

Where has all the inhibition gone? Insights from electrophysiological measures into negative priming without probe distractors

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ABSTRACT

Responses to probe targets that have been distractors in a prime display are slower than responses to unrepeated stimuli, a finding labeled negative priming (NP). However, without probe distractors the NP effect usually diminishes. The present study is the first to investigate ERP correlates of NP without probe distractors to shed light on the processes underlying NP. Based on existing findings in the field, we analyzed two ERP correlates that have been associated with the visual NP effect so far, namely the N200 and the P300. As expected, no behavioral NP effect as well as no N200 modulation emerged. However, the P300 component was enhanced when a prime distractor was repeated as the probe target. This effect is interpreted as reflecting automatic retrieval of the prime episode occurring independently of the presence of probe distractors.

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1. Introduction

It is an accepted finding that, if a to-be-ignored stimulus (distractor) from a prime display becomes the to-be-selected stimulus (target) in the following probe display, then responding to this target will be impaired in terms of reaction time (RT) and accuracy (Dalrymple-Alford & Budayr, 1966; Neill, 1977). Since its original observation, the cost effect of distractor-to-target repetitions has been observed for a wide variety of tasks, stimuli, and populations of participants (Fox, 1995; Tipper, 2001, for reviews) and has finally been labeled negative priming (NP; Tipper, 1985). However, although there is consensus that NP validly taps selective control mechanisms, the functional mechanisms that give rise to the NP effect – are still under debate. A coarse-grained taxonomy of NP theories differentiates between inhibition (Houghton & Tipper, 1994; Tipper, 1985) and retrieval (Mayr & Buchner, 2006; Neill, 1997; Milliken, Joordens, Merikle, & Seiffert, 1998; Rothermund, Wentura, & DeHouwer, 2005) based accounts. Inhibition theory claims that NP mainly arises as a consequence of selecting the prime target against the prime distractor, which may be achieved – at least in part – by inhibiting the cognitive representation of the prime distractor (e.g., Houghton & Tipper, 1994; Tipper, 1985). As a result, when the prime distractor reappears as the probe target (the Ignored-Repetition condi-

tion, IR), sustained inhibition should impair probe-target processing. In contrast, retrieval theories argue that NP is caused by 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 “do-not-respond” or may contain the prime response associated with this stimulus, and the retrieved information interferes with responding quickly and accurately to the current target. Both accounts are well supported by the literature, leading several authors to conclude that both inhibitory mechanisms and retrieval processes contribute to NP (Kane, May, Hasher, Rahhal, & Stoltzfus, 1997; Tipper, 2001).

In a seminal paper Moore (1994) asked ‘Where has all the inhibition gone?’ and referred thereby to the well-known, but still puzzling finding that NP effects usually depend on the presence of distractor stimuli in the probe display (e.g., Allport, Tipper, & Chmiel, 1985; Frings & Wentura, 2006; Lowe, 1979; Milliken et al., 1998; Milliken & Tipper, 1998; Moore, 1994; Tipper & Cranston, 1985). If probe distractors are constantly absent, NP typically does not occur – although some authors found NP without probe distractors given certain specific conditions (e.g., Frings & Wentura, 2006; Moore, 1994; Neill, Terry, & Valdes, 1994; Ortells, Abad, Noguera, & Lupiáñez, 2001) – leading other authors to term this phenomenon the ‘enigma of negative priming’ (cf. Milliken & Tipper, 1998). Yet, this finding remains to be of theoretical significance, since it poses problems for our understanding of the basic processes that underlie NP.

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Usually, the dependence of NP on the presence of probe distractors is interpreted as an evidence against the inhibition account: If it is argued that the prime distractor is inhibited when the *prime* display is presented, variations of the *probe* display should not diminish NP effects, as long as it can plausibly be assumed that the probe trial only tests for the accessibility of the target stimulus. The presence or absence of a probe distractor should be irrelevant here. There have, of course, been attempts to defend the inhibition view of NP. For example, it was argued that participants must be in a selection state for NP to occur; i.e., participants must be in an attentional task set, in which they represent the NP task as a task where the target has to be selected against the distractor. Only in this attentional task set, the target will receive activation and the distractor will receive inhibition. Thus, when participants can anticipate target-only probes and accordingly abandon this selection state, NP will not occur (e.g., Moore, 1994). However, most attempts to reconcile the inhibition theory with the dependence of NP on the presence of probe distractors seemed somewhat post-hoc and far-stretched (cf. Frings & Wentura, 2006).

In contrast, retrieval-based theories of NP provide two possible explanations for why NP diminishes when probe distractors are absent. First, if the context changes between the prime and probe display (e.g., two stimuli in the prime vs. one stimulus in the probe), the likelihood of automatic memory retrieval is lowered (Neill, 1997). Hence, NP will not occur. Second, it has been suggested that in probes without distractors, the algorithmic processing needed to compute the probe response is sufficiently fast that the response may be selected prior to the retrieval of the prime episode (and hence no interference from incompatible episodes occurs; Neill, 1997).

The aim of this study is to shed light on the issue of NP without probe distractors by using electrophysiological measures. In particular, we will analyze the ERP correlates of NP in a visual identity NP task without probe distractors and compare the data pattern with previous ERP studies analyzing the correlates of NP with probe distractors. The EEG measures might help to solve the puzzle what really happens in a NP task without probe distractors. Before we outline our hypotheses, however, we will shortly summarize what so far is known about the ERP correlates of NP (for a review see Mayr & Buchner, 2007).

For visual NP, so far two ERP correlates have been reported. First, an enhanced N200 was observed for identity (Frings & Groh-Bordin, 2007) and location-based (Gibbons, 2006) NP tasks.¹ In addition, Daurignac, Houde, and Jouvent (2006) analyzed NP correlates in a number conservation task similar to those of Piaget and also observed a modulation of the N200. In particular, in these studies, in IR probe trials a more negative going waveform was elicited as compared to control trials mainly at fronto-central recording sites. Usually, such a fronto-central N200 is interpreted in terms of response conflict or response inhibition (e.g., Eimer, 1993; Heil, Osman, Wiegelmann, Rolke, & Henninghausen, 2000; Yeung, Botvinick, & Cohen, 2004); for example, in a flanker task (in which participants respond to a central target flanked by response compatible or response incompatible distractors) the fronto-central N200 is found in trials with response incompatible distractors. On this note, Frings and Groh-Bordin (2007) suggested that the N200 modulation in NP may reflect persisting inhibition from the prime to the probe. They assumed that the response conflict in probe displays in IR trials is particularly strong since the inhibited probe target must be selected against non-inhibited probe distractors. In contrast, in control trials the response conflict is smaller since the probe target was not inhibited

in the prime trial and in turn could be selected with less effort against the probe distractors. The difference in response conflict between IR and control trials is assumed to elicit the enhanced N200.

The second component that has been observed in NP task is the so-called P300, a more positive going waveform at fronto-central or parietal recording sites roughly 300–500 ms after stimulus onset. For example, Kathmann, Bogdahn, and Endrass (2006) analyzed location-based and identity NP. For location-based NP they found reduced P1–N1 amplitudes and a delayed P300 latency in IR probe trials, whereas for identity NP they observed a larger P300 amplitude in IR probe trials as compared to control probe trials. A comparable pattern has been reported by Gibbons (2006) who also found a P300 amplitude modulation in a NP identity task. Typically, the P300 is interpreted as indexing an “updating” of the mental representation of the stimulus environment (cf. Polich & Kok, 1995) or as allocation of attention to new stimulus information (Donchin, Karis, Bashore, Coles, & Gratton, 1986). Both interpretations have also been suggested for the P300 in NP. In particular, Kathmann et al. interpreted the P300 in identity NP as reflecting increased attentional resources for the processing of IR probe trials. In contrast, Gibbons (2006) interpreted the P300 as possibly reflecting retrieval mechanisms. We will discuss the different interpretations concerning the P300 in NP in more detail in the General Discussion.

In sum, some of the ERP studies on NP reviewed above (Daurignac et al., 2006; Frings & Groh-Bordin, 2007; Gibbons, 2006) showed more negative going waveforms in the N200 time window at frontal electrodes in IR relative to control trials – possibly reflecting inhibition processes. In contrast, somewhat later components at central electrodes like the P300 which have been found in other studies (Gibbons, 2006; Kathmann et al., 2006) possibly point to retrieval processes.

Concerning the explanations offered by the theoretical accounts on NP, we expect the following pattern of ERP correlates of NP without probe distractors. First, if the frontal N200 complex is really a correlate of cognitive inhibition as suggested by several authors (e.g., Daurignac et al., 2006; Frings & Groh-Bordin, 2007), the N200 should probably be absent in probe displays without distractors as the behavioral NP effect usually is. The N200 is assumed to tap the conflict between probe target and probe distractor. This conflict should be stronger in IR trials when the representation of the probe target is still inhibited due to the persisting inhibition from the prime display. However, when there is no probe distractor there is obviously no conflict and hence no N200 should emerge. In contrast, the centro-parietal P300 should not be affected by our manipulation at all. Automatic retrieval is assumed to take place even in trials without distractors. Therefore, if the P300 indeed reflects retrieval of the prime episode, we should find a P300 in IR trials independently of the presence of probe distractors and even when there is no behavioral NP effect.

2. Materials and methods

2.1. Participants

Forty four right-handed students from Saarland University participated in this study which was conducted with the understanding and written consent of each subject. Five participants were excluded due to excessive EEG artifacts (since a minimum of 25 trials per condition was considered necessary for inclusion into the Grand Average), leaving 39 subjects for behavioral and ERP analysis (median age 23 years, range 19–30, 22 female). All of them had normal or corrected-to-normal vision.

¹ In fact, Gibbons (2006) argued that the N200 enhancement may also be interpreted as a reduction of the P200. For the sake of readability, however, we will use the term N200 throughout the manuscript.

2.2. Material and apparatus

Four different letter identities (D, F, J, and K) were used as stimuli. Letters were presented in red or green in the center of a 17" CRT monitor (1024 × 768 dpi) against a white background. Stimuli had a size of 1.0 cm vertically and 0.8 cm horizontally and the distance between them was about 0.2 cm; viewing distance was approximately 60 cm. Assignment of stimulus identity to experimental condition was randomized by the computer. Responses were recorded using a QWERTY keyboard, where the four corresponding keys were mapped to the four stimulus identities, and subjects had to respond with their left and right index and middle fingers.

2.3. Design and procedure

The procedure and design closely followed our former study (cf. Frings & Groh-Bordin, 2007, for exact procedure and timing). Prime displays comprised three stimuli, respectively, that were presented simultaneously. In the middle, a red² target letter was shown that was flanked by two identical green distractor letters. Probe display, however, comprised a single red target letter presented at the screen center. Participants were instructed to react as quickly and accurately as possible to red target letters while ignoring the green distractor letters; they received no error feedback during the experiment. Three priming conditions were conducted. In attended repetition trials (AR) only the prime target was repeated as the probe target. In the control condition (C) no stimuli were repeated from prime to probe. In the Ignored-Repetition condition (IR) only the prime distractor was repeated as the probe target. The order of priming conditions and assignment of stimuli to roles as prime distractor, prime target, probe distractor, and probe target were randomly selected by the computer. Overall, 120 experimental trials were conducted with 40 trials for each priming condition. Before the proper experiment, participants performed 60 practice trials to become familiar with the procedure.

For statistical analysis of the behavioral data, only trials with correct prime and probe reactions and with reaction times below 2000 ms were considered. These criteria led to the exclusion of 9.8% of trials (probe error rate 4.4%).

2.4. EEG recording and analysis

The experiment was run in an electromagnetically shielded room. EEG activity was recorded continuously from 64 Ag/AgCl electrodes mounted in a preconfigured cap (Easy Cap, Falk Minow Services, Germany), arranged according to the international 10–10 system. Two electrodes located medially to the right eye, one above and one below, were used to monitor vertical eye movements. Electrodes placed at the outer canthi of the eyes measured horizontal eye movements. Impedances for all electrodes were kept below 10 kΩ. Signals were digitized with a sampling rate of 250 Hz (70 Hz low-pass, 50 Hz notch filter) by an AC coupled amplifier (Brain Amp MR, Brain Products, Munich; time constant 10 s) and referenced on-line to the left mastoid electrode.

For ERP analysis, data were processed as follows: First, electrodes were re-referenced off-line to averaged mastoids. Then, ERPs were extracted during the probe display from –200 to 1000 ms around stimulus onset (an additional analysis on ERP waveforms during prime displays revealed no differences between the later C, AR, and IR conditions). Third, EOG artifacts were corrected off-line (Gratton, Coles, & Donchin, 1983). After-

wards, data were baseline-corrected with respect to the 200 ms pre-stimulus interval and digitally bandpass filtered at 0.2–20 Hz (slope 24 dB). Finally, trials still containing artifacts in any EEG channel (maximum amplitude in the recording epoch $\pm 200 \mu\text{V}$; maximum difference between two successive sampling points $50 \mu\text{V}$; maximum difference of two values in the epoch $200 \mu\text{V}$; lowest allowed activity-change $0.5 \mu\text{V}$ in successive intervals of 100 ms) were excluded from averaging; corresponding to the behavioral analysis, only trials with correct prime-probe sequences were considered. ERPs were then averaged for three different conditions (with the mean number of valid trials per condition as well as the range given in parentheses): Control (38, 30–40), Attended Repetition (39, 36–40), and Ignored Repetition (37, 32–40).

For statistical analysis, ERPs from single electrodes were averaged to the following nine regions of interest (ROIs): Left-Anterior: F5, F7, FC5; Left-Central: T7, CP5, TP7; Left-Posterior: P5, P7, PO7; Mid-Anterior: Fz, FP1, FP2; Mid-Central: Cz, CP1, CP2; Mid-Posterior: Pz, O1, O2; and the right counterparts of left-sided electrode regions. This procedure resulted in a 3 (Caudality) × 3 (Laterality) electrode arrangement. To tap the ERP components that were observed in previous studies (see Introduction) and in order to have a comparable data basis to our earlier study (Frings & Groh-Bordin, 2007), we chose the following two time windows for statistical analysis: The first time range (170–270 ms) encompassed the P200/N200 component, the second time range (340–600 ms) the P300/LPC. Major statistical analyzes of ERPs therefore comprised 3 × 3 × 3 MANOVAs on mean voltages in both time intervals involving the within-subject factors Condition (C, AR, and IR), Caudality (Anterior, Central, and Posterior) and Laterality (Left, Middle, and Right).

3. Results

3.1. Behavioral data

In a MANOVA with reaction time as dependent variable and priming condition (AR vs. IR vs. C) as factor, a significant main effect for priming condition emerged ($F[2, 37] = 83.58$, $p < .001$, $\eta^2 = .82$; see Table 1). To further analyze the effects of priming condition on reaction time, we computed two contrasts, possibly reflecting positive priming effects in AR trials and NP effects in IR trials. AR and C trials differed significantly ($F[1, 38] = 166.99$, $p < .001$, $\eta^2 = .82$), reflecting significantly faster reaction times in the AR condition. In contrast, IR and C trials did not differ significantly ($F[1, 38] = 2.36$, $p = .13$, $\eta^2 = .06$), that is no NP effect emerged in this experiment. The corresponding analysis on error rates mimicked this pattern by showing a significant main effect for priming condition ($F[2, 37] = 21.42$, $p < .001$, $\eta^2 = .54$), which was, however, attributable to fewer errors in the AR than in the C condition ($F[1, 38] = 17.96$, $p < .01$, $\eta^2 = .32$), whereas IR and C did not differ significantly ($F = 1.5$, $p = .23$).

Table 1
Behavioral data.

	Attended repetition	Difference from control	Ignored Repetition	Difference from control	Control
Reaction time	516	108*	612	12	624
Error rate	1.7	3.4*	6.1	–1.0	5.1

Reaction times (in milliseconds) and error rates (in percentage) as a function of priming condition.

* $p < .001$.

² For interpretation of color in Fig. 1, the reader is referred to the web version of this article.

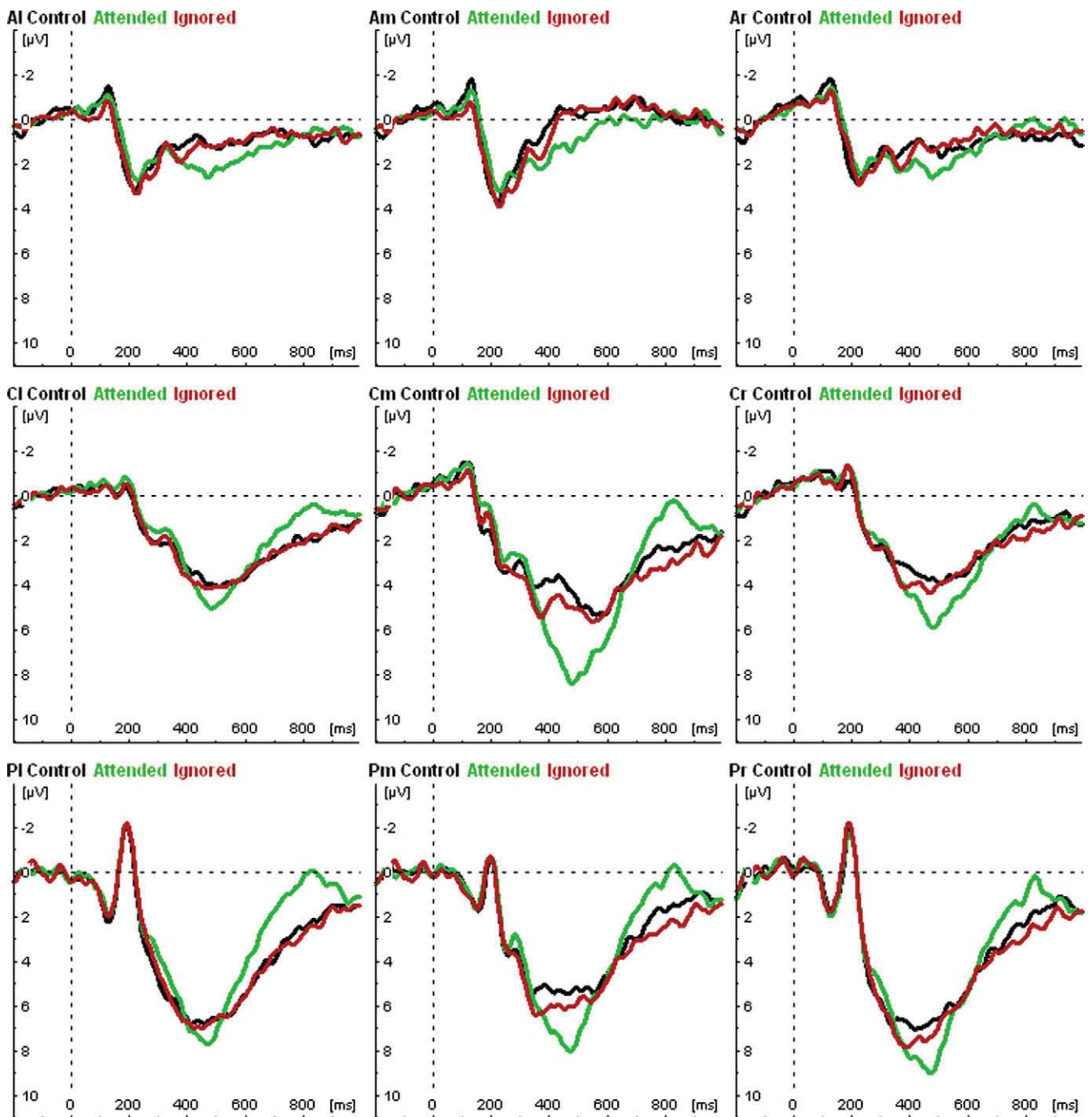


Fig. 1. Grand average waveforms for probe displays at nine regions of interest (ROIs) as a function of Condition (Control, Attended Repetition, Ignored Repetition); A, anterior; C, central; P, posterior; l, left; m, middle; r, right; positive values are displayed downwards.

3.2. ERP data

ERP waveforms for the C, AR, and IR conditions at the nine ROIs are shown in Fig. 1.

In the 170–270 ms interval, statistical analysis revealed no significant effects involving the Condition factor (F s between 0.49 and 2.24, p s between .09 and .85). This pattern is in striking contrast to our previous study where IR trials were specifically associated with a frontal N200 enhancement. Hence, the predicted absence of a behavioral NP effect due to lacking probe distractors in the present study is accompanied obviously by the absence of the IR-related ERP effect from the previous study. In the 340–600 ms interval, MANOVA yielded a significant main effect of Condition

($F[2, 37] = 5.73, p < .01$) along with interaction effects of Condition \times Caudality ($F[4, 35] = 4.41, p < .01$) and Condition \times Laterality ($F[4, 35] = 7.25, p < .001$) as well as a 3-way interaction ($F[8, 31] = 4.05, p < .01$). Post-hoc tests (Tukey HSD) revealed that waveforms for AR trials were significantly more positive than for C (all p s $< .001$) and IR trials (all p s $< .05$) at all ROIs except the left central and left posterior one (all p s $> .90$).³ Furthermore, the rep-

³ Note that these amplitude differences may be – at least in part – due to less latency jitter in AR trials. Although there were no significant differences in the peak latencies of the P300 between the three conditions (C: 491 ms, AR: 480 ms, IR: 467 ms; $F[2,76] = 1.14, p = .33$), the variance of the peak latency was significantly lower for AR trials (SD: 66 ms) than for C (88 ms) and IR trials (97), respectively (Levene Test: $F_s[1,76] > 6.88, p < .011$).

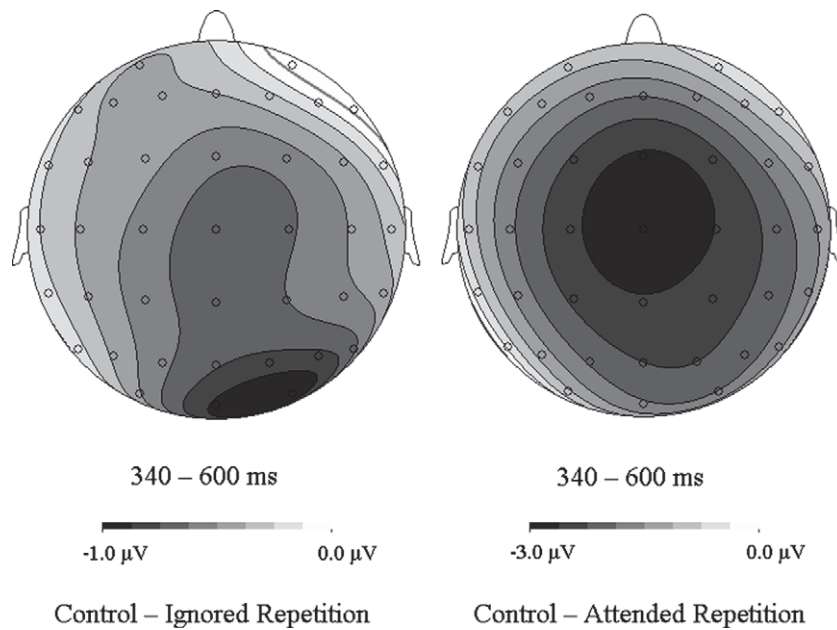


Fig. 2. Spherical-spline interpolated topographical voltage maps of ERP differences in the 340–600 ms interval; IR trials (left-hand side) and AR trials (right-hand side) were subtracted from C trials; the head is depicted from above (with the front facing up, left on left, etc.).

etition positivity for the IR relative to the C condition was significant at the mid-central and mid-posterior ROI ($p < .05$). Fig. 2 shows the topographical distributions of the P300 effects for the IR and AR conditions, respectively.

To sum up, the frontal N200 effect that we found to be specifically associated with the IR condition in our previous study (Frings & Groh-Bordin, 2007) concurrently vanished with the behavioral NP effect in the present study. By contrast, IR trials elicited a significant centro-parietal P300 at midline ROIs that is comparable to the P300 components reported in NP studies with probe distractors (e.g., Gibbons, 2006; Kathmann et al., 2006). However, the P300 modulation was not specific for the IR condition since AR trials showed an even more pronounced P300 increase. The overall picture that thus arises from the present and several previous studies is summarized in Fig. 3. It shows NP-related behavioral and ERP effects for the N200 and P300 component as observed in selected studies, respectively, and illustrates their dependency on the presence/absence of probe distractors.

4. Discussion

To the best of our knowledge, this is the first study investigating ERP correlates of visual identity negative priming without probe distractors. Based on the previous literature, we analyzed two components which have been associated with NP so far, namely the N200 and the P300, possibly reflecting inhibition and retrieval processes, respectively. In an experiment with considerable power ($N = 39$) we observed – as expected – no behavioral NP effect, no N200 component, but a significant modulation of the P300 component in IR as compared to control trials.

Following our former study on ERP correlates of visual identity NP (Frings & Groh-Bordin, 2007) we analyzed the N200 component in the time window from 170 to 270 ms. However, no significant difference between the IR and control trials was observed at any frontal or mid-central ROI. Thus it is justifiable to say that without probe distractors no N200 correlate of NP emerges. As outlined in the introduction, if the N200 modulation observed in previous studies reflects the strong conflict in IR probes (since the probe target is still inhibited and must be selected against the non-inhibited

probe distractor), then no N200 modulation should emerge when there is no conflict in the probe (i.e. when there is no distractor). This pattern is in line with the argument raised by inhibition theories that participants must adopt a ‘selection state’ to show NP (cf. Houghton & Tipper, 1994; Moore, 1994). In sum, it might be said that without probe distractors the prime inhibition becomes irrelevant.

In addition, we analyzed the P300 component in the time window from 340 ms to 600 ms. For IR trials we observed an enhanced P300 as compared to control trials over mid-central and centro-parietal recording sites. This correlate of NP has been reported previously and has been interpreted as reflecting updating the stimulus representation, a more effortful processing, or retrieval mechanisms, respectively (cf. Gibbons, 2006; Kathmann et al., 2006). The observation of a modulation of the P300 component by IR vs. control trials while simultaneously no behavioral NP emerged is quite noteworthy. It should be noted that this pattern is exactly what is predicted by episodic retrieval theory (cf. Neill, 1997). The retrieval mechanism (possibly tapped by the P300, see below) is assumed to be generally at work independently of the presence of probe distractors. However, without probe distractors the response can be computed so quickly that the retrieved episode can not cause (strong) interference and hence no NP occurs. In sum, the modulation of the P300 nicely fits the explanation given by the episodic retrieval theory.

However, two further points should be considered. First, the P300 modulation was not idiosyncratic for IR trials; in fact, AR trials elicited an even more positive P300. Yet, the P300 component in AR trials poses *per se* no problem for the explanation in terms of retrieval since retrieval theories in general explain AR and IR effects by the same underlying retrieval mechanism (cf. Frings, 2008). Comparable to IR trials, the probe target in AR trials leads to automatic retrieval, but in contrast to IR trials the retrieved episode is compatible with the generation of the response and in turn facilitates responding. In AR trials the retrieval is even stronger than in IR trials because the same stimulus is repeated with the same response, in the same color, and at the same location. However, the P300 effect in AR trials may seem nevertheless problematic given that we observed a behavioral AR effect; this leads to the

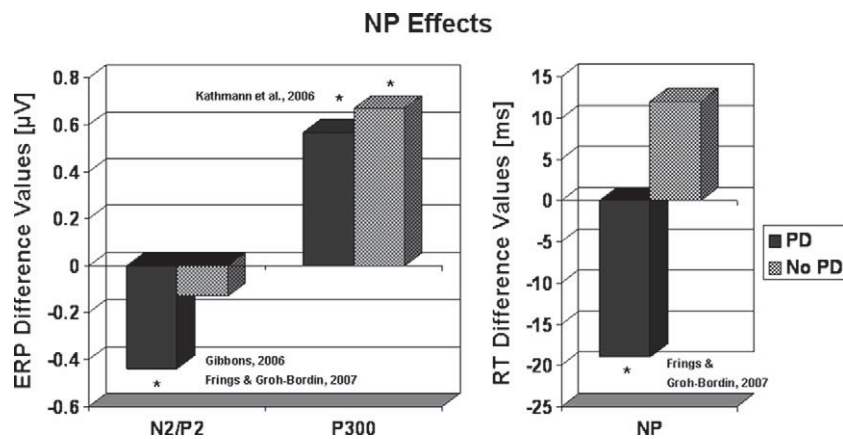


Fig. 3. Schematic overview of NP effects depending on the presence/absence of probe distractors (PD/no PD); mean difference values between IR and C conditions are shown for ERP amplitudes (left-hand side: N200/P200 and P300, respectively) and RTs (right-hand side); for full bars, data are averaged across the indicated studies; (We are grateful to Henning Gibbons for providing the data; data from Kathmann et al. (2006) were estimated from Fig. 3 of the original manuscript.) checkered bars indicate results of the present study; asterisks illustrate where significant differences were reported.

second issue. Why did we even observe a behavioral AR effect when the response generation is so quick that the retrieved episode can not cause (much) interference/benefit? The potential answer lies in the fact that the AR benefit in the present experiment was indeed significantly smaller than in comparable experiments. For example, in the study of Frings and Groh-Bordin (2007), which was exactly identical despite the presence of probe distractors, the benefit in AR trials (141 ms) was significantly larger than the AR benefit (108 ms) in the study presented here ($t[57] = 2.10$, $p < .05$). Thus, since the AR benefit is usually so large in experiments with probe distractors, it still remained significant in the present experiment without probe distractors although the benefit from the retrieved episode was much smaller. Again, the pattern in AR trials fits the explanation in terms of retrieval theory.

One critical question should be considered when linking the P300 to retrieval theory: Does the P300 index retrieval mechanisms in terms of the episodic retrieval theory (cf. Neill, 1997; Rothermund et al., 2005)? The P300 is typically interpreted as indexing an “updating” of the mental representation of the stimulus environment (cf. Polich & Kok, 1995). It has been assumed that this updating process consists of attention mechanisms that are engaged when new information has to be processed (Donchin et al., 1986). Additionally, the P300 can be divided into two functionally distinct subcomponents, the frontal/central P3a (or novelty P300) and the parietal P3b. The former one is assumed to index the operation of an automatic attention network that is responsive to stimulus deviance, while the latter one has been associated with a memory comparison that evaluates the current stimulus in the context of previous stimuli (cf. Polich & Criado, 2006). With respect to the topography of the P300 observed in our experiment (see Fig. 2), it is reasonable to assume that it resembles the P3b and thus reflects the memory comparison process. Furthermore, it is obvious that this process bears a striking resemblance to the retrieval mechanism as conceived by retrieval theories of NP (cf. Neill, 1997; Rothermund et al., 2005).

In addition, a further hint that may corroborate the retrieval interpretation of the P300 effect observed here stems from the large, parietally accentuated, negative-going component for AR trials that starts at about 600 ms and that the attentive reader may have noticed in the present but also in our previous study (Frings & Groh-Bordin, 2007). This component resembles the previously described late posterior negativity (LPN; e.g., Groh-Bordin, Zimmer, & Ecker, 2006; for a review and discussion, see Johansson & Mecklinger, 2003). According to Johansson and Mecklinger (2003), the LPN reflects retrieval processes that try to reconstruct

a prior study episode. In this vein, it is conceivable that subjects in the present NP paradigm are continuously engaged in an evaluation of the stimulus context which they try to recover from the previous prime display. Of course, a direct target-to-target repetition is much more noticeable than a distractor-to-target repetition what might explain why the LPN is observed in AR trials only.

To summarize, with respect to the results presented here and in concert with previous studies, the following conclusions can be drawn. The behavioral NP effect depends on the presence of probe distractors. Yet, electrophysiological data give insight what really happens here. First, the inhibition processes tapped by the N200 component become irrelevant without a conflict in the probe display and hereby the NP effect becomes smaller. Second, the retrieval processes as potentially reflected by the P300 modulation are themselves unaffected by the presence/absence of probe distractors. However, the probe response generation may be so quick that the retrieved episode influences response generation to a far lesser extent (cf. Neill, 1997). As a result, benefits in AR trials and costs in IR trials both become smaller. Together, these data yield evidence for both inhibition and retrieval theories of NP. In particular, the specific assumption of retrieval theories – that the retrieval process is always at work – is supported by our data.

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References

- Allport, D. A., Tipper, S. P., & Chmiel, N. (1985). Perceptual integration and post-categorical filtering. In M. I. Posner & O. S. M. Marin (Eds.), *Attention and performance* (Vol. XI, pp. 107–132). Hillsdale, NJ: Erlbaum.
- Dalrymple-Alford, E. C., & Budayr, B. (1966). Examination of some aspects of the Stroop color-word test. *Perceptual and Motor Skills*, 23, 1211–1214.
- Daurignac, E., Houde, O., & Jouvent, R. (2006). Negative priming in a numerical Piaget-like task as evidenced by ERP. *Journal of Cognitive Neuroscience*, 18, 730–736.
- Donchin, E., Karis, E., Bashore, T., Coles, M., & Gratton, G. (1986). Cognitive psychophysiology and human information processing. In M. Coles, E. Donchin, & S. Porges (Eds.), *Psychophysiology: Systems, processes, and applications* (pp. 244–267). New York: The Guilford Press.
- Eimer, M. (1993). Effects of attention and stimulus probability on ERPs in a go/nogo task. *Biological Psychology*, 35, 123–138.
- Fox, E. (1995). Negative priming from ignored distractors in visual selection: A review. *Psychonomic Bulletin and Review*, 2, 145–173.

- Frings, C. (2008). Analyzing the relationship between target-to-target and distractor-to-target repetitions: Evidence for a common mechanism. *Quarterly Journal of Experimental Psychology*, 61, 1641–1649.
- Frings, C., & Groh-Bordin, C. (2007). Electrophysiological correlates of visual identity negative priming. *Brain Research*, 1176, 82–91.
- Frings, C., & Wentura, D. (2006). Strategy effects counteract distractor inhibition: Negative priming with constantly absent probe distractors. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 854–864.
- Gibbons, H. (2006). An event-related potential investigation of varieties of negative priming. *Journal of Psychophysiology*, 20, 170–185.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468–484.
- Groh-Bordin, C., Zimmer, H. D., & Ecker, U. K. H. (2006). Has the butcher on the bus dyed his hair? When color changes modulate ERP correlates of familiarity and recollection. *NeuroImage*, 32(4), 1879–1890.
- Heil, M., Osman, A., Wiegmann, J., Rolke, B., & Henninghausen, E. (2000). N200 in the Eriksen-task: Inhibitory executive processes? *Journal of Psychophysiology*, 14, 218–225.
- Houghton, G., & Tipper, S. P. (1994). A model of inhibitory mechanisms in selective attention. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory processes in attention, memory and language* (pp. 53–112). San Diego, CA: Academic Press.
- Johansson, M., & Mecklinger, A. (2003). The late posterior negativity in ERP studies of episodic memory: Action monitoring and retrieval of attribute conjunctions. *Biological Psychology*, 64(1–2), 91–117.
- Kane, M. J., May, C. P., Hasher, L., Rahhal, T., & Stoltzfus, E. R. (1997). Dual mechanisms of negative priming. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 632–650.
- Kathmann, N., Bogdahn, B., & Endrass, T. (2006). Event-related brain potential variations during location and identity negative priming. *Neuroscience Letters*, 394, 53–56.
- Lowe, D. G. (1979). Strategies, context and the mechanisms of response inhibition. *Memory & Cognition*, 7, 382–389.
- Mayr, S., & Buchner, A. (2006). Evidence for episodic retrieval of inadequate prime responses in auditory negative priming. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 932–943.
- Mayr, S., & Buchner, A. (2007). Negative priming as a memory phenomenon: A review of 20 years of negative priming research. *Zeitschrift für Psychologie/ Journal of Psychology*, 215, 35–51.
- Milliken, B., Joordens, S., Merikle, P. A., & Seiffert, A. E. (1998). Selective attention: A reevaluation of the implications of negative priming. *Psychological Review*, 105, 203–229.
- Milliken, B., & Tipper, S. P. (1998). Attention and inhibition. In H. Pashler (Ed.), *Attention* (pp. 191–222). East Sussex: Psychological Press.
- Moore, C. M. (1994). Negative priming depends on probe-trial conflict: Where has all the inhibition gone? *Perception & Psychophysics*, 56, 133–147.
- Neill, W. T. (1977). Inhibition and facilitation processes in selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 444–450.
- Neill, W. T. (1997). Episodic retrieval in negative priming and repetition priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23, 1291–1305.
- Neill, W. T., Terry, K. M., & Valdes, L. A. (1994). Negative priming without probe selection. *Psychonomic Bulletin & Review*, 1, 119–121.
- Ortells, J. J., Abad, M. J. F., Noguera, C., & Lupiáñez, J. (2001). Influence of prime-probe stimulus onset asynchrony and prime precuing manipulations on semantic priming effects with words in a lexical-decision task. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 75–91.
- Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology*, 60(2), 172–185.
- Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology*, 41, 103–146.
- Rothermund, K., Wentura, D., & DeHouwer, J. (2005). Retrieval of incidental stimulus-response associations as a source of negative priming: Evidence from task switching studies. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31, 482–495.
- Tipper, S. P. (1985). The negative priming effect: Inhibitory effects of ignored primes. *Quarterly Journal of Experimental Psychology*, 37A, 571–590.
- Tipper, S. P. (2001). Does negative priming reflect inhibitory mechanisms? A review and integration of conflicting views. *Quarterly Journal of Experimental Psychology*, 54A, 321–343.
- Tipper, S. P., & Cranston, M. (1985). Selective attention and priming: Inhibitory and facilitatory effects of ignored primes. *Quarterly Journal of Experimental Psychology*, 37A, 591–611.
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychological Review*, 111, 931–959.