



Priming resolves perceptual ambiguity in visual search: Evidence from behaviour and electrophysiology

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ABSTRACT

Visual search for a target among distractors is often speeded when the target-defining feature is repeated from trial to trial, compared to when it changes. It has been proposed that whether this intertrial priming effect is perceptual in nature or not, and how strong it is, depends on the perceptual ambiguity of the display. Using the event-related potential (ERP) method, Experiment 1 assessed whether perceptual ambiguity indeed resulted in increased priming, by comparing target repetitions and changes in a condition with a target-resembling distractor to a condition without such a distractor. Priming effects on response times were indeed greater in the presence of a distractor. Moreover, EEG analyses revealed latency shifts and amplitude differences in the P1 and N2pc components for the same condition, consistent with a perceptual locus of intertrial priming. Experiment 2 confirmed this by varying the perceptual similarity of the distractor to the target. Priming benefits increased with increasing similarity.

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1. Introduction

To study selective attention, researchers often make use of the visual search task, in which observers scan displays for a relevant object (the *target*) among a number of irrelevant objects (the *distractors*). Findings indicate that selection in visual search is usually not perfect. The wrong object may be selected and interfere with the task when it has a particularly salient appearance (e.g. a distinct color, Theeuwes, 1992; or abrupt onset, Yantis & Jonides, 1984), or it highly resembles the object one is looking for (e.g. a red distractor when the target is also red, Folk, Remington, & Johnston, 1992). Thus, attention appears to reflect a bias in processing that is determined by both the current stimulus and the overall task.

However, the current stimulus and the overall task are not the only factors determining where attention is allocated in visual search. To a large extent, the success or speed with which a target is found on the current trial depends on automatic learning or priming effects stemming from immediately preceding trials (Maljkovic & Nakayama, 1994; Müller, Heller, & Ziegler, 1995; Olivers & Humphreys, 2003; see Los (1996) for a non-search example). In one of the first studies, Maljkovic and Nakayama (1994) showed that response times (RTs) to a red target were speeded when the preceding trial also contained a red target – as opposed to a green target – even though the task was to look for both target types. In fact, such

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intertrial effects occurred even when target repetitions and target changes were perfectly predictable, suggesting that there is little volitional control involved. Maljkovic and Nakayama (2000) therefore attributed these effects to a primitive and automatic priming mechanism that facilitates the return to previously attended objects. This would put the explanation of such effects at the perceptual end of the information processing stream, prior to selection: the priming facilitates the guidance of attention by increasing the relative visual salience of the target. A similar view also returns in *dimension-weighting* and *guided search* theories, which assume that more “attentional weight” is put on the repeated target-defining property. This results in stronger and more rapid activation of that property when the target appears again, leading to an advantage in the competition for selection (Becker & Horstmann, 2009; Found & Müller, 1996; Müller & Krummenacher, 2006; Müller et al., 1995; Wolfe, Butcher, Lee, & Hyle, 2003; see also Bichot & Schall, 2002).

The alternative view has been that intertrial effects on visual search stem from processes solely occurring after selection. Cohen and Magen (1999) found evidence that what is primed is response selection rather than visual selection. According to their account, each stimulus property is assigned its own response module, and when the property re-appears, processing within this response module is facilitated. In support of a response-based account, Kumada (2001; see also Olivers & Meeter, 2006) found intertrial priming effects for *present/absent* search tasks, but not for so-called *compound* search tasks. In the *present/absent* task, the target presence directly drives the response (allowing for direct response priming), whereas in the *compound* search task, the response is

defined by a usually inconspicuous feature that is varied independently from the target-defining feature (thus controlling for response mapping, although the effects of the defining feature and response feature may sometimes interact, e.g. Töllner, Gramann, Müller, Kiss, & Eimer, 2008). Note that in these studies, the search displays were exactly the same for each type of task, making it difficult for perceptual, pre-selection accounts to fully explain the differential priming effects. Nevertheless, a pure response priming account cannot be the full story either. In fact, the original study of Maljkovic and Nakayama (1994) involved a compound search task: participants decided which corner was missing from a diamond-shaped target. Yet they found very robust intertrial effects that have been replicated many times since.

Huang, Holcombe, and Pashler (2004) have proposed that it is not the perceptual stage prior to selection, nor the response selection stage at the end of the information processing stream that is speeded by priming, but a stage in between – the stage that is responsible for verifying or deciding whether a selected object is indeed the target. They found that the repetition of an irrelevant target property (e.g. color when participants were looking for size) actually had a detrimental rather than a beneficial effect on search for a target on switch trials. This cannot easily be explained from a perceptual pre-selection view, which predicts that the repetition of color, if anything, should make the target more salient. Instead, according to Huang et al., the partial mismatch of the target to previous memories creates confusion at a target verification level, which then slows the decision to respond.

2. The ambiguity framework and the present study

To explain the apparently discrepant findings, Meeter and Olivers (2006) have argued that intertrial priming plays a role in resolving *ambiguity* (see also Olivers & Meeter, 2006, 2008). The basic premise of this idea is that as task ambiguity increases, so does the benefit of intertrial repetition. Priming effects may be expressed at different levels, such as perceptual competition or response selection, depending on the level at which the task is ambiguous. For example, when Meeter and Olivers introduced a unique and salient distractor (a *singleton*) in a compound search task, intertrial effects re-emerged. Meeter and Olivers (2006) argued that the presence of a distractor makes the task of determining what the target is perceptually more confusing (or *ambiguous* in their terms). Priming of the target then helps to resolve this perceptual ambiguity. Olivers and Meeter (2006) also found evidence for intertrial priming when the *task* (i.e. stimulus–response mappings) was made more ambiguous, while the stimulus was kept the same. They argued that the decision to respond in a present/absent task essentially suffers from more uncertainty (as it is uncertain whether the target is present) than a compound search (in which a target is always present). Thus, in a present/absent task there is more room for priming to resolve ambiguity. When Olivers and Meeter introduced task-related ambiguity in a compound search task (e.g. by alternating the response requirements), priming benefits emerged even for this task.

In the present study we further assessed priming in visual search under conditions of perceptual ambiguity. Consider Fig. 1a and b, which illustrate two conditions used by Meeter and Olivers (2006) that we will investigate again here. In a compound search task, participants searched for a red or a green diamond among gray distractors, and responded to the direction of an arrow head presented inside the target. The target's color unpredictably changed from trial to trial. In the condition in which there was no singleton distractor (Fig. 1a), Meeter and Olivers found no evidence for intertrial priming. They proposed that this was the case because in such displays there is only one object selected and thus there is little doubt what the

target is. In the other condition, referred to in Fig. 1b as the *similar distractor* condition, there was a blue or yellow singleton distractor present. Now a robust 40 ms intertrial effect emerged. They proposed that this was due to the ambiguous nature of the display: priming helps to resolve the perceptual ambiguity by advancing one object over the other in the competition for selection. Experiment 1 of the current study was designed to test the hypothesis that priming aids in resolving ambiguity. For this purpose, we measured ERPs from the scalp in conditions with relatively low (distractor absent) and high (distractor present) perceptual ambiguity, in response to target repetitions and target changes. Following earlier work (see Luck, 2006, for an overview), we looked to the N2pc component as an index of target selection. The N2pc is a lateralized ERP component that is apparent at posterior electrode locations contralateral to the location of an attended stimulus from roughly 175 ms post-stimulus (Luck & Hillyard, 1994). Our expectation was that the N2pc would show changes in latency or amplitude that followed behaviour, demonstrating that perceptual ambiguity has an impact on target selection. We were additionally interested in changes in the ERP preceding the N2pc that might reflect perceptual priming benefits. To foreshadow, results from the ERP study indeed provide evidence for such early perceptual priming benefits under conditions of increased ambiguity.

Experiment 2 was a behavioural experiment that further tested the role of perceptual ambiguity in intertrial priming. In addition to the no distractor and similar distractor conditions mentioned earlier, Experiment 2 included a *dissimilar distractor* condition, which is illustrated in Fig. 1c. Here the singleton distractor deviated considerably from the remainder of the display items in a number of dimensions. On the basis of the literature we expected that such a salient object would slow down search (e.g. Theeuwes, 1992). Yet at the same time, the display would be less ambiguous, because the distractor is less similar to the target. In other words, on the basis of the ambiguity account, we expected RTs to increase, but priming benefits to decrease.

3. Experiment 1

We measured EEG, RTs and accuracy in response to target repetitions and target switches in visual search under conditions of low and high perceptual ambiguity. Participants searched for a colored target diamond among mostly grey nontarget diamonds. In the distractor-present condition one of the nontargets had a salient color. We expected that priming effects on RT would increase in that condition relative to a distractor absent condition because of increased ambiguity, and that this behavioural pattern would be reflected in the N2pc. We were furthermore interested in the possibility of observing priming effects in earlier components, such as the visual P1, which occurs approximately 100 ms post-stimulus. Evidence of such early modulation would provide a strong argument for a perceptual level of priming.

A previous EEG study by Töllner et al. (2008) is directly relevant here. In this study observers searched for a target that differed from the distractors in either of two dimensions. On half the trials, the target was defined by shape, on the other half it was defined by color. Consistent with earlier findings (Müller et al., 1995), search RTs were faster when the target dimension repeated, compared to when it switched. Together with this behavioural effect, Töllner et al. (2008) found a latency benefit as well as an amplitude increase on the N2pc for repeated vs. switched dimensions, leading them to conclude that priming affects target processing at perceptual stages prior to selection. However, although providing strong evidence for a perceptual locus of priming, Töllner et al.'s data does not provide direct evidence for the claim that priming changes perception *prior* to selection. If we assume that the N2pc reflects the selection process operating on perceptual representations, then a

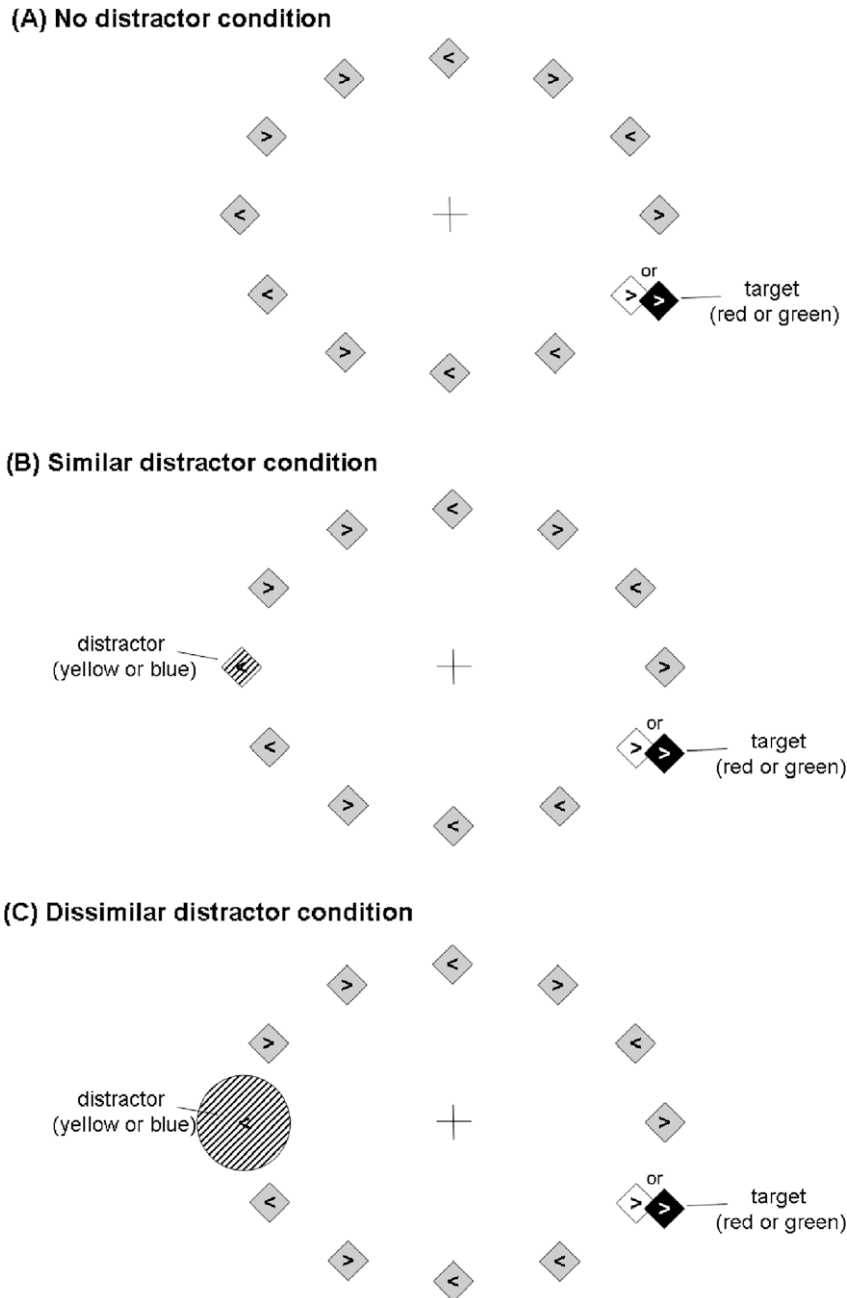


Fig. 1. Example displays for the three conditions of Experiment 2. Targets were red or green diamonds. The nontarget items were all grey (A), except in the similar (B) and dissimilar (C) distractor conditions in which there was a blue or yellow singleton distractor. In Experiment 1, among other differences, only conditions A and B were included, the set size was reduced from 12 to 6, and the diamonds were increased in size. Examples of these displays are shown in Fig. 2.

faster N2pc may reflect stronger perceptual representations, it may reflect a faster selection process, or both. Do repeated targets lead to stronger perceptual representations because they are more likely to be selected, or are repeated targets more likely to be selected because they are perceptually stronger (as suggested by Töllner et al.)? To conclude that priming changes perception prior to selection, we need to find evidence for ERP modulations prior to the N2pc.

Our experiment was designed to extend that of Töllner et al. in several ways. First, we optimized the experiment to enable early perceptual priming. We did this by looking at feature priming rather than dimension priming. In feature priming the two consecutive target features match exactly, possibly allowing for priming to occur at lower level perceptual stages. The idea that feature

priming might act at earlier processing stages is consistent with results from Becker (2008a, see also Becker, 2008b) demonstrating that saccadic latencies are affected by feature priming but not dimension priming. Second, we introduced manipulations of perceptual ambiguity. We feel that the primary benefit of intertrial priming is the resolution of processing ambiguity (cf. Meeter & Olivers, 2006; Olivers & Meeter, 2006), and thus that evidence of perceptual priming is most likely to be detected under circumstances of high perceptual ambiguity. We did this by introducing a salient distractor that was similar to the target.

Our design included stimulus positions that fell on the vertical meridian of the visual search array. This manipulation allowed us to isolate lateralized ERP activity related to target activity when displays contained a salient distractor. This is so because stimuli

presented on the vertical meridian of the display are represented equally in both visual cortices and thus do not have lateralized effects on the visual ERP (e.g. Hickey, McDonald, & Theeuwes, 2006). By presenting the salient distractor on the vertical meridian of the search array we created a circumstance of high perceptual ambiguity without confounding the lateralized response elicited by the distractor with that elicited by the target.

3.1. Methods

3.1.1. Participants

Thirteen volunteers participated for €7 an hour. Two participants were discarded from further analysis due to an apparent inability to maintain fixation during experimental participation. Of the remaining participants six were male and two were left-handed. Age varied between 18 and 26, with an average of 20.4 years. All subjects reported normal or corrected-to-normal acuity and color vision.

3.1.2. Stimuli, design, and procedure

Participants each took part in two recording sessions, each of approximately 1 h. In each session they were seated in a dimly-lit, electromagnetically shielded cubicle at a distance of approximately 60 cm from a 21 in. monitor. Stimulus generation and response recording was done on a standard Windows operated PC using E-Prime software. Examples of search displays are provided in Figs. 3a, 4a, and 5a. Search displays contained six diamonds (diameter $3.3 \times 3.3^\circ$ of visual angle) appearing against a black background, regularly arranged on an imaginary circle (diameter 6.7° of visual angle), such that two items fell on the display meridian, two items fell to the left, and two items fell to the right of fixation. Most of the nontargets were gray (21.6 cd/m^2). The target was a randomly chosen element and was either red (CIE x, y chromaticity coordinates 0.603, 0.344; 21.5 cd/m^2) or green (CIE 0.313, 0.566; 21.6 cd/m^2) for six of the eleven analyzed participants, or blue (CIE 0.170, 0.119; 21.6 cd/m^2), or yellow (CIE 0.450, 0.484; 21.6 cd/m^2) for the remaining five. In the *distractor absent* condition, the target was the only color singleton in the display. In the *distractor-present* condition, one of the nontarget diamonds was given unique color, either blue or yellow for those

subjects in the red or green target condition, or red or green for those subjects in the blue or yellow target condition. Inside each diamond there was either a left- (<) or a right-pointing (>) arrowhead, chosen randomly, and drawn in black. Participants were instructed to ignore the distractors, look for a target, and to respond to the arrowhead inside it by pressing the Z-key for < and the M-key for > while maintaining central fixation. Participants received feedback whenever they made an error and on overall average RTs and accuracy scores after each block.

In addition to *distractor presence*, the other factor of importance was the *target type*. Targets could either *repeat* color from trial to trial, or *switch*. There were 720 trials for each combination of distractor presence (present, absent) and target type (repetition, switch). This resulted in 120 trials for each possible target position prior to the rejection of trials in which participants made eye movements. All trial types were randomly mixed within 12 blocks of 240 trials each, divided between two sessions. Prior to each EEG recording session there was a practice block of 240 trials.

3.1.3. EEG recording and analyses

EEG and electrooculogram (EOG) were recorded from 134 sintered-AgCl electrodes using the Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands). Horizontal EOG was recorded from electrodes located 1 cm lateral to the external canthi and vertical EOG was recorded from electrodes located 2 cm above and below the right eye socket. Electrophysiological signals were digitized at 1024 Hz and down-sampled offline to 500 Hz. Raw EEG was offline filtered using a finite impulse response (FIR) function with half-amplitude attenuation at ~ 0.49 Hz and a 6 dB transition bandwidth of ~ 0.1 Hz, and low-pass filtered using a FIR function with half-amplitude attenuation at 20 Hz and a 6 dB transition bandwidth of 3 Hz.

ERP analysis was conducted using a combination of custom scripts for Matlab (Mathworks, Natick, MA) and the EEGLAB toolbox (Delorme & Makeig, 2004). Independent components were extracted from the data using logistic infomax independent component analysis (ICA) algorithm (Bell & Sejnowski, 1995). The primary component associated with eye movements was identified and used to reject trials in which participants moved their eyes within a 1 s time window beginning 200 ms. before stimulus onset. This resulted in the rejection of 8.3% of total trials per subject ($\pm 4.4\%$ SD). Following this all components associated with blinks, line noise, and other sources of artifact were identified and removed from the data. The resulting epochs were separated into relevant conditions and ERPs were created using standard signal averaging procedures. All ERPs were computed with respect to a 100 ms pre-stimulus baseline period and were referenced to the average of all 128 encephalic electrodes. The ERPs presented in the figures were recorded at lateral occipital electrode sites roughly equivalent to PO7 and PO8 of the international 10–10 electrode placement system (A10 and B7 in Biosemi nomenclature), and all analyses and statistics reported below are based on the signals recorded at these sites. These scalp locations are commonly used in the examination of lateralized P1 and N2pc ERP components. We assessed the N2pc latency difference using a modified jackknife statistical procedure (see Miller, Patterson, & Ulrich, 1998). The jackknife procedure involves creating grand averages for each of the n combinations of $n-1$ subjects. Latency is measured based on these subset grand averages, in this way sidestepping problems inherent to assessing component latency based on low signal-to-noise, per-subject ERPs. Importantly, the jackknife procedure has the effect of artificially reducing variability in the data and this needs to be corrected for during subsequent statistical analysis. All jackknife-based analyses reported below have therefore been corrected as per Miller et al. (1998).

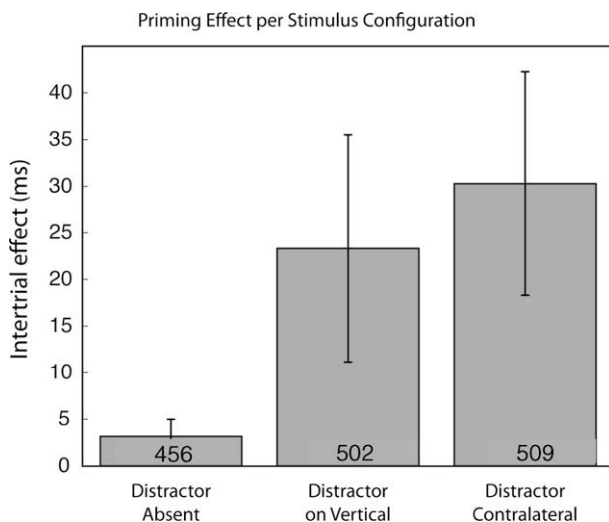


Fig. 2. Mean intertrial effects (RT for target switches minus RTs for target repetitions) for the stimulus configurations used in the ERP analyses of Experiment 1. The target repetition baseline RTs are plotted in numbers inside the columns. Error bars reflect 95% confidence intervals computed for the repeat vs. switch contrast.

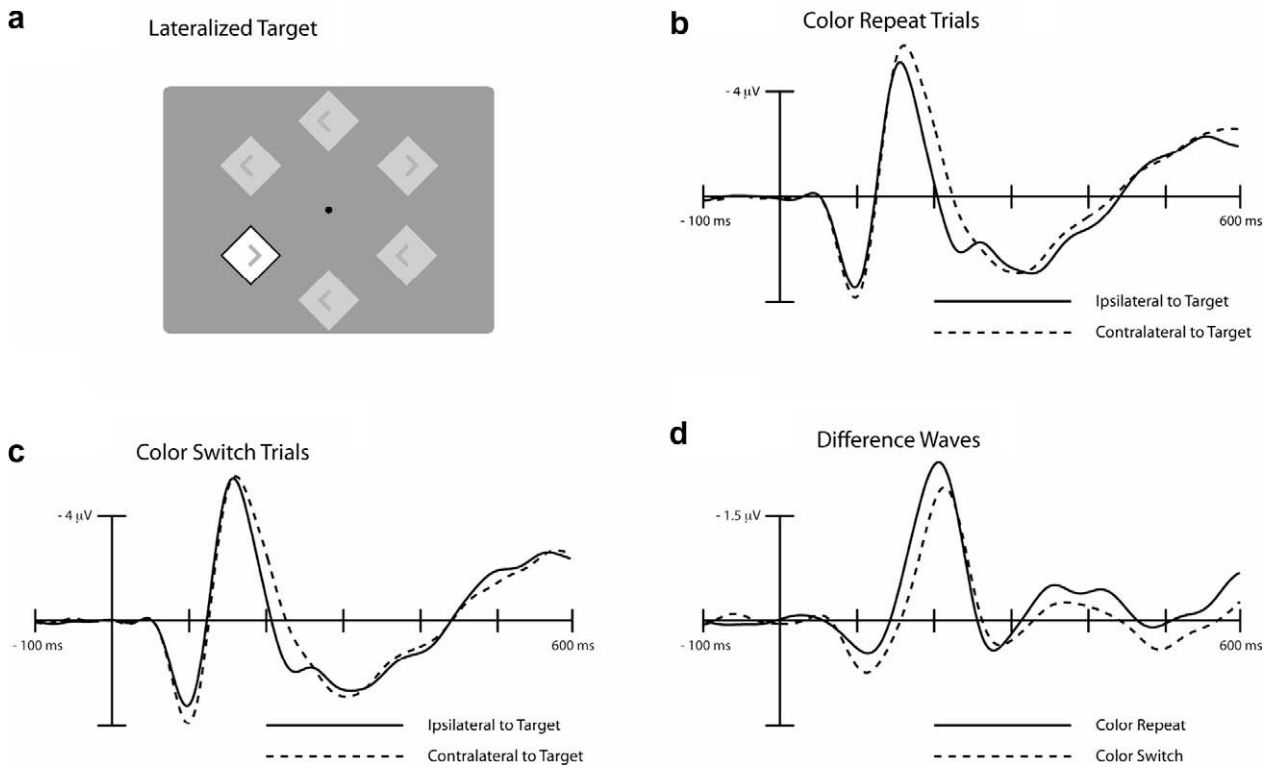


Fig. 3. ERP results of Experiment 1. (a) Example of a lateralized target stimulus configuration in the distractor absent condition, together with the ERPs elicited contralateral and ipsilateral to (b) repeated and (c) switched targets, as well as (d) the difference waves of the contra- vs. ipsilateral contrast. Note that in the ERP waveforms negative is plotted upward and stimulus onset occurred at 0 ms and is indexed by the y-axis.

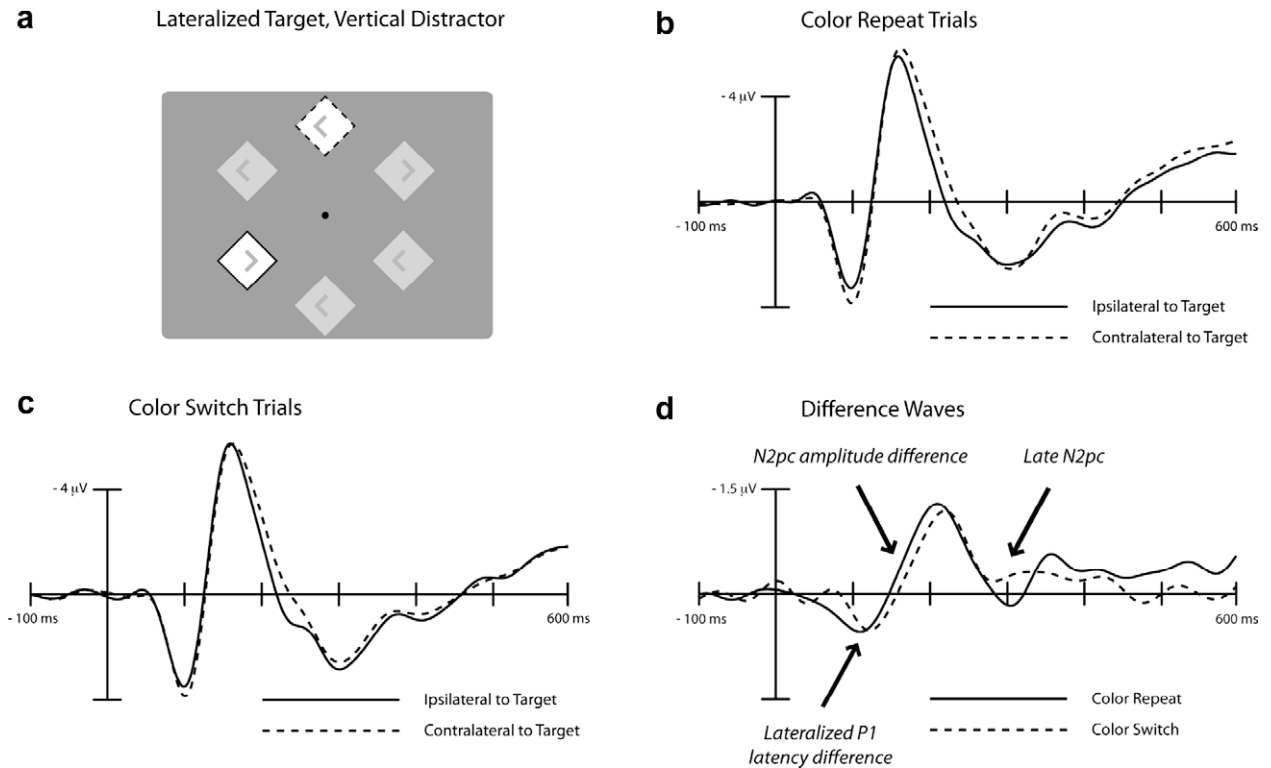


Fig. 4. ERP results of Experiment 1. (a) Example of a lateralized target stimulus configuration in the distractor-present condition in which the distractor was positioned on the meridian (dashed outline), together with the ERPs elicited contralateral and ipsilateral to (b) repeated and (c) switched targets, as well as (d) the difference waves of the contra- vs. ipsilateral contrast. Note that in the ERP waveforms negative is plotted upward and stimulus onset occurred at 0 ms and is indexed by the y-axis.

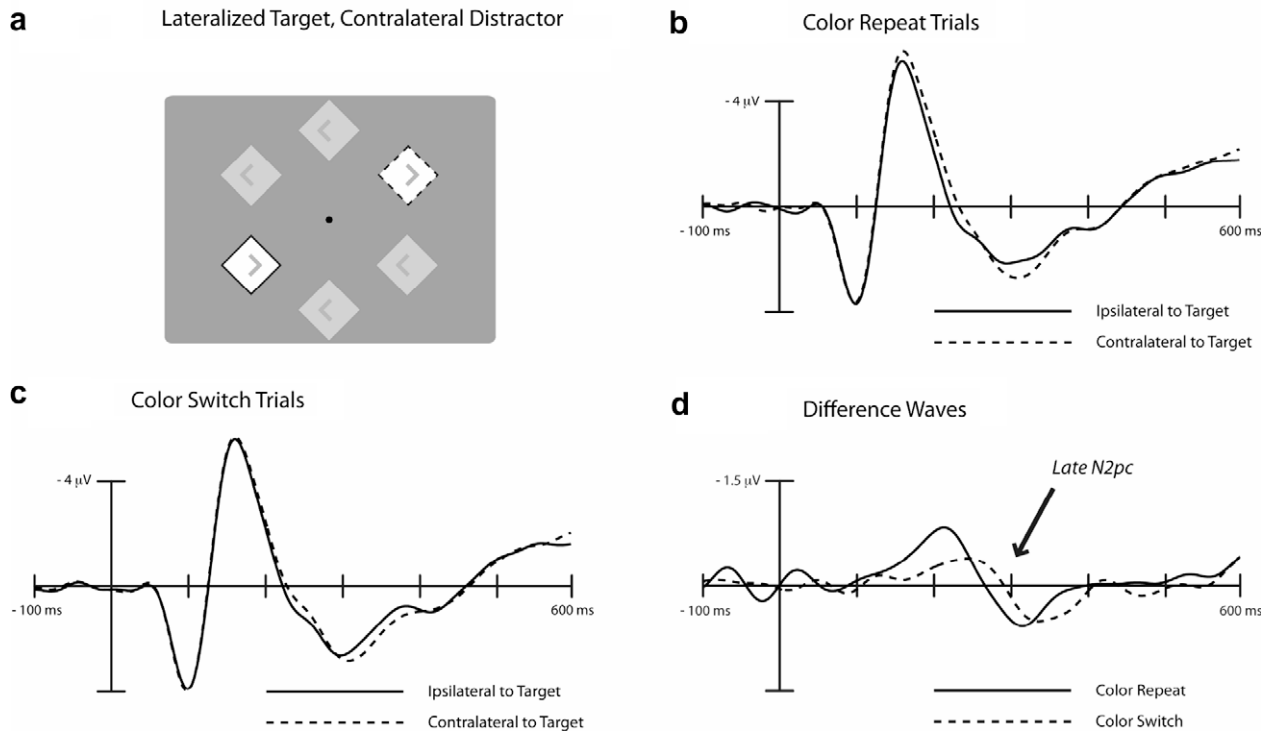


Fig. 5. ERP results of Experiment 1. (a) Example of a lateralized target stimulus configuration in the distractor-present condition in which the distractor was positioned (dashed outline) contralateral to the target, together with the ERPs elicited contralateral and ipsilateral to (b) repeated and (c) switched targets, as well as (d) the difference waves of the contra- vs. ipsilateral contrast. Note that in the ERP waveforms negative is plotted upward and stimulus onset occurred at 0 ms and is indexed by the y-axis.

3.2. Results and discussion

3.2.1. Behavioural results

Error percentages were low overall, at 4.8% when the distractor was absent and the target repeated, and 4.7% when the distractor was absent and the target switched. In the distractor-present condition error rates were 5.3% when the target repeated, and 6.5% when it switched. A repeated measures analysis of variance (ANOVA) with factors for distractor presence (present vs. absent) and target type (repeat vs. switch) revealed a significant main effect of distractor presence ($F(1, 10) = 9.37, \text{MSe} < 0.001, p < 0.02$). No other effects were significant. As will be evident below, accuracy followed the pattern of RTs and there were no signs of a speed/accuracy trade-off. We analyzed the mean of the remaining RTs using the same ANOVA. This revealed significant main effects of distractor presence (absent: 454 ms, present: 492 ms; $F(1, 10) = 40.195, p < 0.001$) and target type (repeat: 474 ms, switch: 506 ms; $F(1, 10) = 31.234, p = 0.001$) and a significant interaction between these factors ($F(1, 10) = 13.078, p = 0.005$). This interaction reflects a reliable 28 ms increase of the intertrial effect in the distractor-present condition relative to the distractor absent condition. Fig. 2 presents the intertrial effects on behaviour associated with three stimulus configurations that were particularly important in the analysis of ERP results: lateralized target with no distractor (Fig. 3a), lateralized target with distractor on the vertical meridian of the display (Fig. 4a), and lateralized target with distractor in the contralateral visual field (Fig. 5a). These ERP analyses are reported next.

3.2.2. Electrophysiological results

Figs. 3b and c, 4b and c, and 5b and c illustrate the ERPs elicited at lateral occipital electrode sites contralateral and ipsilateral to the target in each of three critical stimulus configurations for each of the repeat and switch conditions. Visual examination suggests a series of differences in amplitude and/or latency of the lateralized P1 and N2pc components as a function of target condition. In the lateral

target, distractor absent stimulus configuration, illustrated in Fig. 3, the lateralized P1 difference appears to be larger in amplitude for switch trials (Fig. 3c) whereas the N2pc appears to be both larger and earlier in repeat trials (Fig. 3b). This can be clearly seen in the contralateral-minus-ipsilateral difference waves illustrated in Fig. 3d. The lateralized P1 effect is reflected in the positive deflection in these waveforms beginning at approximately 90 ms, while the N2pc is reflected in the negative deflection beginning at approximately 160 ms. In order to statistically assess the apparent amplitude effects for this stimulus configuration we conducted two repeated measures ANOVAs. Both analyses had factors for laterality (ipsilateral vs. contralateral) and target type (repeat vs. switch). The first ANOVA was based on mean amplitude measured from 115 ms to 125 ms, approximately the peak of the lateralized P1 effect. This analysis revealed a main effect of laterality ($F(1, 10) = 14.855, p = 0.003$) but no main effect of target type ($F(1, 10) < 1$). A significant interaction became apparent ($F(1, 10) = 5.055, p = 0.048$), demonstrating that the increase in lateralized P1 amplitude in the switch condition was reliable.

We should point out here that the lateralized P1 amplitude effect observed in this condition is *opposite* to what would be expected on the basis of perceptual priming. The lateral P1 here is larger in the color switch condition than it is in the color repeat condition, whereas if priming were to facilitate perceptual processing one would expect the P1 to be of larger amplitude in repeat trials. Sensory ERP components are known to be smaller under circumstances of repeated stimulation owing to refractory or fatigue effects (Näätänen & Giard, 1992) and we believe that the reduced P1 in repeat trials might reflect something along these lines. In any case, the P1 amplitude effect observed in this condition did not have a clear behavioural correlate; priming effects in this condition were minimal.

Returning to the ERP effects, a second ANOVA was based on mean amplitude from 150 to 225 ms, constituting the majority of the N2pc conditional difference. This analysis revealed a main

effect of laterality ($F(1, 10) = 19.817, p = 0.001$) but no main effect of target type ($F(1, 10) = 1.077, p = 0.324$). The interaction was significant ($F(1, 10) = 58.766, p < 0.001$), demonstrating that the increase in N2pc amplitude in the repeat condition was reliable. Further analyses revealed a reliable 8 ms shift in peak N2pc latency between the repeat and switch conditions (repeat: 208 ms; switch: 216 ms; $t(10) = 1.930, p = 0.040$).

We would like to note that in this and subsequent conditions we found that the N2pc occurred earlier than is generally observed (e.g. Luck & Hillyard, 1994). One possibility is that this reflects relative ease of selection within the sparse search arrays employed, which contained only five distractor stimuli. This would be consistent with results showing that the N2pc occurs earlier when a target is presented among homogenous distractors rather than heterogenous distractors, circumstances under which target selection would also be facilitated (Mazza, Turatto, & Caramazza, 2009).

To summarize, in the lateral target, distractor absent stimulus configuration the lateralized P1 was larger in the switch condition, while the N2pc both occurred earlier and was larger in the repeat condition.

In the lateral target, vertical distractor stimulus configuration, illustrated in Fig. 4, the lateralized P1 elicited in repeat trials (Fig. 4b) appears to be much the same amplitude as that elicited in switch trials (Fig. 4c), but, it appears to occur earlier (as clear from examination of Fig. 4d). There was a significant 12 ms latency difference (repeat: 110 ms; switch: 122 ms; $t(10) = 2.130, p = 0.030$). Importantly, this P1 latency effect cannot stem from structural differences in the stimuli. The effect was observed in a comparison of ERPs elicited by identical stimulus displays, with the only difference being the type of trial that preceded these displays. In contrast, the ERPs illustrated in Figs. 3 and 4 were elicited by structurally different stimulus arrays; the displays corresponding to the ERPs illustrated in Fig. 4 included a salient distractor, while those corresponding to the ERPs illustrated in Fig. 3 did not. We believe that the presence of the distractor causes the lateralized P1 difference observed in Fig. 4, and that this effect reflects target–distractor interactions that do not occur when the distractor is absent from the display. Far from being a problem or confound, however, these target–distractor interactions are exactly what the experiment was designed to investigate: these interactions are part of the perceptual ambiguity that increases the competition for selection, and thus priming benefits.

In addition to the P1 effects, separate analysis revealed a reliable 10 ms difference in N2pc peak latency (repeat: 210 ms; switch: 220 ms; $t(10) = 2.412, p = 0.017$). A repeated measures ANOVA based on mean amplitude from 150 to 200 ms with factors for lat-

erality and target type revealed a main effect of laterality ($F(1, 10) = 6.588, p = 0.028$) and a significant interaction ($F(1, 10) = 5.209, p = 0.046$), but no main effect of target type ($F(1, 10) < 1$). The N2pc elicited in the switch condition for this stimulus configuration also appears to have a late lateralized component, identified in Fig. 4d as 'late N2pc', that is not present in the repeat condition. We assessed the reliability of this late component in a repeated measures ANOVA based on mean amplitude from 300 to 310 ms with factors for laterality and target type. Neither main effect was significant (laterality: $F(1, 10) < 1$; target type: $F(1, 10) = 3.643, p = 0.0854$), but the interaction was ($F(1, 10) = 6.455, p = 0.028$). This demonstrates that the increase in contralateral negativity was reliable. To summarize, in the lateral target, vertical distractor stimulus configuration the lateralized P1 was earlier in the repeat condition, the N2pc was both larger and earlier in the repeat condition, with a particularly late aspect of the N2pc becoming apparent only in the switch condition.

Finally, in the lateral target, contralateral distractor stimulus configuration, illustrated in Fig. 5, there is little evidence of a lateralized P1 in either the repeat (Fig. 5b) or switch (5c) conditions. However, the analysis revealed a reliable 30 ms difference in N2pc latency (repeat: 214 ms; switch: 244 ms; $t(10) = 7.234, p < 0.001$). A repeated measures ANOVA based on mean amplitude from 150 to 250 ms with factors for laterality and target type revealed a marginally significant main effect of laterality ($F(1, 10) = 4.548, p = 0.059$) and an interaction ($F(1, 10) = 18.378, p = 0.002$), but no main effect of target type ($F(1, 10) < 1$). As in the lateral target, vertical distractor stimulus configuration a late aspect of the N2pc is apparent in the repeat condition. The reliability of this late N2pc activity was assessed in a repeated measures ANOVA based on mean amplitude from 290 to 300 ms with factors for laterality and target type. Neither main effect was significant ($F_s < 1$), but the interaction was significant ($F(1, 10) = 7.320, p = 0.022$), demonstrating that the reliability of this late N2pc for this stimulus configuration. To summarize, in the lateral target, contralateral distractor stimulus configuration, the N2pc both occurred earlier and trended towards being larger in the repeat condition, while again a late aspect of the N2pc was apparent in the switch condition. The latency shifts in P1 and N2pc across different stimulus configurations are summarized in Fig. 6.

As in the earlier ERP investigation of intertrial priming by Töllner et al. (2008) we found that the latency and amplitude of the N2pc was affected by intertrial contingencies. As discussed above, in earlier ERP studies of intertrial priming this modulation of N2pc was interpreted as evidence of perceptual priming. This interpretation relies on the assumption that modulation of N2pc

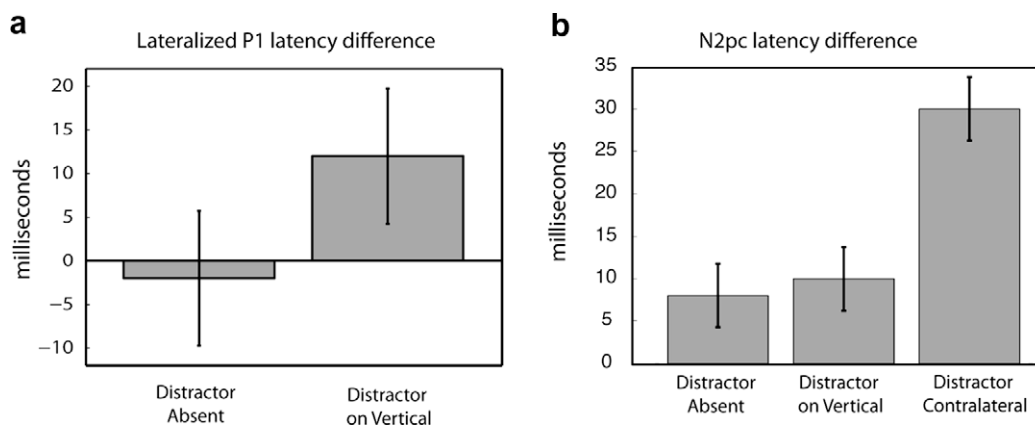


Fig. 6. Mean peak latency differences in Experiment 1 for (a) the P1, and (b) the N2pc, for the target switch vs. target repeat contrast as a function of distractor type (absent, on vertical meridian, or contralateral to the target) of Experiment 1. Error bars reflect 95% confidence intervals computed for the repeat vs. switch contrast per stimulus configuration. Note that no P1 could be estimated for the contralateral distractor condition.

amplitude and latency reflect changes in processing that occur prior to this component. In the current study, we show direct evidence that processing indeed changes in the interval preceding the N2pc when the search display is ambiguous – that is to say, when the target competes for representation with a salient distractor. This change is reflected in a latency shift of the lateral P1, and it was apparent only when the confounding lateralized effect of the salient distractor was nullified by presenting the distractor on the vertical meridian of the search display. Because the lateralized P1 reflects cortical activity involved in early-stage perception, in our view this finding provides clear evidence of perceptual priming.

The ERP results largely matched the behavioural results in that latency benefits of target repetition were small under conditions of low perceptual ambiguity (distractor absent), and became larger under conditions of high perceptual ambiguity (distractor present). Note that in the distractor-present condition, the position of the distractor (lateralized vs. on the meridian) appeared to have had an effect on the N2pc peak latency differences between repeat and switch trials (30 ms vs. 10 ms, respectively), whereas the effect of distractor position was not that large in terms of RT differences (30 ms vs. 23 ms, respectively). However, it seems that when the distractor was on the vertical meridian, the peak latency measure did not quite capture the full extent of the delay or protraction in the N2pc that was evident as the late component in Fig. 4d. In any case, the overall convergence of P1 and N2pc latency measures and amplitude changes with behaviour suggests that intertrial priming effects can be accounted for by changes at perceptual and attentive processing stages, at least under the circumstances created by the current experimental paradigm.

4. Experiment 2

Experiment 1 provided clear evidence that priming affects perceptual processes leading up to selection, and that such priming effects are more strongly expressed under conditions of perceptual ambiguity (i.e. when a distractor was present). In Experiment 2 we sought to extend these findings using behavioural measures only, by varying the nature of the distractor so that it became more or less ambiguous. In Experiment 1, the distractor was very similar to the target, as both were colored diamonds. In Experiment 2, in addition to this what we now call *similar distractor* condition, we included a *dissimilar distractor* condition (illustrated in Fig. 1c). In this condition, the singleton distractor again had a unique color, but now it was big and round (while the other nontargets were still small grey diamonds). Just like the similar distractor, we expected this object to cause considerable slowing, but now on the basis of its strong salience relative to the other items (Theeuwes, 1992), rather than on the basis of its similarity to the target. At the same time, exactly because the distractor was no longer similar to the target, we expected the displays to become perceptually less confusing as to what the target would be. This reduced ambiguity should then result in reduced priming effects. This way, we could also control for an alternative explanation of the results of Experiment 1, namely that the size of the intertrial priming effects simply increases with overall RTs, without having to assume a role for distractor-related ambiguity.

4.1. Methods

4.1.1. Participants

Twelve volunteers participated for €7 an hour. Five were male, of which two were left-handed. Age varied between 16 and 32, with an average of 21.3 years. They all reported (corrected-to-) normal acuity and color vision.

4.1.2. Stimuli, design and procedure

Overall, the set up was very similar to that of Experiment 1, except for the following changes: search displays contained twelve (instead of six) diamonds (diameter $1.1 \times 1.1^\circ$ of visual angle), regularly arranged on an imaginary ellipse (horizontal diameter 10° of visual angle; vertical diameter 8° of visual angle). In the *distractor absent* condition (50% of the trials), all of the nontargets were gray (12 cd/m^2), the target was either red (CIE x,y chromaticity coordinates 0.597, 0.366; 9.51 cd/m^2) or green (CIE 0.254, 0.649; 12.13 cd/m^2). In the *similar distractor* condition (25% of the trials), one of the diamonds was blue (CIE 0.165, 0.154; 11.59 cd/m^2), or yellow (CIE 0.398, 0.527; 37.34 cd/m^2). In the *dissimilar distractor* condition (25% of the trials), one of the diamonds was replaced with a big blue or yellow disk (diameter 3.1° of visual angle). The three distractor conditions were randomly mixed within blocks. As before, targets could either *repeat* from trial to trial, or *switch*. The experiment started with a practice block of 32 trials, followed by 14 experimental blocks of 64 trials each with breaks in between. Participants received feedback after each erroneous response, and feedback on average RTs and accuracy scores after each block.

4.2. Results and discussion

The analyses focused on RTs. Erroneous responses (3.4%) were excluded. Table 1 shows the error percentages, which were analyzed in the same way as the RTs. There were no reliable effects ($ps > 0.2$), except for a general increase in errors after a target switch that approached significance, $F(1, 10) = 3.66$, $MSe = 0.000$, $p = 0.082$. Responses faster than 300 ms or slower than 1500 ms were also removed, resulting in an exclusion of another 2.8% of the trials.

The means of the remaining RTs were subjected to an ANOVA with distractor (distractor absent, similar distractor, dissimilar distractor) and target type (repetition, switch) as factors. There was a main effect of distractor, $F(2, 22) = 44.37$, $MSe = 1925.99$, $p < 0.001$. The presence of a distractor resulted in slower RTs (771 ms for distractor absent trials, 851 for similar distractor trials, and 832 for dissimilar distractor trials). There was also a main effect of target type, $F(1, 11) = 22.26$, $MSe = 740.75$, $p = 0.001$. RTs were overall slower after a target switch than after a repetition (829 ms vs. 808 ms). Finally, there was a distractor \times target type interaction, $F(2, 22) = 12.97$, $MSe = 319.53$, $p < 0.001$, reflecting the fact that intertrial priming effects not only changed as a function of distractor presence, but also as a function of the type of distractor. This is shown in Fig. 7, which plots the intertrial priming effects as a function of distractor type. Separate two-tailed paired *t*-tests revealed that there was no reliable effect of target repetition in the no distractor condition (5 ms, $t(11) = 1.27$, $p = 0.23$). There was a significant priming effect of 42 ms in the similar distractor condition, $t(11) = 5.13$, $p = 0.001$, and smaller, but still significant priming effect of 17 ms in the dissimilar distractor condition $t(11) = 3.21$, $p < 0.01$. Comparing only the similar and dissimilar distractor conditions again revealed a distractor \times target type interaction, $F(1, 11) = 16.06$, $MSe = 214.48$, $p < 0.01$, indicating that the intertrial effects were indeed greater in the presence of a similar distractor than in the presence of a dissimilar distractor. At the same time, on target repetition trials alone,

Table 1
Error percentages in Experiment 2.

Distractor type	Target type	
	Repetition	Switch
No distractor	3.6	3.1
Similar distractor	3.3	4.2
Dissimilar distractor	2.4	3.7

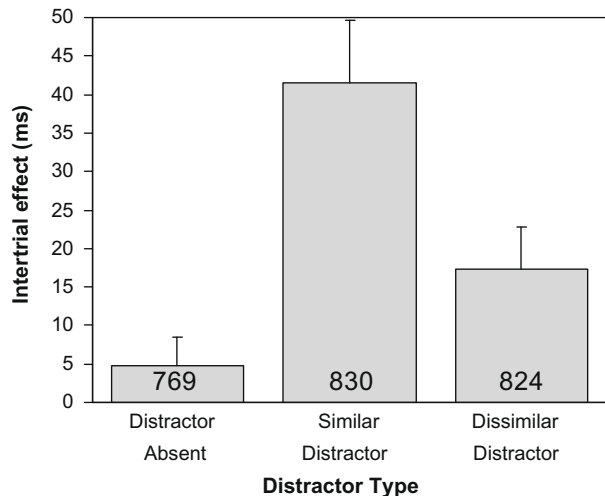


Fig. 7. Mean intertrial priming effects (target switch RT – repetition RT, in ms) for Experiment 2, as a function of distractor type (none, similar, dissimilar), and target type (repetition, switch). The target repetition baseline RTs are plotted in numbers inside the columns. Error bars denote one standard error of the mean. The mean RTs on target repetition trials (relative to which these intertrial effects were calculated) were 769 ms in the distractor absent condition, 830 ms in the similar distractor condition, and 824 ms in the dissimilar distractor condition.

overall RTs were no different for the two distractor types, 830 vs. 824 ms, $t(11) = 1.01$, $p = 0.33$. The main difference was on target switch trials, 872 vs. 841 ms, $t(11) = 3.43$, $p < 0.01$.

The important aspect of the results is that intertrial effects were greater when the display contained a distractor similar to the target, as compared to a more salient, overall equally interfering, but less similar distractor. This means that the differential intertrial priming effects found here and in Experiment 1 were not related to just the overall RTs. Instead, the effects were determined by distractor similarity – in other words, how perceptually confusing the items in the display were. We argue that a similar distractor is more confusing than a dissimilar distractor, even if the latter is very salient. In line with the ambiguity account, this increased perceptual ambiguity leads to stronger priming effects.¹

5. General discussion

There has been a long-standing debate as to what causes intertrial effects in visual search (Becker, 2008a, 2008b; Cohen & Magen, 1999; Found & Müller, 1996; Hillstrom, 2000; Huang et al., 2004; Maljkovic & Nakayama, 1994; Meeter & Olivers, 2006; Müller & Krummenacher, 2006; Olivers & Humphreys, 2003). Notably it has focused on whether the priming of repeated targets operates prior to selection (and thus affects this selection), or whether it operates on post-selection stages, including target verification and response selection. Consistent with earlier proposals (Meeter & Olivers, 2006; Olivers & Meeter, 2006), we show here that at least some priming effects can be measured at a perceptual level, provided there is a degree of perceptual ambiguity in the displays.

¹ One might argue that not the repetition trials but the average performance across both repetition and switch trials is a better estimate of baseline distractor costs. Since the average RT is still lower in the dissimilar distractor condition, one might again expect smaller intertrial effects. To resolve the issue, we looked at only those trials in which the distractor was blue. Blue distractors were overall less salient than yellow ones, leading to reduced RTs. However, these benefits were greater for the similar distractor condition, so that now on average, RTs were exactly on a par with the dissimilar distractor condition (814 vs. 814 ms). Yet again, intertrial priming effects were greater in the similar distractor condition (28 ms) than in the dissimilar distractor condition (6 ms), a significant Distractor Type \times Target Type interaction, $F(1, 10) = 6.10$, $MSe = 247.29$, $p < 0.05$.

The behavioural data of Experiment 1 revealed a considerably stronger intertrial priming effect when a distractor was present, compared to when no such distractor was present. Consistent with a perceptual explanation, the EEG data revealed an early modulation of the latency of the P1 component, around 100 ms post display onset. When a distractor was present, the P1 contralateral to the target was slowed after a target switch, compared to a target repetition, and compared to when no distractor was present. This was then followed by either a weakening, slowing or protracting of the N2pc, the marker for selection. Our findings are thus consistent with the earlier study by Töllner et al. (2008), who measured EEG signals in response to dimension priming rather than feature priming in visual search. They too found a weakened and slowed N2pc in response to a target change. Our work extends these findings by showing that such N2pc effects may originate earlier, from as early as the P1 – thus providing more direct evidence for a perceptual influence.

Moreover, we have shown here that such effects also occur even for more subtle feature changes within a specific dimension (in our case color). This is important, because some recent work suggests that dimension priming may differ from specific feature priming. For example, Olivers and Meeter (2008) showed that the size of feature-based priming does not alter with the presence of dimension-based changes, consistent with (though not conclusive evidence for) independent processes. Becker (2008a, see also Becker, 2008b) has provided more evidence for two different types of priming. Using saccadic latency and fixation duration as measures, she found that a feature change led to longer latencies for the target saccade (without affecting fixation duration), whereas a dimension change led to longer target fixations (without affecting latency). Assuming that saccadic latency reflects processes leading up to selection, and fixation duration reflects decision processes after selection, Becker linked feature priming to a perception stage and dimension priming to a decision stage. This may help explain why Töllner et al. (2008) failed to find any modulations prior to the N2pc: dimension priming effects may have a slightly later locus than feature priming effects.

5.1. Priming aids the resolution of perceptual ambiguity

Of further interest were the results of Experiment 2. Here we manipulated the similarity or confusability of the distractor with the target, and found priming effects to be decreased for less similar, but still very salient, distractors (with overall RTs controlled for). This finding is again in accordance with the idea that perceptual ambiguity determines the strength of intertrial priming effects. However, note that this experiment also forces us to further narrow down the definition of perceptual ambiguity. It appears that ambiguity involves, but is not exactly the same as *competition* between multiple elements in the display. If it is merely any competition between objects that is then biased by priming, then the very salient dissimilar distractor in Experiment 2 should have yielded the same priming effects as the less salient, but more similar object, under the assumption that the similar overall RTs were indicative of equally strong competition in the two conditions. The fact that the priming effects differed between these conditions either means that, despite similar overall RTs, the quantitative strength of the competition was not the same for the two conditions, or it means that there is a qualitative difference between the two types of competition. Salient visual objects generate competition in a bottom-up, stimulus-driven fashion. This type of processing may be limited to a feedforward sweep of activation through the visual pathways. On the other hand, objects that are similar to the target may generate competition in a top-down, goal-driven fashion, as they are modulated by visual feedback mechanisms activated by the target template. Priming in visual search may largely depend on such top-down mechanisms,

and thus may be more strongly expressed in cases of “top-down ambiguity” (i.e. high similarity) than “bottom-up ambiguity” (i.e. high salience).

Further evidence for a role of top-down set in priming comes from studies that manipulate the relevance of different target features to the task. For example, Goolsby and Suzuki (2001) found no repetition effects when the target on the previous trial was cued, or was the only object in the display – conditions under which there is no uncertainty whether the selected object is indeed the target (the target features are even irrelevant to the task). The task on the *current* trial appears even more important: Fecteau (2007) independently manipulated the color and the shape of a target and instructed observers on every trial as to which of these properties was relevant to finding it. For example, the target color could repeat from one trial to the next, but could be relevant in the first, though not the second trial. Fecteau found repetition benefits but only when the repeated feature was relevant for the current task. Taken together then, it appears that intertrial priming effects can occur early in the visual processing stream, but not so early that they are not subject to task-relevant attentional settings.

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