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Priming of pop-out modulates attentional target selection in visual search: Behavioural and electrophysiological evidence

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ABSTRACT

Previous behavioural studies have shown that the repetition of target or distractor features across trials speeds pop-out visual search. We obtained behavioural and event-related brain potential (ERP) measures in two experiments where participants searched for a colour singleton target among homogeneously coloured distractors. An ERP marker of spatially selective attention (N2pc component) was delayed when either target or distractor colours were swapped across successive trials, demonstrating that intertrial feature priming systematically affects the onset of focal-attentional target processing. Results support the hypothesis that priming of pop-out effects are primarily generated at early perceptual/attentional stages of visual processing.

1. Introduction

Visual search for targets that possess unique features (pop-out visual search) is fast, efficient, and subjectively effortless, but is still modulated by the properties of search arrays that were encountered on preceding trials: responses to such feature singleton targets are faster when their properties are repeated across successive trials relative to non-repetition trials. Such intertrial priming effects have been observed both when targets were defined by features (e.g., red colour singleton targets among green distractors, or vice versa; Maljkovic & Nakayama, 1994), and when they were defined in terms of dimensions (e.g., colour vs. orientation; Müller, Heller, & Ziegler, 1995).

While the presence of intertrial priming in pop-out visual search demonstrates that the efficiency to select and report perceptually salient singleton targets is modulated by the properties of preceding search displays, the nature of this modulation is still under dispute. The majority view is that repeating target attributes (features or dimensions) on successive search trials facilitates the early perceptual processing of these attributes, and results in a more rapid and efficient attentional selection of targets on repetition trials (e.g., Chun & Nakayama, 2000; Müller & Krummenacher, 2006; Wolfe, Butcher, Lee, & Hyle, 2003). However, alternative post-perceptual accounts of intertrial priming have been proposed. Huang, Holcombe, and Pashler (2004) suggested that intertrial priming is linked to the retrieval of previous search-relevant events from episodic memory. Response-based accounts (e.g., Cohen & Magen, 1999; Theeuwes, Reimann, & Mortier, 2006) postulate that intertrial priming effects emerge at the stage where target stimuli are translated into their associated responses.

The aim of the present study was to combine behavioural and electrophysiological measures to investigate intertrial 'priming of pop-out' in visual search. This effect was studied by Maljkovic and Nakayama (1994) in experiments where participants searched for green target diamonds among red distractor diamonds, or vice versa. Response times (RTs) were faster in pure blocks where targets and distractors always had the same colour than in mixed blocks where target and distractor colours switched unpredictably across trials (Maljkovic & Nakayama, 1994, Experiment 1). RTs in mixed blocks were faster on repetition trials where target and distractor colours were identical to the immediately preceding trial than on change trials where both target and distractors had switched colour (Experiment 3). The size of this priming of pop-out effect in mixed blocks was determined not just by the immediately preceding trial, but also by trials that appeared earlier in the sequence (Experiment 5).

In a recent functional brain imaging study (Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007), fMRI measures suggested that intertrial feature priming effects are linked to a modulation of areas involved in top-down attentional control (bilateral intraparietal sulci, anterior cingulate, frontal eye fields) as well as in ventral visual areas involved in feature-specific stimulus processing, in line with a perceptual–attentional account of priming of pop-out. Given the poor temporal resolution of hemodynamic brain activity measures, this study cannot provide any precise insights into the onset and time course of intertrial feature priming. To obtain such insights, we used event-related brain

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potential measures to assess how this type of priming affects visual search for singleton targets. We employed visual search procedures similar to those used by Maljkovic and Nakayama (1994). Each visual search display contained four diamond stimuli placed at the corners of an imaginary square (see Fig. 1). Participants had to select the target stimulus that was defined by its unique colour (e.g., red among green distractors, or vice versa), and to report the position of the notch (top vs. bottom) for this target. The critical manipulation was whether target and/or distractor colours were repeated or changed across trials.

To assess whether the repetition or change of target and/or distractor colours on successive trials affects the attentional selection of singleton targets, as suggested by the hypothesis that intertrial feature priming effects are generated at an early stage of perceptual processing, we measured the N2pc component as an established electrophysiological marker of attentional target processing. This component is a negative-going deflection with a maximum over visual areas contralateral to the location of an attended stimulus. The N2pc has been observed in numerous previous visual search experiments, typically between 175 and 300 ms after the onset of the search array. It reflects the attentional selection of target among non-target stimuli, based on target-defining perceptual attributes (e.g., Eimer, 1996; Hopf et al., 2000; Luck & Hillyard, 1994; Woodman & Luck, 1999), and can thus be employed as a temporal marker for the transition from pre-attentive perceptual processes to the focal-attentional processing of target stimuli. Systematic onset latency differences of the N2pc (e.g., an earlier onset on repetition relative to change trials) would demonstrate effects of intertrial feature priming on the time course of perceptual–attentional visual processing stages (see Töllner, Gramann, Müller, Kiss, and Eimer (2008), for initial evidence for this assumption). In contrast, if behavioural priming of pop-out effects were generated exclusively at post-perceptual stages subsequent to the focal-attentional selection of targets, no such N2pc differences should emerge.

Experiment 1 investigated the basic priming of pop-out effects, as described by Maljkovic and Nakayama (1994). The aim of Experiment 2 was to study whether priming of pop-out is associated with a selective facilitation of target features, a selective inhibition of distractor features, or a combination of both processes.

2. Experiment 1

In Experiment 1, participants searched for colour singleton targets presented among uniformly coloured distractors. In pure blocks, target and distractor colours remained constant. In mixed blocks, target and distractor colours were determined randomly on each trial, resulting in 50% repetition trials where both remained unchanged, and 50% change trials where the previous target colour became the distractor colour, and vice versa. In line with

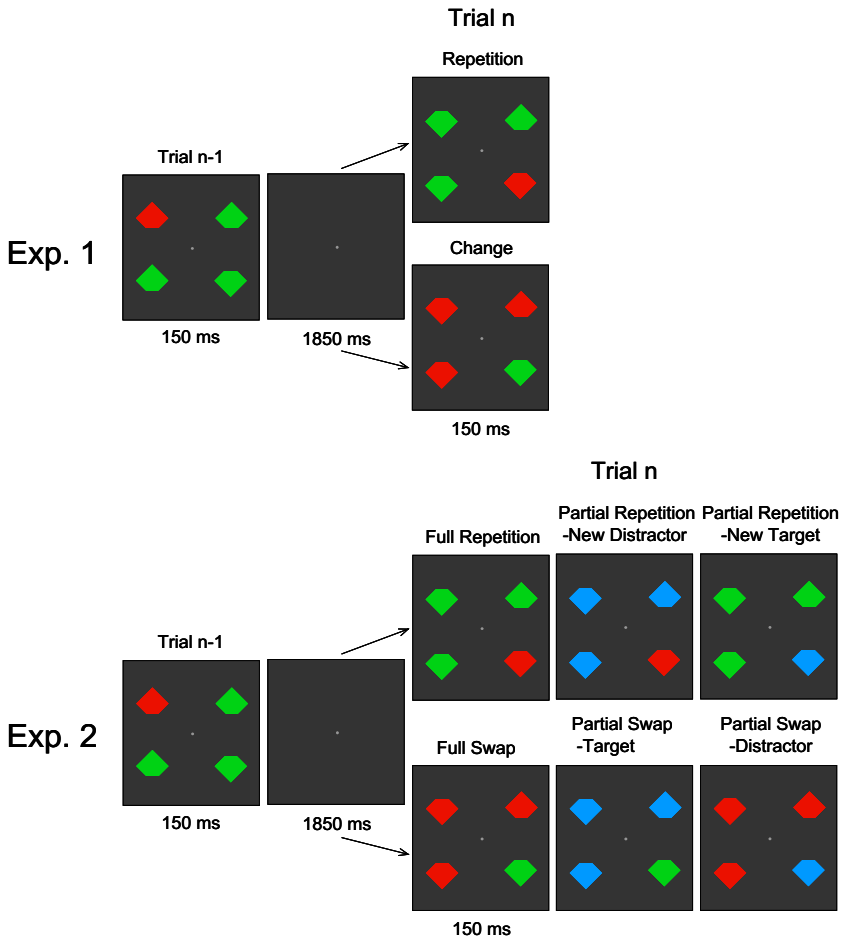

Fig. 1. Example of display sequences for different trial types in Experiment 1 (top) and Experiment 2 (bottom). Participants had to look for the odd-coloured diamond and report the orientation of the notch (top or bottom). In Experiment 1, target and distractor colours either remained unchanged (Repetition trials) or were swapped (Change trials) across successive trials. In Experiment 2, these Full Repetition and Full Change trials were presented among trials where the target/distractor colour remained unchanged, while the distractor/target colour was new (Partial Repetition – New Distractor and Partial Repetition – New Target), and among trials where target colour was the distractor colour of the preceding trial while distractor colour was new (Partial Swap – Target), or vice versa (Partial Swap – Distractor).

the basic priming of pop-out effect reported by Maljkovic and Nakayama (1994), RTs were expected to be faster in pure relative to mixed blocks, and on repetition relative to change trials of mixed blocks. If these behavioural effects were due to intertrial priming affecting attentional target selection, they should be mirrored by latency differences of the N2pc component: the N2pc should emerge earlier in pure relative to mixed blocks. In mixed blocks, an earlier N2pc should be observed for repetition relative to change trials. In contrast, if behavioural priming of pop-out effects were generated exclusively at later post-perceptual stages subsequent to the focal-attentional selection of targets, no such N2pc differences should be observed.

2.1. Methods

2.1.1. Participants

Sixteen paid volunteers participated in this experiment. Four were removed from analyses due to poor eye gaze control (see below). The remaining 12 participants (mean age 23.9 years; range 20–27) were right-handed and had normal or corrected vision.

2.1.2. Stimuli and procedure

Stimulus presentation and response collection were performed using a purpose-written E-Prime script (Psychology Software Tools). Stimuli were presented on a CRT monitor with 100 Hz refresh rate against a black background. Search arrays (150 ms duration) consisted of four coloured diamonds placed at the corners of an imaginary square of 5.6° × 5.6° at equal distance from a central grey fixation point (see Fig. 1, top). Each search array contained one target colour singleton diamond and three uniformly coloured distractor diamonds. Diamonds were approximately equiluminant (~9.3 cd/m^2) red or green (CIE values 0.635/0.339 and 0.298/0.579), and subtended 1.5° × 1.5° visual angle, with a notch of 0.5° at either top or bottom. Notch position was randomly determined for each diamond on each trial. Participants were instructed to search for the odd-colour singleton and report the position of the notch (top or bottom) by pressing one of two spatially corresponding keys with their left or right index finger. The interval between the onset of two search arrays on successive trials was 2000 ms.

Eight blocks with 96 trials per block were run. In four blocks (pure blocks), the target and distractor colours remained constant (two blocks with red target singletons among green distractors; two blocks with green target singletons among red distractors). In the other four blocks (mixed blocks), target and distractor colours were determined randomly for each trial, so that each trial was equally likely to be preceded by a trial with the same target and distractor colours (repetition trials), or by a trial where the colours of target and distractors were reversed (change trials). In all blocks, target position (upper or lower left or right side) varied randomly and unpredictably across trials. Pure blocks and mixed blocks were presented in an alternating order, and the target/distractor colour assignment was reversed between pure blocks. After four blocks, the hand-to-key-mapping was reversed.

2.1.3. EEG recording and analyses

EEG was recorded from 23 scalp electrodes (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8 and Oz) with a sampling rate of 500 Hz. EEG data were amplified with a bandpass of 0–40 Hz, and a 50-Hz notch filter. All electrodes were referenced to the left earlobe during data acquisition, and re-referenced offline to averaged earlobes. Impedances were kept below 5 kΩ. The continuous EEG was epoched from 100 ms prior up to 400 ms after search array onset, and the 100 ms interval prior to stimulus onset served as baseline. Trials containing eye movements (HEOG exceeding ±25 μV), blinks (Fpz exceeding ±60 μV), or muscle activity (activity at any electrode exceeding ±80 μV) were eliminated from analyses, as were trials that contained or immediately followed a response error. On average, 82.5% of trials remained in the analysis for pure blocks and 84.4% for mixed blocks. Four participants were excluded from analyses because their average HEOG after artefact rejection was larger than ±4 μV, indicating a residual tendency to move gaze towards the side of colour singleton targets.

The N2pc component was measured at lateral posterior electrode sites PO7/PO8 contralateral and ipsilateral to the location of colour singleton targets. Mean amplitude values were computed for two time windows (200–270 ms and 270–340 ms after search array onset). N2pc onset latencies were determined with a jackknife-based procedure on the basis of difference waveforms obtained by subtracting ipsilateral from contralateral ERPs. This jackknife procedure estimates onset latencies from grand averages computed for subsamples of participants by successively excluding one participant from the original sample (see Ulrich & Miller, 2001). N2pc onset latency was measured as the time point at which the voltage value on the ascending flank of the difference waveforms for each subsample exceeded 40% of the N2pc peak amplitude. For the latency analysis, *F*-values were corrected (indicated with the label 'F_c') according to the formula given by Ulrich and Miller (2001).

3. Results

3.1. Behavioural data

Response times were faster in pure relative to mixed blocks (557 vs. 680 ms); $t(11) = 8.2$, $p < 0.001$. In mixed blocks, RTs were faster on repetition relative to change trials (648 vs. 703 ms), $t(11) = 7.2$, $p < 0.001$. Error rates were low and did not differ between pure and mixed blocks (3.6% vs. 4.1%); $t(11) = 1$, or between repetition and change trials (3.8% vs. 4.3%); $t(11) < 1$.

3.2. N2pc component

Fig. 2 shows ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the position of a target, together with the resulting contralateral minus ipsilateral difference waveforms, for pure vs. mixed blocks (top panels), and for repetition vs. change trials in mixed blocks (bottom panels). An N2pc was present in all conditions, but varied in both latency and amplitude.

The first set of analyses compared pure and mixed blocks. The onset of the N2pc was 50 ms earlier in pure relative to mixed blocks (168 vs. 218 ms); $F_c(1, 11) = 27.5$, $p < 0.001$. N2pc mean amplitudes were analysed for the factors block (pure vs. mixed), target hemifield (left vs. right) and contralaterality (electrodes contralateral vs. ipsilateral to the target). In the 200–270 time window, a main effect of contralaterality, $F(1, 11) = 31.5$, $p < 0.001$, reflecting the presence of an N2pc, was accompanied by a block × contralaterality interaction, $F(1, 11) = 11.5$, $p < 0.006$, as the N2pc was larger in pure relative to mixed blocks (see Fig. 2, top panel). Follow-up analyses conducted separately for both block types confirmed that an N2pc was reliably present not only in pure blocks, $F(1, 11) = 30.1$, $p < 0.001$, but also in mixed blocks, $F(1, 11) = 24.2$, $p < 0.001$. In the 270–340 ms latency window, a main effect of contralaterality, $F(1, 11) = 10.5$, $p < 0.008$, was again accompanied by a block × contralaterality interaction, $F(1, 11) = 18.9$, $p < 0.001$. Follow-up analyses revealed that while the N2pc was still reliably present in mixed blocks, $F(1, 11) = 37.9$, $p < 0.001$, it had already disappeared within this time window in pure blocks, $F(1, 11) < 1$.

The second set of analyses compared repetition and change trials in mixed blocks. The N2pc started earlier in repetition trials

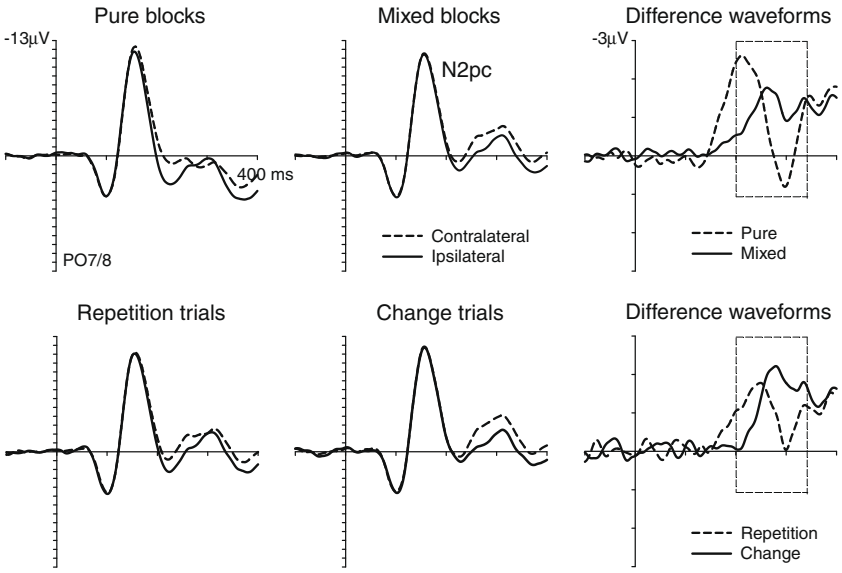

Fig. 2. Grand-average waveforms obtained in Experiment 1 in the 400 ms interval after search array onset at lateral posterior electrodes PO7/PO8 contralateral and ipsilateral to the visual field of the target. Top panel: ERPs obtained in pure blocks and mixed blocks, together with difference waveforms obtained by subtracting ERPs at ipsilateral electrodes from contralateral ERPs (right). Bottom panel: ERPs obtained in Repetition and Change trials of mixed blocks, together with difference waveforms obtained by subtracting ERPs at ipsilateral electrodes from contralateral ERPs (right).

than in change trials (188 vs. 242 ms); $F_c(1, 11) = 10.1$, $p < 0.01$. N2pc mean amplitudes were analysed for the factors trial type (repetition vs. change), target hemifield, and contralaterality. In the 200–270 time window, a main effect of contralaterality, $F(1, 11) = 25.2$, $p < 0.001$, reflecting the presence of an N2pc, was accompanied by a trial type × contralaterality interaction, $F(1, 11) = 6.0$, $p < 0.03$, as the early phase of the N2pc was larger in repetition relative to change trials (see Fig. 2, bottom panel). Follow-up analyses confirmed that an N2pc was reliably present not only in repetition trials, $F(1, 11) = 24.9$, $p < 0.001$, but also in change trials, $F(1, 11) = 14.5$, $p < 0.003$. In the 270–340 ms latency window, a main effect of contralaterality, $F(1, 11) = 38.8$, $p < 0.001$, was accompanied by a trial type × contralaterality interaction, $F(1, 11) = 19.6$, $p < 0.001$, as the late phase of the N2pc was more pronounced for change relative to repetition trials. However, follow-up analyses conducted separately for both trial types found a reliable late N2pc for repetition trials, $F(1, 11) = 8.7$, $p < 0.02$, as well as for change trials, $F(1, 11) = 54.2$, $p < 0.001$.

3.3. Discussion of Experiment 1

The behavioural results observed in Experiment 1 confirmed the basic priming of pop-out effect (Maljkovic & Nakayama, 1994). RTs were faster in pure blocks, where target and distractor colours remained unchanged, than in mixed blocks where repetition and change trials were equiprobable. RTs in mixed blocks were faster for repetition relative to change trials, also in line with Maljkovic and Nakayama (1994). The critical new finding of Experiment 1 was that these RT differences were mirrored by onset latency shifts of the N2pc component: the N2pc emerged earlier in pure blocks relative to mixed blocks, and earlier on repetition trials relative to change trials (see Fig. 2). These observations demonstrate that intertrial feature priming in pop-out visual search has a strong impact on the time course of attentional target selection. The latency modulation of the N2pc appears inconsistent with hypotheses that claim that priming of pop-out is primarily generated at processing stages that follow attentional target selection, such as episodic memory retrieval or stimulus–response translation.

In addition to differences in the onset latency of the N2pc component between pure and mixed blocks, and between repetition and change trials, Experiment 1 also revealed N2pc amplitude differences. The fact that N2pc amplitudes observed during the early measurement window (200–270 ms) were larger in pure blocks and repetition trials relative to mixed blocks and change trials is a simple consequence of the fact that the N2pc emerged earlier on these trials. The reversal of this pattern in the 270–340 ms measurement window, with larger N2pc amplitudes for mixed blocks and change trials, may indicate that the earlier onset of the N2pc in pure blocks and repetition trials was mirrored by an earlier offset. Alternatively, a more sustained N2pc on trials where target and distractor features are changed could also reflect the increased target selection difficulty on these trials. This possibility will be discussed in more detail later.

The results of Experiment 1 provide new electrophysiological evidence that priming of pop-out is associated with systematic differences in the speed of attentional target selection. However, these intertrial priming effects could be linked to two different mechanisms. Attentional target selection may proceed more rapidly on repetition trials because target activation persists across trials, thereby facilitating the processing of target features when these are immediately repeated. Alternatively, target selection may be faster on repetition trials because these include a repetition of distractor features. If distractor inhibition persists across trials, repeating distractor features could facilitate their rejection as non-targets. The aim of Experiment 2 was to separate the effects of target activation and distractor inhibition on the attentional processing of colour singleton targets.

4. Experiment 2

In the typical priming of pop-out paradigm, as employed by Maljkovic and Nakayama (1994) and in the present Experiment 1, both target and distractor colours either remain unchanged across successive trials, or reverse roles, with the previous distractor colour now becoming the target colour, and vice versa. This basic paradigm cannot dissociate the relative contributions of target activation and distractor inhibition to intertrial feature priming.

The N2pc latency differences observed in Experiment 1 between repetition and change trials may thus be exclusively due to the repetition vs. alternation of target colours, the repetition vs. alternation of distractor colours, or a combination of both. Some behavioural studies have investigated the roles of target vs. distractor repetition for priming of pop-out effects. Maljkovic and Nakayama (1994, Experiment 8) studied trial sequences where the distractor colour remained constant across trials while target colour changed on every trial, or vice versa, and found RT priming effects for both target and distractor colour repetitions. They concluded that target activation and distractor inhibition both contribute to intertrial feature priming, although the impact of target activation may be more substantial. Lamy, Antebi, Aviani, and Carmel (2008) calculated behavioural repetition benefits and switch costs that are linked to target colour activation and distractor colour inhibition effects across trials, and found additive contributions of both mechanisms to priming of pop-out, as well as systematic and stable individual differences in the relative role of these mechanisms for intertrial priming. Along similar lines, Kristjánsson and Driver (2008) observed independent effects of target and distractor repetition on intertrial priming, and also identified additional costs resulting from role-reversals of targets and distractors across successive trials.

Experiment 2 investigated how target repetition, distractor repetition, and role-reversals (swaps) affect the speed of attentional target selection, as reflected by the N2pc component. Procedures were similar to the mixed blocks of Experiment 1, except that an additional possible colour for targets or distractors was introduced, and four new trial types were included (see Fig. 1, bottom panel). In Partial Repetition – New Distractor trials, the distractor colour was not present in the previous search array, while target colour remained unchanged. In Partial Repetition – New Target trials, target colour was new, while distractor colour was unchanged. In Partial Swap – Target trials, the previous distractor colour was now the target colour, and distractor colour was new. In Partial Swap – Distractor trials, the previous target colour was now the distractor colour, and target colour was new. In addition, identical repetitions of both target and distractor colours across trials (repetition trials in Experiment 1, now termed Full Repetition trials), and full exchange of target and distractor colours across trials (change trials in Experiment 1, now termed Full Swap trials) were also included.[1]

Experiment 2 was expected to confirm the major findings of Experiment 1, with faster RTs and earlier N2pc onset on Full Repetition relative to Full Swap trials. If these effects were due to target activation, fast RTs and early N2pc onsets similar to those seen on Full Repetition trials should be observed for trials with target repetitions (Partial Repetition – New Distractor). Also, slow RTs and delayed N2pc components similar to those found on Full Swap trials should be seen when the previous target colour was now the distractor colour (Partial Swap – Distractor), as distractors would be more difficult to reject as non-targets. In contrast, if distractor inhibition was primarily responsible for priming of pop-out, RTs and N2pc onsets on trials with distractor repetitions (Partial Repetition – New Target) should be just as fast as on Full Repetition trials. In addition, RTs and N2pc latencies on trials where the target colour is identical to the previous distractor colour (Partial Swap – Target) should be equally delayed as on Full Swap trials, because target selection would have to overcome the persisting colour-specific inhibition. If target activation and distractor inhibition contributed equally to priming of pop-out, no systematic RT and N2pc differences should be observed between the two types of Partial Repetition and Partial Swap trials. In this case, RTs and N2pc onsets should be earlier for Full than Partial Repetition trials, earlier for Partial Repetition than Partial Swap trials, and earlier for Partial Swap than for Full Swap trials.

[1] It should be noted that Lamy et al. (2008) also included the remaining logically possible intertrial sequence condition – trials where both target and distractor colours were new relative to the preceding trial. This trial condition requires the use of four possible target and distractor colours, and was not included in the present Experiment 2.

4.1. Methods

4.1.1. Participants

Nineteen volunteers participated in this experiment. Three were excluded from further analysis because of eye movement artefacts (see below). Thus, 16 participants (7 males) remained in the sample. Mean age was 24.7 years (range 20–33 years). All had normal or corrected vision.

4.1.2. Stimuli and procedure

Stimuli and procedure were the same as in Experiment 1, with the following exceptions. An additional equiluminant colour (blue; CIE values 0.115/0.096) was added to the set of possible target and distractor colours. On each trial, target colour was randomly drawn from the three possible colours, and distractor colour was drawn from the remaining two colours. This resulted in six equally probable intertrial sequence types: Full Repetition trials (both target and distractor colours of the previous trial were repeated); Partial Repetition – New Distractor (target colour remained the same, but distractor colour differed from preceding trial); Partial Repetition – New Target (distractor colour remained the same, but target colour differed from preceding trial); Partial Swap – Target (the previous distractor colour was now the target colour, and distractor colour differed from preceding trial); Partial Swap – Distractor (the previous target colour was now the distractor colour, and target colour differed from preceding trial); Full Swap (previous target colour was now distractor colour, and vice versa). Full Repetition and Full Swap trials were identical to repetition and change trials in the mixed blocks of Experiment 1. As in Experiment 1, eight blocks with 96 trials per block were run.

4.1.3. EEG recording and analysis

These were the same as in Experiment 1. On average, 14.2% of all trials were removed by the artefact rejection procedures. Three participants had to be excluded because their average HEOG after artefact rejection was larger than ±4 μV, indicating a tendency to move gaze towards colour singleton targets. Greenhouse–Geisser corrections for nonsphericity were applied to analyses where appropriate.

4.2. Results

4.2.1. Behavioural data

Fig. 3 shows RTs (top panel) and error rates (bottom panel) for the different trial types. An initial analysis compared RTs on Partial Repetition and Partial Swap trials as a function of whether target or distractor colour was new, or was swapped. For Partial Repetition trials, no significant RT differences were observed between trials with new distractors or new targets, $t(15) < 1$, and data from these two trial types were combined for subsequent analyses. Likewise, on Partial Swap trials, no RT differences emerged between trials with swapped targets or swapped distractors, $t(15) < 1.2$, and these two trial types were also combined.

The omnibus ANOVA with trial type as a 4-level factor (Full Repetition, Partial Repetition, Partial Swap, Full Swap) produced a main effect of trial type on RTs, $F(3, 45) = 58.5$, $p < 0.001$. Planned comparisons were conducted between RTs for different trial types. RTs were faster on Full Repetition than on Full Swap trials (620 vs. 697 ms); $t(15) = 8.5$, $p < 0.001$, confirming the presence of the basic

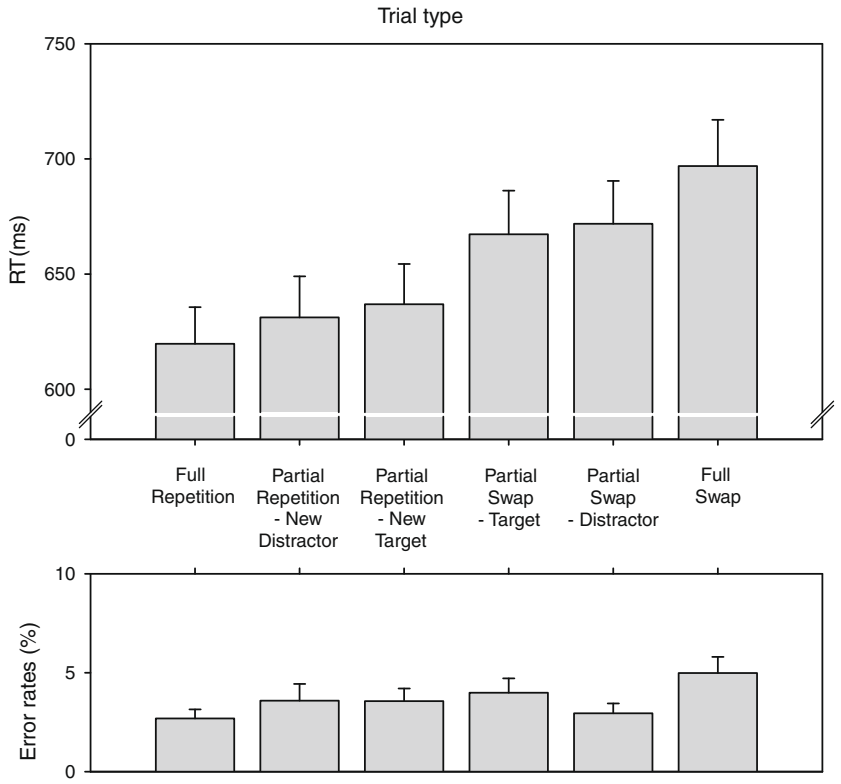

Fig. 3. Mean correct response times (RT) and error rates obtained in Experiment 2 for each of the six trial types. Error bars represent standard errors of the mean.

priming of pop-out effect. Further comparisons revealed faster RTs on Full relative to Partial Repetition trials, $t(15) = 4.3$, $p < 0.001$, on Partial Repetition relative to Partial Swap trials (634 vs. 670); $t(15) = 7.0$, $p < 0.001$, and on Partial relative to Full Swap trials, $t(15) = 5.0$, $p < 0.001$.

Error rates (Fig. 3, bottom panel) were analysed analogously. As for RTs, no significant differences were observed between the two types of Partial Repetition and Partial Swap trials, both $t(15) < 1.4$, both $p > 0.197$. Errors were less frequent on Full Repetition than on Full Swap trials, $t(15) = 3.3$, $p < 0.005$, and on Partial relative to Full Swap trials, $t(15) = 2.9$, $p < 0.02$. Error rates did not differ significantly between Full and Partial Repetition trials, and between Partial Repetition and Partial Swap trials (both $t(15) < 1.5$, both $p > 0.173$).

4.2.2. N2pc component

Fig. 4 shows ERPs for different trial types at lateral posterior electrodes PO7/8 contra- and ipsilateral to the target side. Initial analyses compared N2pc latencies and mean amplitudes within the two measurement windows for Partial Repetition trials as a function of whether new distractors or new targets were presented. This difference had no impact on N2pc latency, $F_c(1, 15) = 1.3$, $p = 0.228$, on amplitude (trial type × contralaterality interaction: $F < 1$ for both time windows), and these two trial types were combined for subsequent analyses. Likewise, no N2pc latency differences, $F_c(1, 15) < 1$, or amplitude differences (trial type × contralaterality interaction: $F < 1$ for both time windows) emerged for Partial Swap trials as a function of whether swapped items were targets or distractors, and these two trial types were also combined.

4.2.2.1. N2pc latency. Fig. 5 shows difference waveforms obtained by subtracting ERPs at electrodes PO7/8 ipsilateral to the target side from contralateral electrodes, separately for Full Repetition trials, Partial repetition trials (collapsed across trials with new distractors and new targets), Partial Swap trials (collapsed across trials with swapped targets and swapped distractors), and Full Swap trials. N2pc onset was delayed for Full and Partial Swap trials relative to Full and Partial Repetition trials, while no N2pc onset difference was apparent between Full vs. Partial Swap trials, and full vs. Partial Repetition trials, respectively. An omnibus ANOVA conducted on N2pc latencies with trial type as a 4-level factor produced a main effect of trial type, $F_c(3, 45) = 4.9$, $p < 0.005$. Separate analyses with trial type as 2-level factor were performed subsequently. The N2pc emerged earlier on Full Repetition relative to Full Swap trials (205 vs. 233 ms); $F_c(1, 15) = 6.7$, $p < 0.03$, confirming the results from Experiment 1. Importantly, further planned comparisons revealed N2pc onset differences also between Partial Repetition and Full Swap trials, $F_c(1, 15) = 16.7$, $p < 0.001$, between Partial Repetition and Partial Swap trials, $F_c(1, 15) = 5.9$, $p < 0.03$, as well as a nearly significant latency difference between Full Repetition and Partial Swap trials, $F_c(1, 15) = 4.4$, $p = 0.054$. In contrast, N2pc onset latencies did not differ between Full and Partial Repetition trials, and between Full and Partial Swap trials (both $F_c < 1$).

4.2.2.2. N2pc amplitude. As in Experiment 1, N2pc amplitudes were analysed for two successive mean amplitude time windows (200–270 ms and 270–340 ms after search array onset), for the 4-level factor trial type and the factors target hemifield and contralaterality. In the 200–270 ms time window, a main effect of contralaterality, $F(1, 15) = 26.1$, $p < 0.001$, reflecting the presence of the N2pc, was accompanied by a trial type × contralaterality interaction, $F(3, 45) = 7.8$, $p < 0.002$. N2pc amplitudes were larger on Full and Partial Repetition trials relative to Full and Partial Swap trials, in line with the earlier onset of this component on the former trials

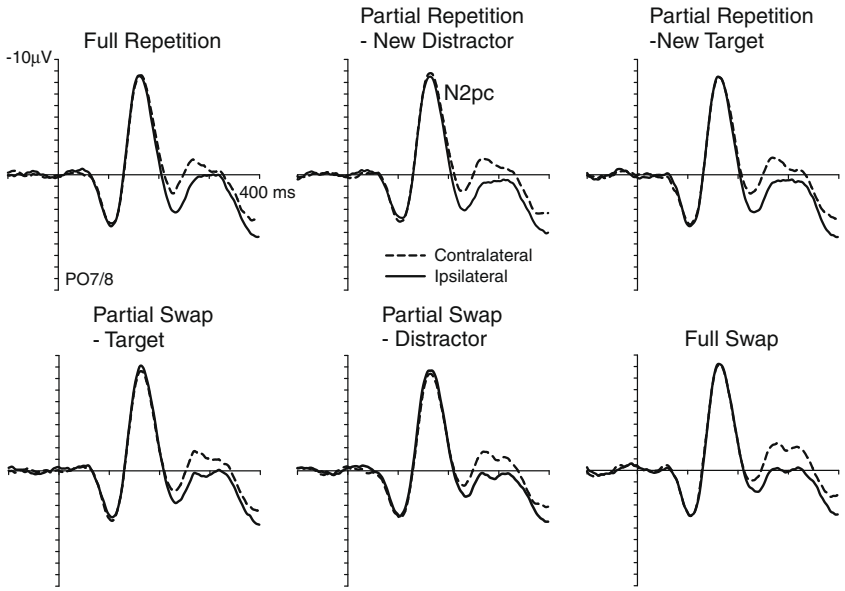

Fig. 4. Grand-average waveforms obtained in Experiment 2 in the 400 ms interval after search array onset at lateral posterior electrodes PO7/PO8 contralateral and ipsilateral to the visual field of the target, shown separately for each of the six trial types.

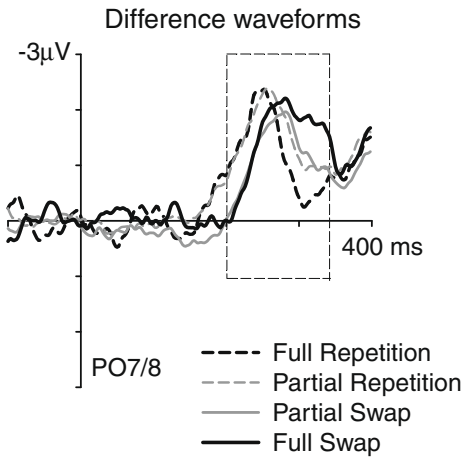

Fig. 5. Difference waveforms obtained in Experiment 2 in the 400 ms interval after search array onset by subtracting ERPs at electrodes PO7/8 ipsilateral to the visual field of the target from contralateral ERPs. Difference waveforms are shown separately for Full Repetition trials, Partial Repetition trials (collapsed across Partial Repetition – New Distractor and Partial Repetition – New Target trials), Partial Swap trials (collapsed across Partial Swap – Target and Partial Swap – Distractor trials), and Full Swap trials.

(see Fig. 5). This was substantiated by planned comparisons which revealed larger N2pc amplitudes for Full Repetition as compared to Full Swap trials (trial type × contralaterality interaction: $F(1, 15) = 6.4$, $p < 0.03$), and between Full Repetition and Partial Swap trials, Partial Repetition and Full Swap trials, and Partial Repetition and Partial Swap trials (trial type × contralaterality interactions: all $F(1, 15) > 10.0$, all $p < 0.007$). No N2pc amplitude differences were present in this time window between Full and Partial Repetition trials, and between Full and Partial Swap trials (both $F < 1$). In spite of these amplitude differences between trial types, analyses conducted separately for each of these four trial types obtained reliable effects of contralaterality, all $F(1, 15) > 8.9$, all $p < 0.009$, confirming the presence of an N2pc for all trial types.

In the 270–340 ms measurement window, a main effect of contralaterality, $F(1, 15) = 69.3$, $p < 0.001$, reflecting the presence of the N2pc, was again accompanied by a trial type × contralaterality interaction, $F(3, 45) = 9.6$, $p < 0.001$. As can be seen in Fig. 5, N2pc amplitudes during this later phase were maximal on Full Swap trials, intermediate on Partial Swap and Partial Repetition trials, and smallest on Full Repetition trials, and this was substantiated through additional planned comparisons. The later phase of the N2pc was larger on Full Swap than on Full Repetition trials (trial type × contralaterality: $F(1, 15) = 18.0$, $p < 0.001$). There was no N2pc amplitude difference between Partial Repetition and Partial Swap trials ($F < 1$). The late phase of the N2pc for both of these trial types was smaller than the late N2pc on Full Swap trials (Partial Repetition vs. Full Swap: $F(1, 15) = 6.1$, $p < 0.03$; Partial Swap vs. Full Swap: $F(1, 15) = 13.1$, $p < 0.003$), but larger than the late N2pc on Full Repetition trials (Partial Repetition vs. Full Repetition: $F(1, 15) = 8.1$, $p < 0.02$; Partial Swap vs. Full Repetition: $F(1, 15) = 7.3$, $p < 0.02$). Even though N2pc amplitudes differed between trial types, additional analyses conducted separately for each of the four trial types obtained reliable effects of contralaterality, all $F(1, 15) > 8.2$, all $p < 0.02$, confirming the presence of an N2pc during the 270–340 ms time window in all trials.

4.3. Discussion of Experiment 2

Experiment 2 confirmed the results found in the mixed blocks of Experiment 1. RTs were substantially faster on Full Repetition than on Full Swap trials, and the N2pc component again emerged earlier on Full Repetition relative to Full Swap trials, supporting the hypothesis that intertrial feature priming effects are generated at the stage of attentional target selection. The critical new question addressed was whether these effects reflect target activation, distractor inhibition, or a combination of both.

The results of Experiment 2 conclusively rule out the possibility that priming of pop-out effects are driven exclusively by target activation, or only by distractor inhibition. In this case, systematic RT and N2pc differences should have been observed between the two types of Partial Repetition and Partial Swap trials. Target activation acting on its own should result in most efficient target selection in both Full Repetition and Partial Repetition – New Distractor trials, most inefficient target selection in both Full Swap and Partial Swap – Distractor trials, and intermediate selection efficiency in the other two trial types. Distractor inhibition on its own would

enable most efficient target selection on both Full Repetition and Partial Repetition – New Target trials, and least efficient selection on both Full Swap and Partial Swap – Target trials, with intermediate selection efficiency in the remaining two trial types. The pattern of RT and electrophysiological data obtained in Experiment 2 is inconsistent with either of these two sets of predictions. Neither RTs nor N2pc latency or amplitude measures revealed differences between the two types of Partial Repetition or Partial Swap trials. In contrast, there were substantial differences between Full and Partial Repetition, Partial Repetition and Partial Swap, and Partial and Full Swap trials. These results suggest that target activation and distractor inhibition processes both contribute equally to intertrial colour priming (see also Lamy et al., 2008).

An equal contribution of target activation and distractor inhibition to priming of pop-out could have been reflected in a gradual increase of RTs and N2pc onset latencies from Full Repetition, Partial Repetition, Partial Swap, up to Full Swap trials. While the RT data obtained in Experiment 2 showed this pattern, N2pc onset latencies did not: the N2pc emerged equally early for Full and Partial Repetition trials, and was equally delayed for Partial and Full Swap trials (see Fig. 5). This suggests that the attentional selection of colour singleton targets was delayed whenever either the target or the distractor colour was swapped across trials. Interestingly, swapping both colours simultaneously (Full Swap trials) did not produce an additional N2pc delay. Likewise, the N2pc emerged just as early on Partial Repetition trials where only one item (target or distractor) was repeated as on Full Repetition trials. An early N2pc on Full and Partial Repetition trials, and a delayed N2pc on Partial and Full Swap trials, suggests that the speed of attentional target selection is determined by whether or not at least one role-reversal occurs across trials (see also Kristjánsson & Driver, 2008).

However, this account cannot explain the full pattern of RT effects, which also included delayed RTs on Partial relative to Full Repetition trials, and delayed RTs on Full as compared to Partial Swap trials (see Fig. 3). In other words, there were RT costs for trials where only one of the target and distractor colours instead of both of them were repeated, and for trials where both colours instead of just one were swapped. If these performance differences are not caused by differences in the speed of attentional target selection, as reflected by N2pc onset latencies, how could they have been produced? An inspection of the N2pc waveforms shown in Fig. 5 suggests a possible answer. While N2pc components on Partial vs. Full Repetition trials, and on Partial vs. Full Swap trials were initially indistinguishable, these two pairs of waveforms differed reliably during the late N2pc time window (270–340 ms after search array onset). Here, N2pc amplitudes were larger for Full relative to Partial Swap trials, and larger for Partial relative to Full Repetition trials. A more sustained N2pc in trials where RT costs emerged could reflect a longer duration of focal-attentional target processing under conditions where intertrial priming results in increased demands on selective attention. In Full Repetition trials, persisting target colour activation and distractor colour inhibition ensure that target selection and distractor rejection are fast and efficient, resulting in an early but transient N2pc component. In Partial Repetition trials, where either the target or the distractor colour is new, only one of these facilitatory processes is activated, producing less efficient selective processing and a relatively more sustained N2pc. In Full Swap trials, persisting target activation and distractor inhibition both interfere with target selection and thus maximize the demands on selective attentional processing, resulting in its temporal extension and a sustained N2pc. On Partial Swap trials, only one source of interference is active, allowing relatively more efficient selective target processing, which is reflected by a reduced late N2pc.

Although this line of argument is speculative at present and will need support from further ERP investigations of intertrial priming, it is in line with previous studies that have found links between N2pc amplitudes and the difficulty of attentional target selection (e.g., Luck & Hillyard, 1994). It implies that behavioural priming of pop-out effects may have two distinct sources: on the one hand, the onset of spatially selective attentional target processing is delayed whenever there is at least one role-reversal between targets and distractors on successive trials. On the other hand, the efficiency and duration of focal-attentional processing is further modulated by target activation and distractor inhibition that persist from the preceding trial.

5. General discussion

In both experiments, RTs were faster when both target and distractor colours were repeated across successive trials relative to trials where these colours were swapped, thus confirming previous observations (e.g., Lamy et al., 2008; Maljkovic & Nakayama, 1994). Critically, these RT differences were accompanied by earlier onsets of the N2pc component for Full Repetition as compared to Full Swap trials. As the N2pc has previously been shown to be a marker of the spatially selective processing of target events in visual search displays (e.g., Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999), this N2pc latency difference provides new electrophysiological evidence that the repetition vs. alternation of task-relevant features across trials has a systematic effect on the speed of selective attentional processing. This conclusion is in line with the hypothesis that priming of pop-out effects are primarily generated at early visual processing stages, where the perceptual analysis and attentional selection of target events is facilitated by feature repetition (Chun & Nakayama, 2000; Maljkovic & Nakayama, 1994; Wolfe et al., 2003), but not with alternative models that postulate a purely post-perceptual locus of intertrial priming effects, such as retrieval of from episodic memory (Huang et al., 2004) or stimulus–response translation (e.g., Cohen & Magen, 1999; Mortier, Theeuwes, & Starreveld, 2005). If priming of pop-out effects were primarily generated after the focal-attentional selection of target events, no effects of intertrial feature priming on N2pc latencies should have been observed in the present experiments. The fact that the onset of the N2pc component was strongly affected by the properties of the search arrays encountered on the preceding trial provides clear-cut support that priming of pop-out modulates the latency of processes that are involved in the selective attentional processing of target stimuli.

Importantly, Experiment 2 revealed that these N2pc onset latency shifts were determined by the presence vs. absence of a role-reversal of targets and distractors across trials, thus suggesting that delays in the onset of spatially selective attentional target processing are not simply elicited on all non-repetition trials, but depend more specifically on a swap of either target or distractor features across trials. On swap trials, persisting target colour activation interferes with the rejection of distractors as non-targets, and persisting distractor colour inhibition interferes with the attentional selection of the current target. The results of Experiment 2 suggest that either of these processes on its own is sufficient to produce a delay in the onset of focal-attentional target processing.

Even though the role-reversal of targets and distractors across trials affected N2pc latency in both experiments, behavioural priming of pop-out effects may not be exclusively produced by a delay in the onset of spatially selective attentional target processing, but might also reflect an additional modulation of later stages. In Experiment 1, the magnitude of behavioural priming of pop-out effect in mixed blocks was virtually identical to the N2pc onset latency difference observed between repetition and change trials, suggesting that the RT effect might be fully accounted for by differ-

ences in the onset of attentional target processing, as reflected by the N2pc. In contrast, the RT difference between pure and mixed blocks (123 ms) in Experiment 1 was substantially larger than the corresponding difference in N2pc onset latencies between these two types of blocks (50 ms), suggesting that additional factors might have contributed to the RT effect. Along similar lines, the RT differences between Full Repetition and Full Swap trials observed in Experiment 2 were substantially larger than the corresponding N2pc onset latency differences, indicating that additional processes beyond the delay of focal-attentional processing might be involved.[2] This assumption is further supported by the fact that N2pc onsets did not differ between Full and Partial Repetition trials, and between Partial and Full Swap trials, in spite of the fact that reliable RT differences were obtained between these conditions. As argued above, the observation that the late N2pc was more sustained on trials where relative RT costs were observed (Partial relative to Full Repetition trials, and Full relative to Partial Swap trials, respectively) suggests that these RT differences may be associated with differences in the efficiency and duration of focal-attentional target processing that result from intertrial priming.[3] Even though behavioural priming of pop-out effects may not exclusively reflect differences in the onset of the focal-attentional stage of target processing, but also differences in its duration, both of these mechanisms represent effects of intertrial feature priming on the spatially selective attentional processing of visual search targets, rather than on post-selective stages such as episodic memory retrieval or response selection. In this respect, the current findings are still in line with previous suggestions that priming of pop-out effects are related to a modulation of processes that are involved in the attentional selection of visual search targets (Chun & Nakayama, 2000; Maljkovic & Nakayama, 1994; Wolfe et al., 2003).

It is important to underline that the current results do not imply that all intertrial priming effects in visual search are generated at relatively early perceptual or attentional processing stages. This is illustrated by a recent study by Töllner et al. (2008), who studied electrophysiological correlates of intertrial priming in a compound visual search task where targets were either colour or shape singletons, distractor features remained constant across trials, and the repetition vs. alternation of the target-defining dimension and the required manual response were varied independently. The N2pc emerged earlier and was larger on trials where the target dimension was repeated than on dimension-change trials. In line with the current results, this observation suggests that the repetition of target features allows a faster and more efficient allocation of focal attention. Importantly, the repetition vs. alternation of responses across trials had no effect whatsoever on the N2pc, but instead affected the amplitudes of the Lateralised Readiness Potential, which is an electrophysiological marker of response activation and execution. This pattern of results strongly suggests that intertrial priming effects associated with repetitions vs. changes in target dimensions or responses are generated at separable perceptual–attentional and response-related processing stages.

6. Conclusions

The present study has provided new electrophysiological evidence that intertrial feature priming modulates processing stages that underlie the spatially selective attentional processing of target stimuli in pop-out visual search. The attentional selection of such targets is delayed when either targets or distractor features are swapped across successive trials. In addition, persisting target activation and distractor inhibition can also modulate the efficiency and duration of attentional target processing.

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[2] This difference between experiments may be partially due to the fact that a relative amplitude criterion was used to estimate N2pc onsets. This can be problematic when component amplitudes vary across trial conditions, with an overestimation of onset latencies for conditions with larger component amplitudes, and an underestimation with smaller amplitudes. In Experiment 1, N2pc peak amplitudes were larger for change trials than for repetition trials, which may have accentuated the N2pc onset differences between these two trial types. In Experiment 2, N2pc amplitudes tended to be larger on Full Repetition relative to Full Swap trials, thus possibly resulting in an underestimation of N2pc onset differences between these conditions.

[3] The observation that in Experiment 1 N2pc latency shifts could fully account for RT differences between repetition and change trials, may be linked to the fact that full repetitions of target and distractor colours were much more frequent (50% of all trials) than in Experiment 2, resulting in a higher probability of identical target and distractor colours appearing on three or more successive trials. This difference may account for the earlier N2pc onset on Full Repetition trials relative to Experiment 2, and could thus have amplified the effects of intertrial priming on the onset of selective attentional target processing, as estimated on the basis of N2pc latencies.