contralateral activity had a more dorsal and medial scalp distribution than the N2pc. Although not conclusive, this evidence adds to the present results in suggesting a functional distinction between these two ERP activations.

Our findings suggest the existence of two distinct ERP correlates of dissociable cognitive stages in the processing of task-relevant visual events. The N2pc is elicited as a result of the attentional selection of a target item in a visual array (see also Eimer 1996; Woodman and Luck 1999), while the later lateralisation represents finer in-depth analyses of selected visual item. It is interesting to note that in spite of the substantial differences in the perceptual demands imposed by the localisation and discrimination tasks (which were reflected in a response time difference of almost 200 ms), the N2pc triggered during these two tasks was virtually indistinguishable (Fig. 1d). This suggests that the initial attentional processing of visual target events, as reflected by the N2pc, is largely unaffected by variations in task demands, at least when targets are salient and therefore easily distinguishable from non-target stimuli.

Our interpretation of the late sustained activation is consistent with previous suggestions that the active maintenance of representation in VSTM is reflected by a sustained lateralised activity at posterior scalp sites that is triggered during the delay period of a visual memory task (Vogel and Machizawa 2004). Although our task was not a typical memory task, it should be noted that visual search arrays were presented for only 150 ms. It is thus likely that in the discrimination task, where a further processing stage was required, target analysis was based on VSTM representations rather than on-line visual information. This interpretation is consistent with recent findings by Robitaille and Jolicoeur (2006), who asked participants to identify a target stimulus while varying its visibility and found, similarly to the present study, the presence of a late sustained contralateral activity even when no masking was used.

Alternatively, one could interpret the late lateralisation as the correlate of a specific target feature selection (the target shape) that is contingent on a previous selection of the target location. This type of processing is usually reflected by a sustained negative activation at around 180–300 ms (selection negativity, SN, see Hillyard and Munte 1984). Although this interpretation is possible, any direct comparison between the SN and the late lateralisation found here is problematic, as very different paradigms were used in studies where the SN was observed. While the SN is computed by comparing ERPs in response to relevant versus irrelevant spatial and non-spatial features, there was no relevant shape feature in our experiment, as both left-cut and the right-cut shapes were equally important for the task. In addition, there are also systematic latency differences, as the SN is typically triggered at a shorter latency than the lateralised activity found here. Perhaps most importantly, the sustained negativity observed in the present discrimination task was elicited at contralateral posterior electrodes (PO7/PO8), whereas the SN is much more broadly distributed, and, crucially, is not lateralised. Hence, it is unlikely that the late contralateral negativity observed here is equivalent to an SN, in the sense that it reflects the selective processing of shape that is contingent on target location. We, therefore, suggest that under conditions where the visual system has to perform a finer analysis of a target singleton, the N2pc (reflecting the initial allocation of attention to the target) is followed by a subsequent (re)activation of the visual areas needed to perform the discrimination task, resulting in two separable successive ERP activations.

Two recent ERP studies (Dell'Acqua et al. 2006; Jolicoeur et al. 2006a) have measured the N2pc and the sustained posterior contralateral negativity (SPCN) to investigate the neural basis of the attentional blink (Raymond et al. 1992) under conditions where two successive target stimuli appeared during rapid serial visual presentation among distractors. Both components were suppressed when the second target was presented during the attentional blink interval, suggesting that the processing of the first target interferes with the attentional selection of the second target event, as well as with its subsequent encoding and/or maintenance in VSTM. However, the fact that N2pc and SPCN components were equally affected by the attentional blink in these two studies makes it impossible to rule out the possibility that these components are not distinct, and that the SPCN might just reflect the late part of the N2pc (but see Jolicoeur et al. 2006b, where some preliminary evidence suggesting a dissociation was provided). The main finding of the present study that the N2pc and the later lateralised activity can be dissociated when task demands are systematically varied strongly suggests that this alternative interpretation is not warranted, and that these two components may indeed reflect distinct stages in visual cognition.

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