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Non-spatial attentional effects on P1

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Abstract

Objective: It has been suggested that P1, the earliest endogenous visual potential, is influenced primarily by spatial location. However, we have found that attention to non-spatial visual features can affect both the latency and amplitude of this component.

Methods: A series of studies are reviewed, starting with 4 using simple geometric forms, and either serial presentation of single stimuli or presentation of stimulus arrays followed by two studies using natural complex images.

Results: With simple stimuli, latency and amplitude effects are seen on the P1, but differ among the paradigms, depending on the demands of the task. The data further showed a facilitation effect and that binding occurs in parallel with single feature processing. For complex stimuli we found P1 shorter to faces than inverted faces, eyes or non-face stimuli, and larger to animal than non-animal pictures. The above effects were present in children as well as in adults.

Conclusions: These findings demonstrate that very early stages of processing can be modified by top-down attentional influences across a range of ages and experimental paradigms, concordant with visual processing models showing very rapid and dispersed activation with feedback at early cortical levels. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Attention; P1; Visual; Non-spatial; Development

1. Introduction

Attention has been a focus of interest for event-related potential (ERP) studies for decades, and its influence on later ERPs and with spatial attention is well documented (see Woods, 1990; Luck and Hillyard, 2000). Effects of attention are readily measured on components such as N2 and P3, but these later peaks can also be affected by many other factors, and disentangling the various influences is difficult. Also, as more studies have examined the early ERP components, the sensitivity of early stages of processing to cognitive factors is becoming evident. P1 is often considered the earliest endogenous visual ERP component and although it has been shown to be sensitive to manipulations in spatial information (Hopf and Mangun, 2000; Martinez et al., 2001), recent studies have also shown effects of attention on early stages of processing other visual information (Han et al., 2000; Mouchetant-Rostaing et al., 2000a).

One of the major strengths of ERP research is the ability for fine temporal discrimination, reflecting the timing of information processing in the brain. These results in turn can have important ramifications on models of visual processing. Recent papers have shown that visual areas are activated almost simultaneously with visual input and receive very rapid feedback to basic levels of processing (Bullier, 2001a; Foxe and Simpson, 2002), although the hierarchical model of visual processing is still widely referenced (e.g. Riesenhuber and Poggio, 1999). It is only very recently that the interactive feedback model has been successfully applied to human studies; the present paper also suggests that it can also be validated by developmental data. This paper briefly reviews a series of developmental ERP studies of visual attention and categorization processing, focussing primarily on the early P1 component and factors that influence it.

The studies were all run in normal subjects, young adults and/or children (within the age range of 4–15 years). The recording methods were similar across studies; ERPs were recorded from 30–35 electrodes set in electrode caps (ECI or EasyCap) with the Neuroscan system and Synamps (bandpass 0.1–100 Hz) using an averaged reference montage. The first series investigated the processing of features (colour, form) either singly or in conjunction. The second series investigated the processing of complex visual stimuli.

There is a wealth of studies in the adult behavioural litera-

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ture that have used visual search paradigms to elucidate the extent of attentional processing required for visual detection. Much discussion has focussed on whether attention is required for single feature as well as conjunction tasks or whether there is pre-attentive or parallel processing of single features (Wolfe et al., 1989; Treisman, 1988). As developmental studies are an important means for testing the validity of theoretical models (Enns, 1993), the first study investigated these issues of automatic or parallel versus serial or intentional processing in children. Single feature pop-out tasks of colour and form were used to assess parallel processing and a conjunction of features task was used to study serial processing in 7-12 year old children (divided into 3 groups: 7–8, 9–10, and 11–12 years, n = 42; Taylor and Khan, 2000). Stimulus arrays contained 8 rectangles. For the parallel tasks they were all the same colour (blue) and size for the standard stimulus arrays, or contained one red rectangle (colour pop-out array) or one larger rectangle (form/size pop-out array). Within the parallel task series, both types of pop-out stimulus arrays were presented, although only one or the other was designated as the target per task. For the conjunction or serial task, the size and colour of the items in the array varied, with a target array being defined as one that contained a large red rectangle. Arrays were presented for 400 ms with an inter-stimulus interval (ISI) of 1500 ms. Early ERP components were measured, as we were particularly interested in the initial stages of visual search processing; P1 and N1 were measured posteriorly and P2 anteriorly. The latencies of all 3 components decreased with age, and the latencies also showed effects that varied with task. What was most surprising to us at the time was that with arrays containing a colour pop-out, P1 was earlier when those arrays were targets than when the same arrays were non-targets (within the form task). This was the case for all 3 age groups; there was no interaction with age (Fig. 1a). Thus, when the children were attending to arrays with a colour pop-out, such stimuli were processed faster starting at the P1 latency than when the same stimuli were presented but when the children were attending to form. P1 amplitude to all categories of targets was larger than to non-targets (Fig. 1b). An amplitude effect to targets had been reported in adults (Han et al., 1997); this was the first report of this effect being present also in school-aged children. Serial processing was seen most clearly in the non-target trials (Chun and Wolfe, 1996) in P2 amplitude modulations, but P1 also had a shorter latency to the serial targets than non-targets, due, we believe, to the inclusion of colour as one of the features to be conjoined. Thus, feature-specific top-down processing was found developmentally, starting at P1 latency, which was particularly sensitive to attention to colour. This demonstration of top-down modulation of processing is consistent with the guided search model of visual processing (Wolfe et al., 1989), as were the effects seen on P2 (Taylor and Khan, 2000).

These tasks used stimulus arrays, however, raising the

question of possible confounding of the binding or conjoining of stimulus features with the visual search of the array (Woods et al., 1998). To disambiguate the processing of features and their conjunction from the visual search through an array for a target, in a subsequent study, items were presented singly in a rapid serial visual paradigm. The visual stimuli consisted of 4 coloured rectangles constructed

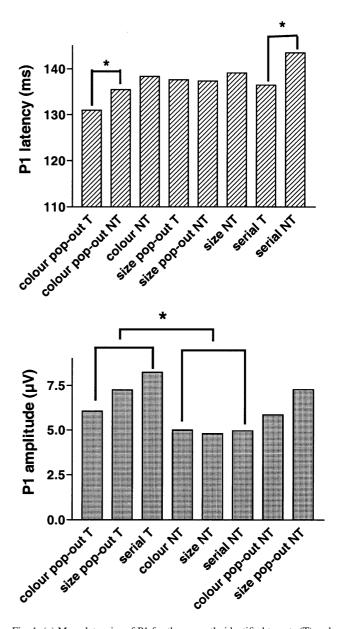


Fig. 1. (a) Mean latencies of P1 for the correctly identified targets (T) and the non-targets (NT) pop-out as well as NT standard stimuli for the colour and size single feature tasks and for the conjunction task. As there were no interactions with age, these latencies are averaged across age groups (7–12 years of age); asterisks mark significant differences (P < 0.05) between colour pop-outs, whether they were targets (left) or non-targets, and between the targets and non-targets in the serial task (right). No effects were seen for the size task at the P1 latency. (b) Mean amplitudes of the P1 for the same 8 trial types. The 3 types of target (T) trials (on the left) had significantly larger amplitudes (P < 0.03) than their corresponding nontarget (NT) trials (in the middle) (adapted from Taylor and Khan, 2000).

using two colours (blue and violet) and two orientations (horizontal and vertical) (Cortese et al., 1999). Stimuli were presented centrally, rapidly on a black background on the computer screen, one at a time and in a pseudorandom order for 57 ms with a variable ISI of 400-800 ms. Subjects were presented with 3 different blocked conditions, i.e. colour, orientation, and conjunction, in which they pressed the space bar whenever a stimulus with the designated colour regardless of orientation was presented, or the designated orientation was presented regardless of its colour, or when a stimulus with a specified combination of features (e.g. blue and horizontal bars) was presented. Each block of trials included 240 stimuli; in all cases target stimuli constituted 25% of trials. There was always a minimum of two distractors presented between successive targets. Compared with adults, children (10-12 years of age) had longer N1 and P2 latencies, and larger P1 and P2 amplitudes (Theunissen et al., 2001). Amplitude asymmetries were consistent with differing cortical regions being implicated in the processing of colour and form (e.g. Corbetta et al., 1991), and the differences between the adults' and children's data suggest that this develops with age. There were, however, no ERP latency effects as a function of single feature tasks versus the conjunction task, suggesting that when stimuli are presented rapidly, the binding of features proceeds in parallel with the processing of single features. No extra time was used for processing conjunction targets compared to single feature targets from 85 to 210 ms. These data are consistent with recent models of perceptual processing (Bartels and Zeki, 1998; Wolfe et al., 1989) and suggest that at the stages of processing we measured there appeared to be no binding problem in children or adults; binding of features occurred in parallel with single feature processing at P1 through to P2 latencies.

The processing of colour and form and their conjunction was further investigated with serial presentation of single stimuli, but using a sustained attention paradigm, i.e. at a slow rate; stimuli were presented for 650 ms at an ISI of 1100-2000 ms. Stimuli were one of 4 shapes (circle, diamond, triangle or cross) and one of 4 colours (red, blue, yellow or pink), and subjects had to respond 'yes' to targets and 'no' to non-targets (run in blocks where targets were defined by colour, form or a conjunction of colour and form). Twenty-nine adults and 65 children (7-8, 9-10 and 11-12 years) were tested (Taylor et al., 1999, 2001a). There were age effects with latency and amplitude of P1 decreasing with age. In the 7-8 year olds P1 was at a mean of 135 ms and 9 μ V, while in adults it was 120 ms and only about $1.2 \mu V$. However, the most interesting effects were those seen as a function of task. Across age groups the P1 was at shorter latencies for the conjunction than single feature targets. This effect was most marked in the adults; they showed a decrease of 15 ms for the P1 in the conjunction task, compared to both single feature tasks. This effect of shorter latency for the conjunction targets was also seen for N1. Thus, when two features had to be conjoined to define

the target, this was done more rapidly than the processing of a single feature. There were also further task effects: shape targets had shorter N1 latencies than colour targets and, in adults only, a left-sided distribution. The most important finding, however, was that at this initial stage of processing at 115-130 ms, when a conjunction of features had to be used to detect a target in a sustained attention task, the processing was faster than for either single feature. This facilitation effect has been reported in the behavioural literature (Woods et al., 1998; Wolfe et al., 1989), but the locus of the facilitation from the present data appears to be very early in the information processing. It is also intriguing that this facilitation effect was seen, albeit reduced, from 7-8 years of age. Again, there was no indication of a problem in binding features, but rather facilitation with this slower presentation rate.

The final study in this section returned to the classical paradigm of visual arrays, but varied the number of items in the array. Adult subjects were presented with arrays containing 5, 9 or 17 coloured rectangles. Targets were those arrays that contained a blue vertical bar, and the distractors were bars that differed from the targets in colour (green or pink) and/or orientation (± 45 degrees). Targets could be discriminated on either the basis of colour (only one item was blue), orientation (all rectangles were blue; only one was vertical) or a conjunction of colour and orientation (arrays contained a mixture of the 3 colours and two orientations; for target arrays, there was only one vertical and blue bar). The target arrays occurred with 50% probability and all conditions and all 3 array sizes were presented randomly intermixed (Taylor et al., 2001b). Subjects pressed 'yes' to targets and 'no' to non-target arrays. Thus, unlike Taylor and Khan (2000), the target was constant throughout the study, although there was no predicting from trial to trial as to either the number or the type of distractors (colour, orientation or conjunction) that would be presented. Behavioural effects were seen in the orientation and conjunction conditions for the higher array sizes (increased RTs for target-absent); accuracy only decreased for target-present trials in the conjunction task. For the ERPs, however, an unusual effect was seen: across tasks, without any interaction, P1 latency was significantly shorter for the array size 17 (Fig. 2). Amplitude also increased with array size 17, particularly at the more lateral temporo-parietal sites. The latency effect was seen at the N1 as well, although P3 showed the classical effects of increased latencies with larger arrays, related to task difficulty. We interpreted these P1 results as showing a strategy shift under the more difficult conditions of array size 17 to a more rapid global processing. This is consistent with recent studies showing that global information is processed before finer features (Sugita, 1999; Bullier, 2001a). This global processing was possibly more superficial, as suggested by the error rates, but nevertheless effective for the single feature discriminations and target-absent trials, even in the conjunction trials. Thus, when the stimulus complexity

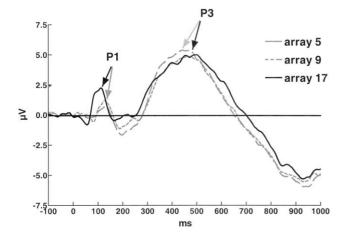


Fig. 2. Grand averaged visual ERPs at Pz electrode for the 3 array sizes, showing the shorter latencies, larger P1s for array size 17, but longer latency P3 (dark arrows) than for array sizes 5 and 9 (grey arrows). These are averaged across colour, orientation and conjunction conditions, as this ERP effect was seen regardless of whether it was a single feature or conjunction trial.

made the task more difficult, the strategy changed and the early processing occurred more rapidly, seen in both the P1 and N1 peaks. This change, however, had to occur 'on line', as the array sizes and distractor conditions were intermixed, and thus must reflect an automatic processing option, rather than the more traditional expectation of top-down modulations.

These first 4 studies used simple stimuli, consisting of geometric forms in which colour and size or orientation were manipulated. Although common to visual search paradigms, such stimuli are not particularly ecologically valid. The final two data sets included complex 'real' visual stimuli. In the first, various facial and control stimuli were used. Faces and eyes are critical social stimuli which adults process with ease, but relatively little is known about how this expertise develops. The aim of the study was to investigate the development of neural changes in processing facial stimuli; attention was focussed on N170, the component widely investigated as a face-sensitive peak (e.g. McCarthy et al., 1999), but P1 was also measured. A large series of unknown faces were presented, upright and inverted, intermixed with scrambled faces, eyes-only, flowers and checkerboard targets (720 stimuli in total; 400 ms presentation at an ISI of 1800-2200 ms). Ninety children (4-15 years of age) and 38 adults were included; the early ERP components were measured over posterior-temporal sites to non-target stimuli (Taylor et al., 2001c). We found that P1 decreased significantly in latency with age for all categories of stimuli, being at 160 ms for the 4-5 year olds and at 110 ms for adults. However, across all 7 age groups P1 was at consistently shorter latencies (by 10-15 ms; Fig. 3) to upright faces than to inverted faces or the control stimuli. This had been reported with MEG recordings in adults, but only comparing upright and inverted faces (Linkenkaer-Hansen et al., 1998), an effect recently confirmed with ERPs (Itier and Taylor, 2002). The developmental data demonstrated that this effect, which we interpreted to be due to the salience of upright faces over other categories of stimuli, is present very early in life. Even when there was no task requirement regarding facial stimuli – they were all non-targets, and hence did not have attention specifically directed to them – this early stage of processing was faster. P1 did not show other interactions with the face stimuli, as was found with N170, suggesting that it does not have the same sensitivity to faces as N170, but reflects earlier, more global information processing (categorizing stimuli as faces), comparable to recent reports in monkeys (Sugase et al., 1999).

The final study investigated categorization, in an animal/ non-animal go/no-go task. Categorization is a process that starts to mature very early, and has important ramifications for learning in general, but few studies have examined its evolution over childhood. The stimuli were 540 colour photographs of natural scenes that included an animal, or animals, in the picture on 25% of the trials (Batty and Taylor, 2002). Subjects (n = 62; children aged 7–15 years (7-8, 9-10, 11-12, 13-15 years; n = 48), and young adults) pressed the space bar whenever an image presented contained an animal. The pictures were presented very briefly (80 ms) at an ISI of 1100-1500 ms and none were repeated. There was no indication as to what species of animal (mammal, bird, insect, etc.) or background (trees, underwater scenes, landscapes, etc.) would be shown. This was expected to be a difficult task, but in fact it was performed with very high accuracy (96-98%) even in the youngest group. Thus, the categorization ability for this task appeared mature at 7-8 years, although underlying processing was still developing, according to the ERPs. P1 showed

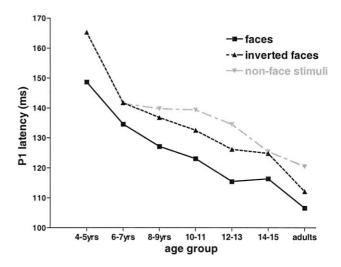


Fig. 3. Mean P1 latencies across 7 age groups, showing the consistently shorter latencies to faces compared to inverted faces and control stimuli (phase-scrambled faces and flowers). There were 15 children in each of the 6 age groups and 38 adults (adapted from Taylor et al., 2001c).

little latency change across age, but there was an enormous decrease in amplitude from an average of 25 μ V in the 7–8 year olds to 5 μ V in the adults. There were no latency effects of target versus non-target, but across age groups there was small but consistent and significantly larger amplitudes to targets. Thus, the pictures that contained animals produced larger P1s, even in the 7-8 year olds. This suggests that with stimuli that have biological importance to humans, as also seen with faces, early processing is affected – having either faster latencies or larger amplitudes - compared to other categories of stimuli. These data are consistent with other reports in adults of very early effects of complex stimuli that were suggested to be due to biological significance (Seeck et al., 1997; Mouchetant-Rostaing et al., 2000a,b). The current studies demonstrated that this facilitation at initial encoding stages of visual information is present and mature at a relatively young age, suggesting that this is not a learned effect.

2. Conclusions

Although it has been argued that the visual P1 component is sensitive only to spatial attention, we demonstrate that it shows both amplitude and latency changes that are sensitive to various demands in non-spatial visual tasks. The robustness of these effects is underlined by their presence in children. Investigations that include developmental data are important in confirming models of cognitive processing based only on results from adults (Enns, 1993); in the examples included here models of visual search and issues surrounding binding were elucidated.

P1 reflects early, rapid processing of both simple and complex stimuli that is sensitive to task demands and the stimuli presented. P1 is influenced by top-down modulation, which can speed up the processing time for the attended feature of colour, as well as show facilitation effects in a conjunction task. Other factors that affect P1 are task load, as with increased load the processing time shortens likely due to an automatic shift in strategy, and salience, as P1 appears sensitive to stimuli that have particular importance to humans, such as animals and upright human faces.

These data are consistent with the models of visual processing that posit rapid, widespread activation through the visual sensory pathways, which allow time for feedback to sensory areas well before the P1 latency (Bullier, 2001a; Foxe and Simpson, 2002). Thus, the effects on P1 are very likely the result of feedback and interactive processing that can impact rapidly on very early stages of cortical processing (Bullier, 2001b); these mature very quickly, or are present from a young age.

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