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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 to both identify and localise a relevant stimulus in the scene, the late sustained activity reflects the subsequent in-depth analysis and identification of these stimuli.

Keywords

visual-spatial attention; visual cognition; visual working memory; attentional control; event-related brain potentials

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 (e.g., Treisman & Gelade, 1980; Treisman, 1996).

The aim of the present study was to investigate whether the process of localising relevant items in the scene, as reflected by attentional orienting processes, 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 twelve coloured diamond shapes that had a corner cut off on the left or right side (see Figure 1; also see Bravo & Nakayama, 1992). One of these items had a unique colour (colour singleton: red among green, or vice versa). In the localisation task, participants simply reported the visual hemifield where the singleton was presented. In the more difficult discrimination task, they reported which side of the colour singleton was trimmed.

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Based on previous research (Luck, Girelli, McDermott & Ford, 1997; McPeck, Maljkovic & Nakayama, 1999; Theeuwes, 1991) we predicted that spatial attention would be allocated to the singleton in both tasks. However, compared to when the singleton has only to be localised, further processing should be involved when a detailed analysis of its shape is required, which in turn may involve the contribution of visual short-term memory (VSTM) to maintain the singleton representation active until a decision is made (Bravo & 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 (Eimer, 1996; Hickey, McDonald & Theeuwes, 2006; Luck & Hillyard, 1994; Wascher & Wauschkuhn, 1996). The N2pc is typically elicited at post-stimulus latencies of 200 to 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 (e.g., Turatto & 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 (Dell'Acqua, Sessa, Jolicoeur, & Robitaille, 2006; Vogel & Machizawa, 2004). This lateralised and sustained activity is thought to reflect the maintaining of visual representations in VSTM for further cognitive or response-related operations. If this sustained lateralisation represents VSTM processes that are distinct from the initial attentional selection of visual objects 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 ($0.1^\circ \times 0.1^\circ$). Each diamond ($0.8^\circ \times 1^\circ$) had a 0.25° corner trimmed on the left or right side (see Figure 1). 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 (see Figure 1), 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 1500 ms. The intertrial interval was 1500 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 K Ω for all electrodes. Amplifier bandpass was 0.1 to 40 Hz, and digitisation rate was 200 Hz. Trials with horizontal eye movements (HEOG exceeding $\pm 20 \mu\text{V}$), eye blinks, head movements, and other artefacts (any electrode exceeding $\pm 80 \mu\text{V}$) 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 ipsilateral 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, $F(1,9)=247.0$, $p<.001$. Participants were also faster for right targets ($M=540$ ms, $SE=19.6$) than for left targets ($M=555$ ms, $SE=20.2$), $F(1,9)=5.3$, $p<.05$, 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 ($M=96\%$, $SE=.012$), $F(1,9)=9.0$, $p=.015$, confirming that the discrimination task was more difficult.

ERP results

As can be seen from Figure 2, 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 (see Figure 2C), 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, $F(1,9)=41.4$, $p<.001$, but no evidence of any contralaterality $\times$ 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, $F(1,9)=42.4$, $p<.001$, as well as for the discrimination task, $F(1,9)=32.7$, $p<.001$. A very different pattern was obtained for the subsequent sustained negative activity (350-600 ms post-stimulus). Here, a main effect of contralaterality, $F(1,9)=12.7$, $p<.007$, was accompanied by a significant contralaterality $\times$ task interaction, $F(1,9)=11.2$, $p<.009$, thus demonstrating that the sustained negative 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: $F(1,9)=16.75$, $p<.003$). In contrast, no significant effect of contralaterality was present in the localisation task, $F(1,9)=4.2$, $p>.068$, 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 had only 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 element (the target) was presented together with eleven 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 (e.g., Luck & 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 sensory stages of stimulus processing. To examine this, we conducted a statistical analysis on the mean amplitudes recorded at posterior electrodes (PO7, 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 $p>.19$, 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 in the present experiment were primarily due to the physical asymmetry in the displays.

A different issue relates to the general 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 sustained 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 (see Figure 2C), especially in the case of 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 $\times$ lateralisation $F(1,9) = 1.08$, $p > .3$, thus demonstrating that the N2pc and the subsequent sustained negative activity were clearly separated in time. It should be noted that some previous studies have also uncovered successively triggered lateralised activities in visual arrays that contain several potentially relevant items (e.g., Hickey et al., 2006; Woodman & Luck, 1999), and have interpreted these lateralised 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 suggestions of a functional distinction between the two activations come from the study by Vogel and Machizawa (2004), where they found that whereas the number of memory stimuli strongly affects the late contralateral negativity, it has no effect on the N2pc. Interestingly, in a recent study (McCollough, Machizawa & Vogel, 2007) it was found a distinction in the scalp distribution of the two activities, in that the sustained late contralateral activity had a more dorsal and medial distribution than the N2pc. Although not conclusive, this evidence adds to the present results in suggesting a distinction between these two ERP activations. This distinction, however, should not be interpreted as evidence of hierarchical properties of the visual system. One possibility is that every time the system needs to perform a finer analysis of that item, a subsequent (re)activation of the visual areas be needed to perform the task correctly, and this results in two separable and subsequent ERP activations.

Given these observations, we conclude that our findings suggest the existence of two distinct electrophysiological 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 & Luck, 1999), while the late 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 (see Figure 2C). 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 & 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 particularly 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 accordant with some recent findings by Robitaille and Jolicoeur (2006), who asked participants to identify a target stimulus in three conditions of visibility and found, similarly to the present study, the presence of a late sustained contralateral activity even when no masking procedure 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 location. Previous studies have shown that this type of processing is reflected by a sustained negative activation at around 180-300 ms (selection negativity, SN, see Hillyard & Munte, 1984). In principle we do not disregard this interpretation, however any direct comparison between the SN and the late lateralisation found here is unwarranted, as very different paradigms were used in those studies. For

instance, the two activations strongly differ in latency, having the SN a shorter latency than the sustained activity found here. In addition, the SN is computed in relation to the ERPs of the relevant features versus the irrelevant features. In our experiment, however, there was no relevant feature in terms of shape, as both the left-cut and the right-cut shapes were equally important for the task.

Two recent ERP studies (Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006; Dell'Acqua et al., 2006) have measured the N2pc and the sustained posterior contralateral negativity (SPCN) to investigate the neural basis of the attentional blink (see Raymond, Shapiro, & Arnell, 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, Sessa, Dell'Acqua & Robitaille, 2006, where some preliminary evidence suggesting a dissociation was provided). The main finding of the present study that the N2pc and the late sustained and 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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Figure 1.

On each trial eleven 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).

Figure 2.

A-B. 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 (A) and the discrimination task (B). **C.** 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: $\pm 2.3 \mu\text{V}$ for both tasks; Late sustained contralateral negativity: $\pm 1.1 \mu\text{V}$ for the localisation task; $\pm 1.5 \mu\text{V}$ for the discrimination task).