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Flanker negative priming from spatially unpredictable primes: An ERP study

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ABSTRACT

In a typical flanker task, a to-be-selected central target is flanked by two to-be ignored, identical distractors. The flanker negative priming (NP) effect denotes increased reaction time and error percent when the distractor of a first display serves as the target in the next. Most theories of NP are consistent with the idea that during processing of the first display, the identity of the distractors is inhibited. If the target of the subsequent display has the same identity, NP occurs because of persisting or retrieved inhibition. However, in the standard flanker task stimuli appear at the same screen locations for all trials, allowing for anticipatory spatial selection. No strong additional inhibition of stimulus *identities* may then be required. Therefore, besides the standard flanker task we employed a modified task in which the location of the stimulus triplet slightly differed across trials, thus disabling spatial pre-selection. Event-related potentials (ERPs) were recorded to identify brain correlates of NP in the two tasks. Behavioral NP was present in the modified task but absent in the standard task. An ERP correlate specific to NP in the modified task concerned larger amplitude of a left-posterior processing negativity. Results support the idea that stronger inhibition of distractor identities contributes to NP in the flanker task when spatial pre-selection is disabled.

1. Introduction

It is well accepted that, if a to-be-ignored stimulus (distractor) from a first prime display becomes the to-be-selected stimulus (target) in a subsequent probe display, then a person's response to this target will be impaired in terms of latency and/or accuracy (Dalrymple-Alford and Budayr, 1966). This phenomenon has been labeled negative priming (NP; Tipper, 1985).[1] NP is a robust empirical finding which has been observed in a wide variety of different tasks, stimuli, and populations (see Fox, 1995; Tipper, 2001, for reviews). For example, in a typical NP task based on the flanker task (Eriksen and Eriksen, 1974), participants respond to the identity of a central target stimulus (e.g., a digit) which is flanked by two identical distractor digits different from the target. In the *ignored-repetition* (IR) condition, the prime distractor serves as the target in the subsequent probe, whereas in the *control* condition no prime digits are repeated in the probe. The NP effect is computed as the difference in RT and/or error percent between IR and control conditions.

A coarse-grained taxonomy of NP theories differentiates between persisting-inhibition (e.g., Frings and Wühr, 2007; Houghton and Tipper, 1994; Tipper, 1985) and episodic-retrieval accounts (e.g., Mayr and Buchner, 2006; Neill et al., 1992; Rothermund et al., 2005). Inhibition theory assumes that, in identity-based NP tasks, the distractor stimulus identity is actively suppressed by mechanisms of selective attention during the processing of the prime display and that this inhibition persists until the next display. Thus, when in the IR condition the prime distractor serves as the target of the subsequent probe, a still-inhibited representation has to be activated in order for the participant to respond, and this causes the NP effect.

By contrast, retrieval theories argue that NP is due to the fact that perceiving a target activates memory traces associated with that particular stimulus. In the IR condition, the last memory trace of the current target stimulus may contain information like "distractor" or "do-not-respond" (Neill et al., 1992), or it will retrieve the (incompatible) prime response (Rothermund et al., 2005). This information then interferes with a person's ability to respond quickly and accurately to the target. Both accounts are well supported by the literature, and several authors concluded that both persisting inhibition and episodic retrieval may contribute to NP (see Kane et al., 1997). Note however that both frameworks are compatible with the idea of *distractor inhibition* as a major source of NP (Tipper, 2001).

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[1] It should be emphasized that, although the present study investigated the effect of a spatial manipulation on NP, it is still concerned with identity-based NP and not with spatial NP (or, NP from localization tasks). In visuo-spatial NP, pre-defined targets have to be localized, that is, a button has to be pressed that spatially corresponds to the location of the target on the screen ("select what, respond where", cf., Tipper et al., 1990). By contrast, in the present flanker task – even in the modified varied-locations variant – the correct response critically depends on the identity of the central stimulus ("select where, respond what"; cf. Tipper et al., 1990). In general, the distinction between identity-based and location-based (spatial) NP is an important one because different mechanisms seem to be involved (Fox, 1995; May et al., 1995).

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According to Tipper (2001), the original episodic-retrieval (e.g., Neill et al., 1992) and persisting-inhibition views (e.g. Tipper, 1985) may only differ with respect to the assumption of whether inhibition allocated to the prime distractor is actively reinstated by a retrieval mechanism during probe processing, or passively persists from the prime to the probe.

Recently, there have been attempts to use event-related potentials (ERPs) to enhance our understanding of the processes involved in NP. In the following, we briefly summarize this literature (see Mayr and Buchner, 2007, for a review). Mainly three different ERP components have been found sensitive to visual NP. First, NP-related enhancement of (frontal) N200 components was observed in target identification (Frings and Groh-Bordin, 2007; Hinojosa et al., 2009) and target localization (Gibbons, 2006) tasks. Also Daurignac et al. (2006) found NP in a number conservation task similar to those of Piaget to be accompanied by larger N200. Generally, the N200 NP effect was assumed to reflect persisting inhibition. For example, Frings and Groh-Bordin (2007) suggested that in IR trials the still-inhibited probe target has to be selected against non-inhibited probe distractors. Since this persisting inhibition may already affect *early* probe processing, it implies the risk that IR probe distractors can quickly activate their associated response. This may require immediate response inhibition and hence can explain the frontal N200 (cf., Eimer, 1993; Heil et al., 2000).

Second, in several studies a modulation of the P300 complex was observed. For example, Kathmann et al. (2006) reported larger P300 amplitude to accompany identity-based NP. This finding was interpreted as reflecting increased attentional resources to be required for the processing of IR probe displays. Although the authors originally did not draw this conclusion, larger P300 seems well in line with persisting-inhibition view of NP (cf., Stahl and Gibbons, 2007). However, three studies (Gibbons, 2006; Gibbons, 2009; Stahl and Gibbons, 2007) found NP-related P300 amplitude *reduction* in flanker-like identification tasks, which was interpreted as a correlate of retrieval processes. More specifically, it was argued that smaller P300 reflects perceived prime–probe similarity which may correspond to a central concept of episodic-retrieval theories, i.e., the “retrieval cue”. Interestingly, also with auditory NP tasks smaller late posterior positivity in the IR condition was found (Mayr et al., 2003, 2006), and interpreted as support for episodic-retrieval view.

A third ERP correlate of NP was recently reported by Gibbons (2009) who employed a flanker task and distinguished reduced amplitude of left-posterior early P300 (300–400 ms; this finding was not specific to the IR condition, see below) from an *IR-specific* P300 amplitude reduction in a later time range (400–500 ms). This latter effect was interpreted as an N400-like processing negativity which overlapped the late P300 time range specifically in the IR condition and may reflect more effortful processing.

The present study aimed at testing a prediction that can be derived from the notion of distractor inhibition being a major source of NP (cf., Tipper, 2001). To be specific, a strong anticipatory spatial selection component can be assumed to be at work in the standard flanker task. With all triplets appearing at the center of the screen, selection can benefit from inhibition of *any* information at the fixed lateral flanker locations. Moreover, the more effective this spatial (stimulus-unspecific) inhibition, the less additional (stimulus-specific) distractor inhibition should be required for successful target selection. Note that only the latter, stimulus-specific inhibitory component of selection would contribute to a flanker NP effect that is caused by distractor inhibition. Interestingly, with fixed and therefore predictable locations of the flanker triplets, NP diminished to a non-significant level when the distance between target and flankers was too large (Fox, 1994; Ruthruff and Miller, 1995). In sum, it can be concluded that the standard flanker task with fixed locations may not provide optimal conditions for the investigation of a possible distractor-inhibition component of NP.

We therefore developed a modified, *varied-locations* variant of the flanker task, with locations of the stimulus triplets slightly differing between subsequent trials (here, “trial” refers to a pair of consecutive prime and probe displays). Whereas the probe always appears in exactly the same screen location as the preceding prime, locations may slightly change between a probe and the next prime. Thus, anticipatory inhibition of the upcoming prime distractor locations is disabled. With this modified task, then, the prime distractors should no longer suffer from *a-priori* processing disadvantage caused by their appearance in already spatially inhibited screen locations. This should result in deeper processing of the prime distractor stimuli (i.e., their identity-specific conceptual representations are more strongly activated) before they are eventually inhibited when the prime target is selected. According to Houghton and Tipper (1994), stronger initial distractor activation should call for stronger subsequent distractor inhibition. If distractor inhibition is indeed a major source of NP, this should result in a stronger NP effect in the modified, varied-locations task, compared to the standard, fixed-location task.

Against this background, the present study aimed at a comparison of behavioral NP effects and ERP correlates of NP in the two tasks, to further investigate the role of inhibition of distractor identities in NP. The first prediction relates to larger behavioral NP for the varied-locations compared to the fixed-location task. Moreover, the larger NP effect in the modified task should have a distinct ERP correlate which is not observed in the fixed-location task. Given the above considerations about an inhibitory mechanism operating at a relatively *advanced level of distractor processing*, one would expect late-range ERP correlates. By contrast, NP in the varied-locations task may not be accompanied by early ERP effects in the N200 time range (e.g., Frings and Groh-Bordin, 2007). As noted earlier, N200 effects may indicate inhibition of the response associated with the distractors in IR probe displays, and hence be specific to NP operating at relatively early levels of processing, causing advantage for the probe distractors over the still-inhibited IR probe target early during probe processing.

Examples of late-range ERP correlates of visual NP concern P300 amplitude modulations (e.g., Kathmann et al., 2006; Stahl and Gibbons, 2007) or amplitude increase of an N400-like processing negativity (Behrendt et al., in press; Gibbons, 2009); similar findings can be expected for the present modified flanker task with variable prime locations. According to Donchin and Coles (1988), P300 reflects the effort with stimulus identification. For example, unexpected stimuli evoke a larger P300 because their internal representations are not pre-activated in a given context. Critically, distractor-inhibition accounts of NP predict that the representation of an IR probe target can be less easily activated, either because inhibition of this representation has persisted from the prime, or is reactivated during probe processing. Thus, like in Kathmann et al.'s (2006) study, larger P300 may accompany the present NP effect, particularly in the varied-locations task designed to strengthen the distractor-inhibition component of NP.

However, more effortful processing can also manifest itself in *reduced* P300 amplitude caused by a processing negativity (PN) overlapping the P300 time range (Kok, 2001). This interpretation was suggested by Gibbons (2009) for his late-range (400–500 ms), left-posterior ERP correlate of flanker NP. Importantly, the PN could be distinguished from an early (300–400 ms) P300 amplitude reduction in the IR condition, which had similar topography but was also found in yet another priming condition, the attended-repetition (AR) condition. In the AR condition the prime target is repeated as the probe target, which usually results in a strong facilitation of responding known as positive priming (PP). Therefore, the joint AR/IR effect on early P300 reported by Gibbons (2009) cannot be an index of more effortful processing in the IR condition. Interestingly, unlike the early P300 effect, the late P300/PN effect was functionally related to behavioral NP, insofar as it was more pronounced in participants showing an above-median individual behavioral NP effect. For the varied-locations task, therefore, NP effects on late P300/PN can be expected, but should be carefully distinguished from AR effects in this time range.

2. Method

2.1. Participants

22 right-handed undergraduate volunteers (12 males) with normal vision and no known history of neurological disorder participated in the study for partial course credit. Mean age was 23.5 years (SD = 4.5 years). All participants were naïve to the purpose of the experiment and provided written informed consent. Due to distorted EEG recording, ERP data from one female participant were not applicable; therefore, EEG analysis was based on 21 participants.

2.2. Apparatus and stimuli

For presentation of stimuli, an IBM compatible computer equipped with a 17″ SVGA monitor was used. Stimuli were triplets composed of the digits 1, 2, 3, and 4, presented in white on a black background. The central digit was always different from the two identical flanking digits (see Fig. 1). Each triplet subtended a horizontal visual angle of 2.1° and a vertical visual angle of 0.7°. Horizontal target–distractor distance was 0.5°. Triplets could appear in one of four sets of locations arranged around the center of the screen (see Fig. 1, panel A). Neighboring sets of locations were shifted by 0.5° in vertical direction and by approximately 0.3° in horizontal direction. Responses were recorded with an accuracy of 1 ms using a four-button response board labeled 1–4.

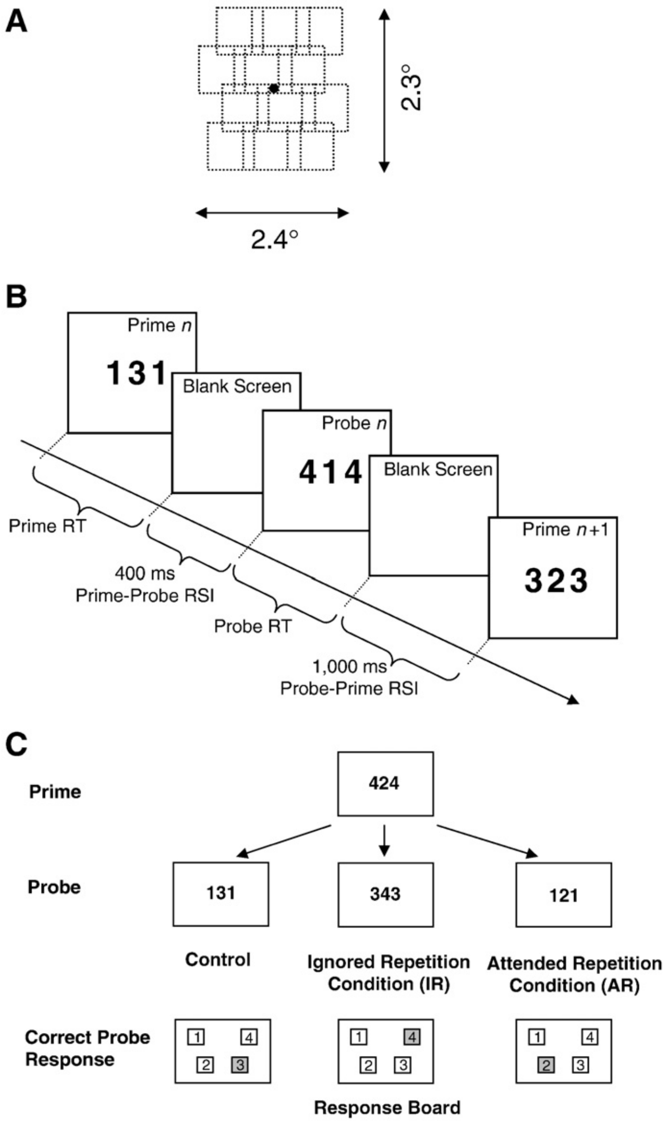

Fig. 1. Panel A: Arrangement of the four different prime locations (i.e., groups of three horizontal positions) around the center of the computer monitor (black dot; did *not* appear in the presentations). Panel B: Sequence of trial events. Panel C: Examples for the three different priming conditions (IR, AR, and control). Correct probe responses are indicated in gray on the response board.

2.3. Procedure

Participants were instructed to keep fixation “at the center of the screen” throughout the experiment; no fixation cross was however employed to increase uncertainty about the exact position in which the next triplet would appear. They were asked to respond as quickly and accurately as possible by pressing the button labeled with the digit that appeared in the center of the triplet, and to ignore the flankers. The experiment was conducted in a sound-attenuated, dimly lit room; viewing distance was 60 cm. The four response buttons were operated by index and middle fingers of both hands (left hand: digits 1 and 2; right hand: digits 3 and 4; see Fig. 1).

There were two experimental tasks, employing varied as opposed to fixed prime locations, which were run in two consecutive parts of the experiment. In the experimental part with *fixed prime location*, there were four different blocks. Within one block, all stimulus triplets appeared in one and the same location. For each of the four locations one block was run. There were 72 trials in each block, consisting of the prime display followed by the probe display, of which 24 trials each belonged to the priming conditions IR, AR, and control. In the control condition, two digits that had not appeared in the prime served as target and flanker stimuli in the probe display (e.g., a prime 424 was followed by a probe 131; see Fig. 1). In the IR condition the prime distractor was repeated as the probe target, and prime target and probe distractor were different (e.g., a prime 424 was followed by a probe 343). In the AR condition, the prime target was repeated as the probe target while prime and probe distractors were different (e.g., a prime 424 was followed by a probe 121).

The experimental task with *varied prime location* consisted of one block of 288 trials (96 control, 96 AR, and 96 IR trials). At the beginning of each trial, the prime location was randomly drawn from the four locations, with the restriction that each prime location had to be employed in one fourth of the trials (i.e., 72). Furthermore, in each of these sets of 72 trials, each of the 24 possibilities to construct AR, IR, and control trials had to be included once. The probe location always was identical to the prime location, thereby excluding effects of prime–probe location priming on the responses. The order of experimental tasks (varied vs. fixed prime location) was balanced across participants. Within the fixed-location task, order of the four blocks corresponding to the four locations was balanced across the first 20 participants. Within each block, priming conditions were presented in random order. There was a 1-min break after every 144 trials. At the beginning, 24 practice trials with fixed prime location were administered, to practice stimulus–response assignments.

A trial began with the presentation of the prime, which remained on the screen until a response was made. If the response to the prime was correct (i.e., the button assigned to the central target letter was pressed), after 400 ms the probe display appeared and remained on the screen until a response was made. In case of wrong responses to prime or probe, error feedback [50-ms tone; 1100 Hz; 40 dB SPL(A)] was presented. No response within 1500 ms after prime/probe onset was prompted with a 150-ms tone (1100 Hz). After wrong/missing prime responses, the trial was cancelled. False/missing probe responses were recorded and classified accordingly. Each trial ended with a correct probe response, or with the offset of error feedback. After a 1000-ms inter-trial blank-screen interval, the next trial started (see Fig. 1).

2.4. Analysis of behavioral data

To demonstrate the general validity of the experimental manipulation concerning the task factor (varied vs. fixed prime locations), in a first step planned comparisons between the two tasks for RT on correct *prime* responses (both means and medians) and prime error percent were performed, using two-tailed *t* tests. Regarding priming effects, as dependent variables both mean and median[2] probe RT (from trials with correct prime *and* probe responses), and probe error percent (from trials with correct prime responses) were determined for each individual and each of the three priming conditions (IR, AR, and control).

Then, 3 × 2 repeated-measures ANOVAs with factors Priming Condition (IR, AR, and control) and Task (varied and fixed prime location) were performed, separately for median RT, mean RT, and error percent. Since the present study focused on task effects on the *NP* effect, additional repeated-measures 2 × 2 ANOVAs were performed, employing a two-level factor Priming Condition (IR, control) in addition to the Task factor. Planned comparisons were used to follow up significant effects (expecting PP from AR trials and NP from IR trials).

2.5. EEG recording

Electrical brain activity was recorded from 27 scalp locations of the 10–20 system (Jasper, 1958), using an electrode cap (Electrocap Inc.) with sintered Ag/AgCl electrodes. Left and right mastoids served as active and passive references, respectively. Vertical and horizontal EOG were monitored from electrodes below and above the right eye, and from the outer left and right canthi, respectively. EEG was recorded continuously using a 32-channel digital Synamps amplifier and Acquire software (NeuroScan Inc.). Sampling rate was 500 Hz and bandpass ranged from 0.1 to 70 Hz. The EEG was re-referenced against algebraically linked mastoids and epoched off-line, with epochs ranging from 100 ms before until 1000 ms after probe display onset. Epochs were baseline-corrected with respect to the 100-ms interval preceding probe display onset. All data were screened for artifacts (amplitudes exceeding ±100 µV), and contaminated trials were rejected (less than 8% for each participant and condition). EOG correction was performed according to Gratton et al. (1983). Epochs accompanying wrong responses were discarded. Waveforms were then averaged, separately for each individual, electrode, and priming condition.

2.6. ERP analysis

ERPs were separately analyzed for the two tasks (varied and fixed prime locations). Selection of the specific ERP components and time windows to be analyzed was mainly based on the former task, because only here behavioral NP was significant.

In the *varied-locations task*, visual inspection suggested ERP priming effects mainly in three time windows, that is, in the N200 time range (230–330 ms), where ERPs were relatively more negative-going in the AR condition, between 380 and 430 ms, where a left-posterior processing negativity (PN) was specifically observed for the IR condition, and in the late P300 range (430–480 ms), where mid-central late P300 was largest in the AR condition (see Fig. 2). To statistically corroborate these findings, nine electrode clusters were formed from the 27 electrodes (left anterior: F7, F3, FC3; medial anterior: FP1, Fz, FP2; right anterior: F8, F4, FC4; left central: FT7, T3, C3; medial central: FCz, Cz, CPz; right central: FT8, T4, C4; left posterior: T5, CP3, P3; medial posterior: O1, Pz, O2; and right posterior: T6, CP4, P4). Separately for participants, priming conditions, and electrode clusters, N200 amplitude was measured as mean voltage in the (230, 330 ms) interval covering the N200 range. Analogously, PN and late central P300 amplitudes were quantified as mean voltage in the (380, 430 ms) and (430, 480 ms) intervals, respectively (see Fig. 2). N200, PN, and late P300 amplitudes were subjected to separate repeated-measures ANOVAs, each involving the three factors Priming Condition (IR, control, AR), Caudality (anterior, central, posterior), and Laterality (left, medial, right). Greenhouse–Geisser correction was applied if appropriate, and significant effects of Priming Condition were further investigated using Tukey's HSD test. To confirm functional significance of the NP effect on left-posterior PN, PN amplitude in the left-posterior cluster was compared between IR and control conditions by means of planned comparisons (*t* tests), separately for the groups of strong-NP participants (with individual NP effects – computed as median RT for IR/varied minus median RT for control/varied – greater than or equal to 15 ms, $N = 13$) and weak-NP participants (NP effect <15 ms, $N = 8$).

In the *fixed-location task*, visual inspection suggested only one priming effect in a time range similar to the late P300 effect in the varied-locations task, however, in a larger time window at around 500 ms, and with a left-frontal focus. Late P300 amplitude was quantified as mean amplitude between 430 and 550 ms, and subjected to 3 × 3 × 3 ANOVA with repeated measures on Caudality, Laterality, and Priming Condition. In addition, to demonstrate that the NP effect on left-posterior PN was specific to the modified, varied-locations task, also in the fixed-location task a 3 × 3 × 3 ANOVA for mean PN amplitude in the (380, 430 ms) time window analogous to PN analysis in the varied-locations task was computed, employing factors Caudality, Laterality, and Priming Condition. Finally, an ANOVA analogous to N200 analysis in the varied-locations task was also performed for the fixed-location task.

3. Results

3.1. Prime RTs

The planned comparison of median *prime* RTs in the fixed- and varied-locations tasks revealed a significant difference, $t(21) = 4.8$, $p < .001$. Mean median prime RTs were 618 ms in the fixed-location task and 644 ms the varied-locations task. Comparable results were found when individual means instead of medians were analyzed; $t(21) = 4.3$; $p < .001$; fixed location = 648 ms; varied location = 677 ms. These differences support our assumption that prime selection was more difficult with varied as opposed to fixed prime locations.

3.2. Prime errors

The planned comparison for prime error percent did not indicate significant differences between tasks, $t(21) = 0.6$, $p = .56$.

3.3. Probe RTs

In a first systematic approach, median RTs were subjected to repeated-measures 3 × 2 ANOVA employing factors Priming Condition (IR, AR, and control) and Task (varied vs. fixed prime location). The main effect of Priming Condition was significant, $F(2, 42) = 169.2$, $p < .001$, $\varepsilon = .84$. Mean median RTs were 506 ms, 616 ms, and 627 ms in conditions AR, control, and IR, respectively. Planned two-tailed comparisons for RT

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[2] Medians rather than means were the preferred measure of central tendency because of their greater resistance to outliers. This was necessary to obtain reliable estimates of the individual NP effects, to allow for a selection of strong-NP and weak-NP groups. Moreover, medians are more appropriate than means for *ERP studies* of NP. An NP effect on mean RT may be due to very slow RTs on just a few trials in the IR condition, which however may be insufficient to cause pronounced NP effects in the ERP averaged across all IR trials. By contrast, an NP effect on median RT is a stronger finding because it indicates that the NP-relevant process is present in many trials of the IR condition (the whole distribution of RTs is shifted to the right). This increases the chance of finding NP effects in the averaged ERP.

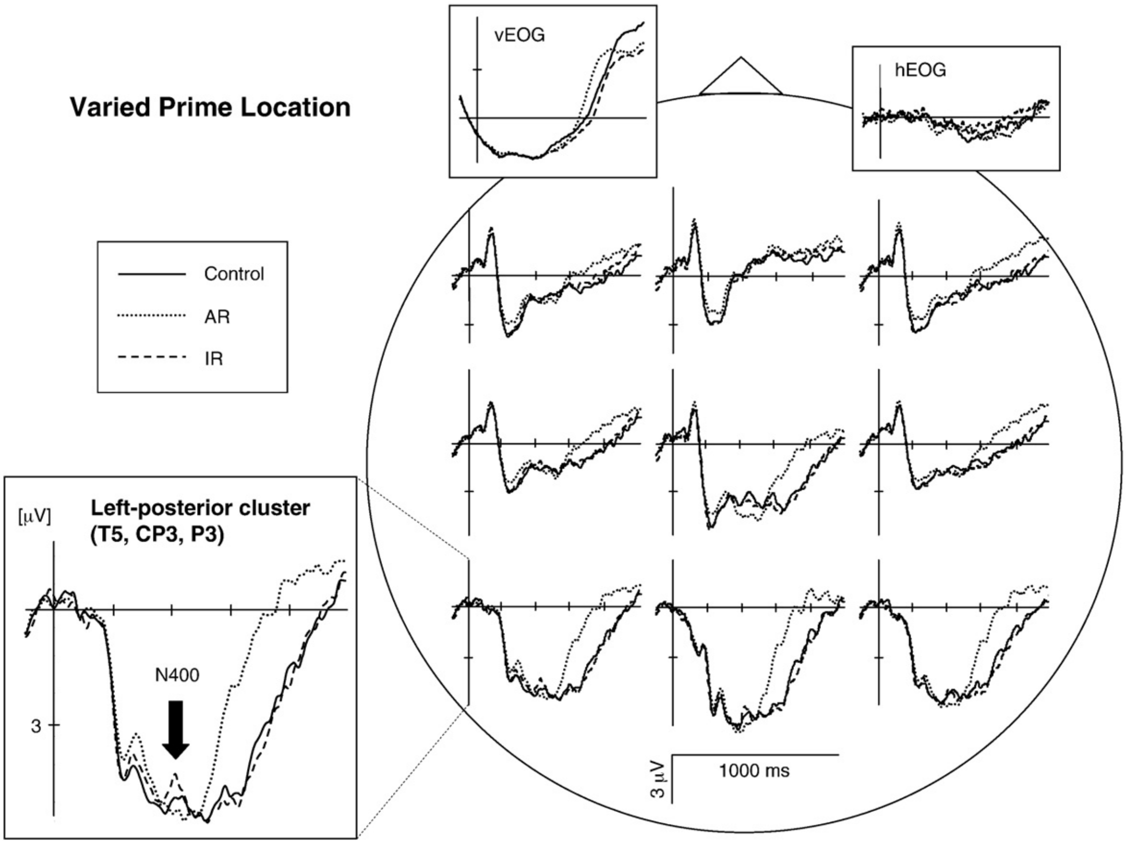

Fig. 2. Grand-average probe ERPs in nine electrode clusters in the condition with varied prime location, as a function of priming condition (IR, AR, and control). Note the increased relative negativity (processing negativity, PN) in the IR condition in the left-posterior cluster (enlarged) relative to both, AR and control.

Table 1
Mean median response time (median RT), mean response time (mean RT), and error percent (*E*%) as a function of Priming Condition (AR, control, and IR) and Task (varied and fixed prime location).

	Varied prime location						Fixed prime location					
	AR		Control		IR		AR		Control		IR	
	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
Median RT	505	14.8	613	13.9	629	13.2	506	14.4	620	17.7	624	15.9
Mean RT	531	15.8	642	14.8	657	14.2	535	16.5	644	18.2	646	17.4
E%	0.6	0.3	2.9	0.5	4.3	0.6	1.3	0.3	2.8	0.6	4.4	0.6

Note: AR = attended repetition; IR = ignored repetition.

combined across tasks revealed significant PP and NP effects of $M = 110$ ms, $t(21) = 13.1$, $p < .001$, and $M = 11$ ms, $t(21) = 2.9$, $p < .01$, respectively. The Task main effect was not significant, $F(1, 21) = 0.1$, $p = .79$, as was the interaction Priming Condition × Task, $F(2, 42) = 1.8$, $p = .19$, $\varepsilon = .83$ (see Table 1).

The analogous analysis using individual mean RTs as the dependent measures yielded highly similar results: The main effect of Priming Condition was significant, $F(2, 42) = 148.2$, $p < .001$, $\varepsilon = .59$; mean RT was 533 ms, 643 ms, and 652 ms for conditions AR, control, and IR. Both the Task main effect, $F(1, 21) = 0.09$, $p = .77$, and the interaction Priming Condition × Task were not significant, $F(2, 42) = 2.7$, $p = .08$, $\varepsilon = .91$ (see Table 1). Both PP and NP effects in mean RTs were significant, $t(21) = 11.1$, $p < .001$, and $t(21) = 2.7$, $p = .01$, respectively.

However, the foregoing type of analysis with a three-level factor Priming Condition is dominated by the PP effect which was (as usual) much stronger than the NP effect, and moreover, appears to be insensitive to Task (see Table 1). Investigation of the NP effect and its task dependence therefore required additional analyses, employing repeated measures on two two-level factors Negative Priming (IR, control) and Task (varied vs. fixed prime location).[3] In the analysis for median RT, the main effect of Negative Priming was significant, $F(1, 21) = 8.3$, $p < .01$, and further qualified by a significant interaction by Task, $F(1, 21) = 6.4$, $p < .05$. According to planned comparisons NP was highly significant in the varied-locations task, $M = 16$ ms, $t(21) = 4.6$, $p < .001$, but absent in the fixed-location task, $M = 4$ ms, $t(21) = 0.9$, $p = .36$. Note that the significant interaction indicates a significant between-task difference in size of the NP effect.

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[3] An ANOVA with a three-level factor Priming Condition (AR, IR, and control) was employed for a first, systematic approach to the data, but is not optimal for the investigation of task differences in behavioral NP. Because the AR condition shows *much* lower RTs than both, IR and control conditions, it accounts for most of the RT variability between priming conditions. Moreover, if this PP effect is not sensitive to Task, as with the present data, no significant Priming (AR, IR, control) × Task interaction will appear, and any potential between-tasks differences in behavioral *NP* will be masked. An investigation of task effects on behavioral NP that is independent of task effects on behavioral PP therefore requires an analysis with a two-level factor Task (varied vs. fixed prime location) and a two-level factor Negative Priming (IR, control).

The Task main effect was not significant, $F(1, 21) = 0.07$, $p = .79$. The analysis of mean RTs again revealed highly similar results: There was a significant main effect of NP, $F(1, 21) = 7.2$, $p = .01$, and a significant Task × NP interaction, $F(1, 21) = 5.0$, $p < .05$. NP in mean RTs was significant in the varied-locations task, $M = 15$ ms, $t(21) = 3.8$, $p = .001$, but not in the fixed-location task, $M = 2$ ms, $t(21) = 0.5$, $p = .62$. The Task main effect was not significant, $F(1, 21) = 0.4$, $p = .51$ (see Table 1).

3.4. Probe errors

In the 3 × 2 ANOVA for error percent, employing a three-level factor Priming Condition, the main effect of Priming Condition was significant, $F(2, 42) = 34.7$, $p < .001$, $\varepsilon = .99$. Both PP and NP effects in errors were significant, $M = 1.9\%$, $t(21) = 4.7$, $p < .001$, and $M = 1.5\%$, $t(21) = 4.6$, $p < .001$, respectively. The main effect of Task, $F(1, 21) = 0.5$, $p = .51$, and the interaction by Priming Condition, $F(2, 42) = 0.8$, $p = .44$, $\varepsilon = .77$, were not significant. In the 2 × 2 ANOVA focusing on NP, the main effect of Negative Priming was significant, $F(1, 21) = 13.3$, $p < .001$. More errors were committed in the IR condition compared to control (4.3% vs. 2.9%). Neither the main effect of Task, $F(1, 21) = 0.01$, $p = .90$, nor the two-way interaction, $F(1, 21) = 0.05$, $p = .83$, was significant.

3.5. ERPs

3.5.1. Varied-locations task

Visual inspection suggested NP effects on amplitude of a left-posterior processing negativity (PN) and PP effects in the N200 time range and on a mid-central late P300 (see Fig. 2). Separate repeated-measures ANOVAs with factors Caudality (anterior, central, posterior), Laterality (left, midline, right), and Priming Condition (AR, control, IR) were computed for N200, PN, and P300 amplitudes. Only effects involving Priming Condition are reported.

3.5.1.1. N200. The 3 × 3 × 3 ANOVA for mean amplitude in the time window between 230 and 330 ms, covering the N200, revealed a significant main effect of Priming Condition, $F(2, 40) = 3.8$, $p < .05$, $\varepsilon = .77$. According to post-hoc Tukey's HSD test, in the N200 time range ERPs were more negative in the AR condition compared to both, the control condition and the IR condition (both $ps < .05$; see Fig. 2), with no significant difference between the latter two conditions ($p = .90$). No other effect of Priming Condition was significant (all $Fs < 1.5$).

3.5.1.2. PN. The 3 × 3 × 3 ANOVA for mean amplitude in the 50-ms time window between 380 and 430 ms, covering the peak of the left-posterior PN, revealed a significant interaction Caudality × Priming Condition, $F(4, 80) = 4.2$, $p < .05$, $\varepsilon = .50$. Over posterior recording sites, the PN was larger for IR than AR ($p < .001$). Moreover, the interaction Laterality × Priming Condition was significant, $F(4, 80) = 3.8$, $p < .05$, $\varepsilon = .84$. There was larger relative negativity for IR compared to both control ($p < .05$) and AR ($p < .01$) at left-side electrodes, with no significant difference between AR and control ($p > .90$). At medial electrodes, PN amplitude was larger for both IR ($p < .001$) and control ($p < .01$) relative to the AR condition. The midline PN amplitude difference between IR and control was not significant ($p > .90$). Finally, there was a significant three-way interaction, $F(8, 160) = 3.4$, $p < .01$, $\varepsilon = .57$. Specifically in the left-posterior cluster of electrodes (T5, CP3, P3), PN amplitude was increased for IR relative to both control ($p < .01$) and AR ($p < .001$; see Fig. 2), with no significant difference between the latter two conditions ($p = .96$). In the remaining eight electrode clusters, all IR-relevant contrasts were not significant (all $ps > .20$).

An additional analysis for those participants showing individual behavioral NP effects (median RT for IR/varied minus median RT for control/varied) of 15 ms and larger ($N = 13$) suggested functional significance of IR-related left-posterior PN increase. A planned comparison of PN amplitudes in the left-posterior cluster revealed a significant difference between IR and control in strong-NP participants; mean $= -1.0$ µV; $t(12) = 2.3$, $p < .05$ (Fig. 3, left panel). The remaining eight participants who had individual NP effects of less than 15 ms did not show this left-posterior PN effect; mean $= -0.02$ µV; $t(7) = 0.03$, $p = .98$ (Fig. 3, right panel).

3.5.1.3. Late P300. The 3 × 3 × 3-ANOVA for mean amplitude in the (430, 480 ms) time window covering the late mid-central P300 yielded a significant interaction between Laterality and Priming Condition, $F(4, 80) = 5.9$, $p = .001$, $\varepsilon = .79$. At midline electrodes, late P300 was significantly larger for AR compared to both control ($p < .001$) and IR ($p < .05$). Also the three-way interaction was significant, $F(8, 160) = 3.4$, $p < .01$, $\varepsilon = .63$. Only in the mid-central cluster (FCz, Cz, CPz) was there larger late P300 in the AR condition compared to both control ($p < .001$), and IR ($p < .05$; see Fig. 2).

3.5.2. Fixed-location task

Absence of a behavioral NP effect prevented a meaningful investigation of independent ERP correlates of NP in the fixed-location task. Rather, for reasons of comparison, all ERP components that had been shown sensitive to priming in the varied-locations task were analyzed in exactly the same time windows, except for late P300 which could be more optimally assessed in a (450, 550 ms) time window.

3.5.2.1. N200. In the 3 × 3 × 3 ANOVA with repeated measures on Caudality, Laterality, and Priming Condition, there were no significant effects; Priming main effect, $F(2, 40) = 0.9$, $p = .41$, $\varepsilon = .99$; interaction by Caudality, $F(4, 80) = 0.7$, $p = .49$, $\varepsilon = .55$; interaction by Laterality, $F(4, 80) = 1.9$, $p = .14$, $\varepsilon = .68$; three-way interaction, $F(8, 160) = 1.5$, $p = .21$, $\varepsilon = .59$.

3.5.2.2. PN. A further 3 × 3 × 3 ANOVA was computed for PN, covering the same (380, 430 ms) time window that was employed for the varied-locations task, to confirm specificity of the NP effect on left-posterior PN for the varied-locations task. In this analysis, the main effect of Priming Condition just failed to reach significance, $F(2, 40) = 3.5$, $p = .053$, $\varepsilon = .78$. ERPs tended to be more positive for AR than control ($p = .06$) and IR ($p = .08$); the difference between IR and control was not significant ($p = .99$). While the interaction between Priming Condition and Caudality was not significant, $F(4, 80) = 0.7$, $p = .50$, $\varepsilon = .53$, the interaction between Priming Condition and Laterality was, $F(4, 80) = 4.5$, $p < .01$, $\varepsilon = .66$. At left and medial clusters, ERPs in the AR condition were more positive compared to both control and IR (all $p < .001$). This effect was less pronounced over right clusters of electrodes (all $p < .06$). For all levels of Laterality, however, was the difference between IR and control not significant (all $p > .99$). Finally, also the three-way interaction Priming Condition × Caudality × Laterality was significant, $F(8, 160) = 7.5$, $p < .001$, $\varepsilon = .59$. In seven of the nine clusters of electrodes, amplitude was more positive for AR than IR (all $p < .01$), except for the right anterior ($p > .50$) and the right-central cluster ($p > .99$). Moreover, at all three medial clusters and at left-anterior and left-central clusters, AR differed significantly from control ($p < .001$). Also at left and right posterior clusters was the AR-control difference significant ($p < .05$). At right-anterior and right-central clusters, AR did not differ significantly from control ($p > .50$). ERPs in the PN time range did not differ between IR and control conditions at any of the nine clusters of electrodes (all $p > .36$). Thus, there was no evidence for a left-posterior PN effect in the IR condition of the fixed-location task.

3.5.2.3. Late P300. Mean amplitude between 450 and 550 ms (see above) was subjected to 3 × 3 × 3 ANOVA analogous to the previous analyses. The main effect of Priming Condition was not significant, $F(2, 40) = 2.5$, $p = .11$, $\varepsilon = .80$. Both two-way interactions Priming Condition × Caudality, $F(4, 80) = 1.0$, $p = .37$, $\varepsilon = .44$, and Priming Condition × Laterality, $F(4, 80) = 2.1$, $p = .11$, $\varepsilon = .75$, were not significant. However, the three-way interaction Priming Condition × Caudality × Laterality was

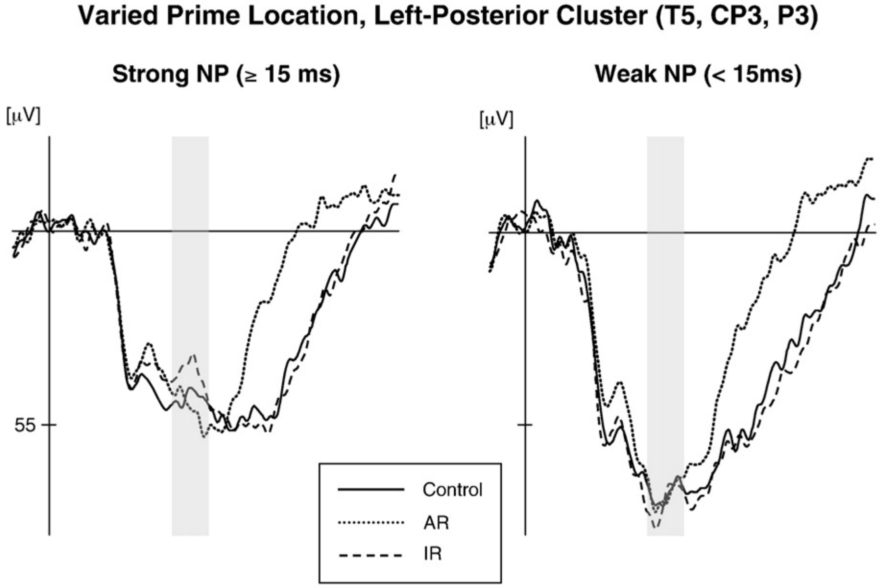

Fig. 3. Averaged left-posterior ERPs for IR and control in the condition with varied prime location, separately for strong-NP participants (NP effect ≥15 ms, $N=13$) and weak-NP participants (NP effect<15 ms, $N=8$). Only strong-NP participants (left panel) show an IR-related increase in left-posterior PN amplitude.

significant, $F(8, 160)=5.0$, $p<.01$, $\varepsilon=.44$. Post-hoc Tukey's HSD test revealed no priming effects over posterior electrodes (for all pair-wise comparisons between priming conditions, $p>.61$) and in the right-central cluster (all $p>.10$). In the mid-central cluster, ERPs were more positive for AR compared to both, IR ($p<.001$) and control ($p<.001$), and for IR than control ($p<.001$). In the left-central cluster, only the difference between AR and control ($p<.001$) was significant (all other $p>.18$). In the anterior clusters, ERP amplitude was more positive for AR than control (all $p<.05$) and for IR than control (all $p<.05$), while AR–IR differences were not significant (all $p>.08$). In sum, in the fixed-location task was there no specific ERP correlate of NP; ERPs were more positive at around 500 ms for IR than control, but even more so in the AR condition (Fig. 4).

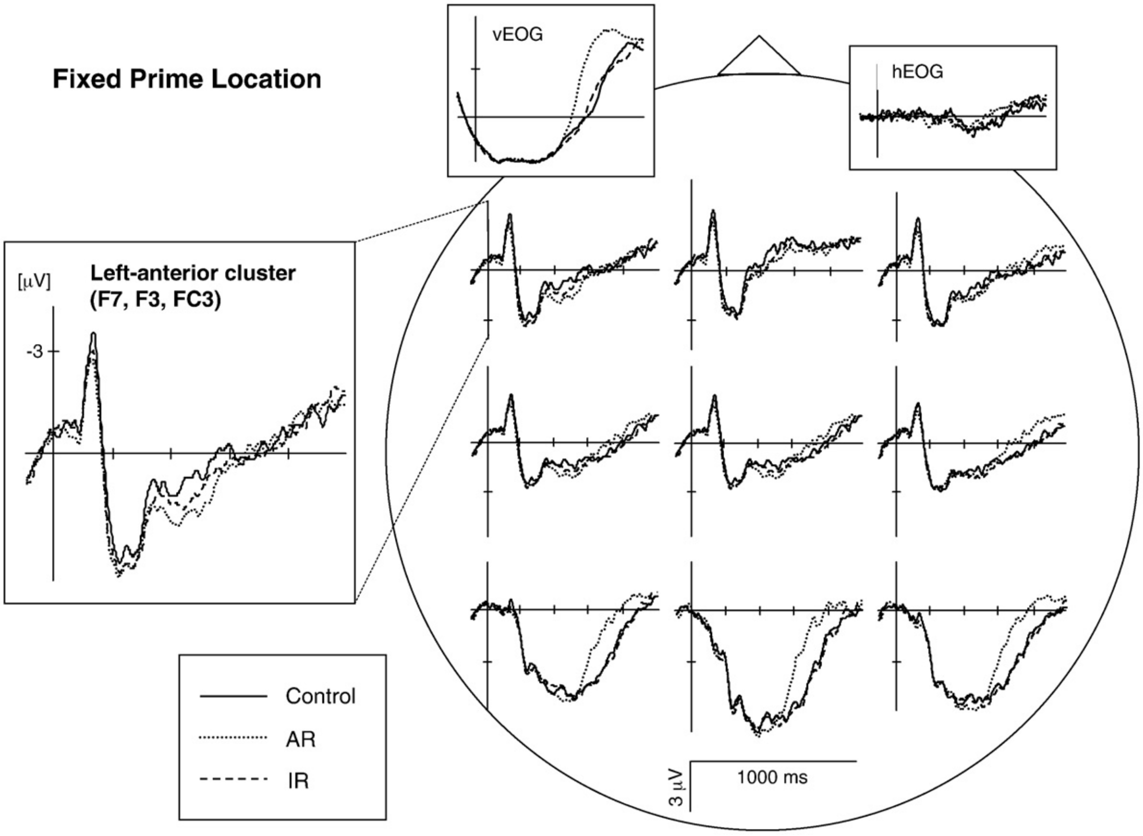

Fig. 4. Grand-average probe ERPs in nine electrode clusters in the fixed-location task, as a function of priming condition (IR, AR, and control).

4. Discussion

The present study is, to the best of our knowledge, the first ERP investigation of NP that goes beyond the traditional approach of comparing ERPs in an IR condition and a control condition in just one single task. Rather, the size of the behavioral NP effect was experimentally varied through manipulating spatial prime uncertainty. This was based on a theory-guided attempt to strengthen the distractor-inhibition component in identity-based NP. This way, those ERP correlates of NP that were sensitive to variations in the behavioral NP effect and hence might be particularly strongly related to inhibition of distractor identities could be isolated. Both, a standard flanker task with all stimuli appearing in the same (central) screen location, and a modified task in which location of the prime flanker triplets slightly varied between consecutive trials were employed. In the latter task, anticipatory spatial selection of the prime distractor locations was disabled, which should result in deeper processing of the prime distractors and, hence, call for stronger distractor inhibition.

4.1. Effects of spatial prime uncertainty on behavioral NP

The present flanker NP effect was clearly sensitive to the manipulation of spatial prime uncertainty: with fixed locations of the triplets, where prime selection could benefit from anticipatory spatial selection, the NP effect was not significant, while in the condition with varied prime locations not allowing for anticipatory spatial selection, significant NP was observed. As indicated by the significant Task × NP interaction on RTs, also the *difference* between tasks in size of the NP effect was significant. Note that in case of unpredictable prime locations, participants cannot ignore the distractor positions already before onset of the prime display and thus have to engage additional processes for successful target selection. This assumption of more effortful prime selection in the varied-locations task is supported by the finding of a significant 26-ms increase of *prime* RT, compared to the fixed-location task.

We argue that in this modified flanker task, prime distractors are more deeply processed, compared to the standard flanker task allowing for spatial pre-selection. This seems plausible because in the varied-locations task, after onset of the prime triplet the participants first have to re-adjust their focus of attention at the screen, before *selective* information processing can start. Thereby, the period of time during which similar initial processing of all stimuli takes places is lengthened, and the target has to be selected against distractors whose processing is already relatively advanced. Then, however, prime selection necessitates stronger inhibition of non-spatial features defining the identity of the prime distractors. Stronger prime distractor inhibition, in turn, should lead to stronger behavioral NP from IR trials, irrespective of whether inhibition is assumed to persist from prime to probe, or to be retrieved during probe processing (see below). The larger behavioral NP effect in the task with varied as opposed to fixed prime location can therefore be explained in terms of additional effort due to persisting/retrieved inhibition at the level of stimulus identities.

Although the fact requires further discussion that NP was absent (and not only reduced) in the fixed-location task (see below), the present pattern of results has one specific advantage: The NP effect in the varied-locations task is most likely *not* a composite effect of at least two different subcomponents (one that is also present in the standard task, and one additional component in the modified task). Instead, it may represent a relatively pure measure of inhibition of distractor identities, since the critical difference between tasks should be the degree to which inhibition of distractor identities at advanced levels of processing is required (see above). Consequently, an ERP effect that is seen exclusively in the IR condition of the modified, varied-locations task might exactly tap those mental processes that may be responsible for a distractor-inhibition component in NP, as it has been implemented, for example, in Houghton and Tipper's (1994) model.

The absence of NP in the present standard, fixed-location flanker task is at variance with earlier reports using three-stimuli flanker displays (e.g., Fox and de Fockert, 1998; Neill, 1997; Stadler and Hogan, 1996), also from our own groups (e.g., Frings and Groh-Bordin, 2007; Gibbons, 2009; Stahl and Gibbons, 2007). A possible explanation might concern target-to-distractor distance. For example, whereas this distance was 2 mm in Stahl and Gibbons (2007) and in Gibbons (2009), it was 5 mm in the present task. Without additional demands on selection processes, as they may have been introduced by the spatial prime-uncertainty manipulation, this target-to-distractor distance may have been too large to require distractor inhibition to an extent sufficient for establishing NP under *standard conditions* (i.e., fixed display location; cf., Fox, 1994; Ruthruff and Miller, 1995). Note, however, that for the present purpose of investigating the influence of spatial prime uncertainty on behavioral and ERP effects of NP, the finding of a significant *difference* between tasks in size of the NP effect is most important. This expected between-task difference indeed could be observed.

Note that with prime location randomly drawn from four possible locations, also in our varied-locations task there was a 25% probability for location repetitions between a probe and the next prime. Interestingly, behavioral NP was *not* stronger in an analysis of the 75% of trials on which a location change *actually* occurred (14 ms as compared to the 16-ms NP effect from all trials of the varied-locations task; see Results). Thus, stronger NP in the varied-locations task seems to be related to the fact that a location change can be *expected* with high probability. This additional finding is in line with our idea that NP is stronger in the varied-locations task because anticipatory spatial prime selection is disabled, and adds to earlier findings of strategic effects on NP (e.g., Frings and Wentura, 2006; 2008; Kane et al., 1997).

4.2. An ERP correlate of behavioral NP from spatially unpredictable primes

The only ERP effect specific to NP was found in the modified, varied-locations task and concerned left-posterior PN amplitude increase.[4] It is important to note that the PN effect distinguished the IR condition from both, the control condition and the AR condition involving prime–probe target repetition. Thus, NP-related PN amplitude increase is not due to the repetition of prime stimuli *per se*, and instead appears to *directly* reflect those mental processes that are responsible for the present behavioral NP effect (in contrast, a shared AR/IR effect on the ERP can only be indirectly related to behavioral NP; see Gibbons, 2009, for details). The claim of functional significance of the left-posterior PN effect for behavioral NP also receives strong support from an individual differences approach to the present data. Only in the group of participants showing a sizeable individual NP effect (≥ 15 ms; $N = 13$) in the modified task, IR-related left-posterior PN increase was observed, whereas the PN effect was absent in weak-NP participants ($N = 8$; NP$<$15 ms).

The present left-posterior PN effect resembles the "N400-like" ERP correlate of flanker NP reported by Gibbons (2009; see below). In the literature, N400 amplitude is usually interpreted as reflecting the mismatch between a stimulus and the context; this context is often provided by a preceding word or sentence (e.g., Holcomb, 1988).

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[4] The visually most prominent priming ERP effect was the increased late P300 component over central recording sites. This effect was however specific to the AR condition (see Results), and is not discussed here in detail because the present paper focuses on NP. Briefly, it seems plausible that in the AR condition where the prime target repeats as the probe target, stimulus identification and/or closure of trial information processing takes place more rigorously and with lower temporal variability. The AR effect on central P300 may thus represent an example of larger P300 in situations of high decision confidence (cf., the symbolic distance effect on P300; Grune et al., 1993).

Recently, however, Bermeitinger et al. (2008) have argued that in priming experiments the N400 component might also be directly related to the access to stimulus representations. For the present study, the N400-like processing negativity may reflect increased effort with the activation of identity-specific internal representations of a stimulus that has been ignored during processing of the preceding prime. As suggested above, in the varied-locations task prime distractors should be more deeply processed than in the fixed-location task; hence, successful selection of the prime target should involve stronger distractor inhibition at relatively advanced levels of processing. If the distractor then becomes a target in the subsequent probe display, the relevant stimulus representations may still be in a state of inhibition, and their activation above a critical threshold would require more effort, which in turn is reflected in larger N400-like processing negativity overlapping the P300 time range. The rather untypical left-posterior predominance of the present processing negativity may partly be due to the fact that simple number stimuli were used, as opposed to the typical complex word stimuli used in N400 experiments.

4.3. Comparison of the present ERP correlate of NP with previous ERP findings

The present NP effect on amplitude of an N400-like component is in line with a recent finding by Gibbons (2009), in several respects: First, the specificity of the effect to the IR condition (i.e., absence of a similar effect in the AR condition), second, the left-posterior predominance of the effect, and third, functional significance of the effect for behavioral NP (that is, the N400-like effect was stronger in strong-NP participants). The present ERP correlate of NP in the modified flanker task thus may also be interpreted as a processing negativity (cf. Kok, 2001) which is superimposed on P300 whenever stimulus identification requires the recruitment of additional resources. This fits well with the idea that the present varied-locations task involves particularly strong distractor inhibition, which implicates more effortful processing when a prime distractor serves as target in the subsequent probe. However, Gibbons (2009) observed an N400-like ERP correlate of NP also in the standard flanker task, which seems to contrast with the present N400-like effect being specific to the modified, varied-locations task. This apparent inconsistency may be resolved by referring to differences between studies: With the smaller target-to-distractor distance (approximately 0.2° or 2 mm, as opposed to approximately 0.5° or 5 mm in the present tasks), also in the standard flanker task by Gibbons (2009) distractor inhibition may have been required to an extent sufficient to produce NP. Thus, the fact that Gibbons (2009) observed an N400-like ERP correlate of NP in the standard task is still consistent with the idea that this ERP effect reflects a distractor-inhibition component of NP. In conclusion, there may be different possibilities to strengthen the distractor-inhibition component of NP, for example, by using a relatively small target-to-distractor distance (Frings and Wühr, 2007; Gibbons, 2009), or by presenting the primes in unpredictable locations, as in the experiment reported here.

No NP effects on N200 and P300 components were observed in the present study. With regard to (frontal) N200, we suggest that in the present modified, varied-locations task prime distractors are relatively deeply processed and distractor-specific inhibition can only operate at relatively advanced levels of processing. Therefore, distractors in IR probe displays may not benefit from *early* processing advantage over the still-inhibited probe target, inhibition of their associated response may not be necessary, and no N200 occurs. By contrast, in previous ERP studies (e.g., Frings and Groh-Bordin, 2007; Hinojosa et al., 2009) NP may have operated at earlier levels of processing, thereby activating an N200-related mechanism of response inhibition.

Regarding P300, we only observed a larger mid-central P300 for AR trials compared to both, IR and control trials, which precisely replicates Frings and Groh-Bordin (2007) and Gibbons (2009) and most likely indicates earlier completion of stimulus evaluation (cf., Donchin and Coles, 1988) in the AR condition. No NP-related increase in (posterior) P300 amplitude, like it has been reported by Kathmann et al. (2006), was found in the present study. These divergent findings might be explained by differences in the experimental tasks; for example, the earlier study used overlapping digits instead of the present flanker task. Also, absence of an AR condition in Kathmann et al. (2006) may have had effects on the selection strategies adopted by the participants (see Frings and Wentura, 2008) and, hence, P300 amplitude.

4.4. Consequences for theories and research on NP

The present study replicated a relatively novel ERP correlate of identity-based NP, left-posterior N400-like processing negativity (PN) in the IR condition (Gibbons, 2009). Moreover, our study adds to previous work insofar as it suggests that this PN component may be closely related to a distractor-inhibition component of NP. Both behavioral NP and its N400-like ERP correlate were only found in a modified flanker task designed to strengthen the distractor-inhibition component of NP, but absent in the standard flanker task. In this modified, varied-locations task, anticipatory spatial prime selection was disabled, thus implicating deeper processing of the prime distractors. We suggest that the left-posterior PN reflects the increased effort with activation of internal representations of a stimulus that has been ignored immediately before. This may be particularly true for the present varied-locations task, where distractors are relatively deeply processed (e.g., up to the object level or even up to the conceptual level) before inhibition can be applied. Both, the left-posterior predominance and the late time range of the present NP-related ERP effect indicates that NP in the varied-locations task operates at the level of conceptual representations. If so, the inhibitory processes contributing to this NP effect should be subject to capacity limitations (cf., Engle et al., 1995; Lavie et al., 2004), and hence be reduced under increased cognitive load. This hypothesis should be tested in future behavioral and/or ERP studies, by using dual-task arrangements.

The above interpretation also sheds new light on the analysis of NP processes in general, because it emphasizes the importance of level of processing for NP. Neill (2007) has recently argued that the distinction between NP effects that emerge on perceptual vs. object vs. motor levels of processing is highly relevant to the debate as to whether NP reflects retrieval or inhibition processes. In fact, ERP correlates might help resolve this issue. For example, it might be speculated that the N200 effect observed in previous studies reflects conflict on a motor level of processing, as the frontal N200 is often interpreted as an index of response inhibition (e.g., Eimer, 1993; Heil et al., 2000).

It is less clear, however, whether NP on an object level exclusively relies on memory processes, as proposed by Neill (2007). One prominent inhibition-based model of NP (Houghton and Tipper, 1994) suggests inhibition of to-be-ignored stimuli on the level of abstract stimulus representations. This mechanism closely resembles our understanding of the present NP effect in the varied-locations task. Indeed, the present modified flanker task was developed to investigate distractor-inhibition components of NP (which lead us to expect stronger distractor inhibition with unpredictable prime locations). If this reasoning is correct, amplitude of the present left-posterior PN can be understood as an index of the amount of activation needed for target identification. In IR trials, more activation is needed; activation of the internal representation of an IR target may be below baseline during the relevant period of probe processing. Importantly, this could be due to at least two mechanisms, *persisting* inhibition from the prime to the probe (Houghton and Tipper, 1994;

Tipper, 1985), or retrieval/ reactivation of inhibition during probe processing (Tipper, 2001). Even traditional episodic-retrieval view, claiming the retrieval of a “do-not-respond” tag for IR probe targets (Neill et al., 1992) can incorporate the present findings, if the do-not-respond tag is understood as a metaphor for the retrieval of inhibition of a stimulus identity. Thus, based on the present results one cannot ultimately decide between the two major theories as potentially valid explanations of the present NP effect, and NP effects in general.

Clearly, further research is necessary to analyze NP at different levels of processing while using ERPs. The present study represents a first step in this direction, insofar as the effects of an experimental manipulation on both, behavioral NP effects and their ERP correlates, have been simultaneously assessed. Results support the notion that different ERP components may be sensitive to the behavioral NP effect, depending on the level of processing at which NP operates in a given task.

A final cautionary note concerns the fact that, to still more convincingly support distractor-inhibition accounts of NP, the full set of all possible prime–probe distractor–target relationships should be employed (cf., Christie and Klein, 2008). This way, one can definitively rule out the possibility that NP was unrelated to the repetition of the prime distractor as the probe *target*, and instead reflects some less specific repetition effect. For example, a condition where the prime distractor repeats as the probe *distractor* while prime and probe targets are different should *not* produce an RT cost of similar magnitude as the NP effect from IR trials.

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