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Brief article

ERP correlates of auditory negative priming[☆]

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Abstract

Negative priming refers to slowed down reactions when the distractor on one trial becomes the target on the next. Following two popular accounts, the effect might be due either to inhibitory processes associated with the frontal cortex, or to an ambiguity in the retrieval of episodic information. We used event-related brain potentials (ERPs) to identify the processing stage primarily associated with negative priming. In an auditory categorization task, reactions in negative priming trials were compared to reactions in a standard control (unrelated primes and probes) and a repetition control (attended prime = ignored probe) condition. Reactions were slower for negative priming than for standard control (Δ32 ms) and repetition control trials (Δ64 ms). The corresponding ERP effect was reflected in an attenuation of a sustained parietal positivity extending from 300 to 600 ms. Because corresponding ERP components were found to be sensitive to stimulus recognition and familiarity, the results may be interpreted to support an episodic retrieval account of negative priming.

Keywords: Auditory processing; Negative priming; Attention; Event-related brain potentials

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1. Introduction

The negative priming effect refers to the phenomenon of slowed down or more error-prone reactions to a stimulus that had to be ignored recently (Neill, 1977; Tipper, 1985). The standard paradigm consists of two consecutive presentations of pairs of stimuli, called

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prime and probe. In each pair one stimulus has to be attended (target) and the other has to be ignored (distractor). In the negative priming condition the prime distractor becomes the probe target whereas in the control condition primes and probes are usually unrelated. Although most experimental approaches used the visual domain to induce negative priming (Fox, 1995; May, Kane, & Hasher, 1995), the effect is apparently even more pronounced in the auditory modality (Banks, Roberts, & Ciranni, 1995; Buchner & Steffens, 2001).

Negative priming has been discussed primarily within two theoretical frameworks. According to Tipper (Houghton & Tipper, 1998; Tipper, 1985) negative priming is the result of a forward-acting **suppression mechanism**. In order to process an attended target efficiently, representations of competing distractors are actively suppressed in the sense that the processes that mediate between distractor representations and overt responses are inhibited. The processing of an inhibited representation will be impaired when it becomes the subsequent target.

An alternative explanation is the **episodic retrieval account** (Neill & Valdes, 1992; Neill, Valdes, Terry, & Gorfein, 1992). Instead of a forward-acting suppression mechanism based on the processing of the prime, the negative priming effect is assumed to be generated by a backward-acting memory process triggered by the probe episode. In a typical negative priming trial, the probe target is identical to the prime distractor so that the probe target may cue the retrieval of the perceptually similar prime episode. This reinstatement of the previous processing episode is transfer-inappropriate because the requirement to respond to the target conflicts with the retrieved 'no-response' information for this stimulus from the prime episode. Resolving this response competition is time-consuming and slows down reactions.

Physiological measures might be useful to differentiate between the two accounts. For instance, inhibitory processes have often been associated with enhanced frontal event-related brain potential (ERP) activity. For example, enhanced frontal activity has been found in paradigms where the suppression of an inappropriate response was required (Eimer, 1993; Falkenstein, Hoormann, & Hohnsbein, 2002; West & Alain, 2000). Assuming a central suppression mechanism, one could argue that frontal activation would also be associated with negative priming. Indeed, proponents of a central suppression mechanism of negative priming (Houghton & Tipper, 1994, 1998) have already discussed the specific role of the prefrontal lobe for attentional control. In contrast, an episodic memory effect should exhibit a more posterior topography, comparable to the "parietal P3" that has been interpreted as the reflection of context or memory updating processes (Coles & Rugg, 1995). We are aware of only one study investigating the physiological correlates of the negative priming phenomenon (Steel et al., 2001). In the negative priming condition of this fMRI study a widespread cortical network was activated involving left temporal, inferior parietal as well as frontal areas. The activation pattern did not directly falsify any of the possible theoretical accounts of the phenomenon. One purpose of the present study was to extend these findings using an ERP technique which is more suitable to tracking the time course of the mental processes underlying the negative priming phenomenon.

In the present study, reaction times (RT) and ERPs were recorded when participants reacted to a target sound while ignoring a distractor sound.

2. Method

2.1. Subjects

EEG recordings and behavioural data were obtained from 16 persons who were naive as to the purpose of the experiment. One data set was not analyzed because the person had produced excessive error rates. The remaining 15 subjects (eight female, seven male, aged between 19 and 35) had no history of neurological disorders or hearing disabilities.

2.2. Stimuli and procedure

The stimuli were digitized sounds, three of which were played by musical instruments (piano, guitar, and cornet), and three were animal sounds (frog, bird, and hen). Each sound was 300 ms long. The sounds were presented via headphones (KOSS-C35) at approximately 70 dB SPL.

A monaural 20 ms metronome click cue indicated the ear (left or right) at which the to-be-attended sound would be presented. After a 750 ms cue-target interval, the prime pair of sounds (the target sound to the cued ear, the distractor to the other ear) was presented. Subjects reacted by pressing the “animal” or “instrument” key, depending on the category of the target. A sagittal response key arrangement prevented spatial compatibility effects between the target’s location and the required response. Following a 1500 ms interval, the probe cue was presented to the ear opposite to that of the prime cue. The temporal parameters and the subjects’ task were identical for the prime and probe sound pairs. Subjects received no feedback about the correctness of their responses. They initiated the presentation of the next prime-probe pair by an arbitrary key press.

Three basic types of prime-probe trials defined the experimental conditions. In 72 negative priming trials, the ignored prime was repeated as the to-be-attended probe sound; the remaining two sounds differed. In 72 standard control trials, all prime and probe sounds were different. In order to control for ERP effects evoked by stimulus repetition, we introduced 72 repetition control trials in which the previously attended sound became the to-be-ignored sound in the probe; the remaining two sounds differed.

The 216 negative priming, standard control, and repetition control trials were parallel in that the response categories of the prime target and distractor were different (Buchner, Zabal, & Mayr, in press). Due to the nature of the negative priming trials, the same was true for the attended prime and probe response categories. To control for response bias, 216 filler trials were included in which the prime and probe target categories were identical. Examples of the stimulus configuration are given in Fig. 1.

The sequence of 432 trials (72 negative priming, 72 standard control, 72 repetition control, and 216 filler) was random. Within the restrictions outlined above, prime and probe sounds were selected randomly. Post-hoc analyses showed that the frequencies of individual sounds as well as their combinations were approximately equal in the three experimental conditions. The instructions emphasized correctness, but reactions were also to be made as quickly as possible. To reduce false classifications of sounds, 48 trials were presented in a training session preceding the main experiment.

	Prime	*Probe*
Negative Priming:	L: Frog **R: Piano**	**L: Frog** R: Trumpet
Standard Control:	L: Bird **R: Piano**	
Repetition Control:	L: Bird **R: Trumpet**	
Filler Trials Repetition:	L: Trumpet **R: Bird**	
Filler Trials Standard:	L: Piano **R: Bird**	

Fig. 1. Stimulus configuration examples for the different experimental conditions. Depicted are parallel trials which share the same probe pair but vary in the construction of the prime pair. The target sound is printed in bold font, the distractor sound in normal font. The single letters "L" and "R" indicate the ear (left, right) to which the sound was presented. Technical details of auditory presentation are given in the text.

2.3. EEG recording and data analysis

An elastic cap with predefined electrode positions (Falk-Minow-Services, Munich) was mounted on the subject's head. The 30 active silver-silver chloride electrodes were referenced to linked mastoids, with impedance kept below 5 kOhm. Vertical and horizontal EOGs were recorded to control for ocular artefacts. Biosignals were recorded continuously (EEG-8 amplifiers, Contact Precision Instruments, London), sampled at 250 Hz, and online band pass-filtered (0.03–200 Hz). Offline, EEG data were segmented according to the sound onset in each trial (−100–1000 ms epoch length), filtered (0.5–40 Hz, −48 dB cut-offs), and baseline corrected (−100–0 ms). Single EEG sweeps containing muscular or ocular (vEOG, hEOG) artefacts were excluded from the analysis. The remaining sweeps were averaged according to the stimulus type (prime, probe), experimental condition, and electrode position. ERP responses evoked in filler trials, as well as the ERPs evoked by primes will not be discussed in detail, but note that prime ERPs did not differ between experimental conditions.

Based on the grand-averaged ERPs, four time windows were determined (80–130, 250–300, 300–450, and 450–600 ms) which represented distinct transient components (N1 complex, frontal negativity (FN), and late positive complex) and the time course of a sustained ERP effect. Mean reference-to-baseline amplitudes within these windows were computed for each subject, experimental condition, and electrode. Topographical effects were considered by splitting the electrodes according to the spatial factors 'caudality' (anterior, central, posterior), and 'laterality' (left, middle, right).

2.4. Design

The main independent variable for the behavioural data was the experimental condition (negative priming, standard control, repetition control). For the ERP data, the design also included electrode position caudality (anterior, central, posterior) and laterality (left, middle, right) as independent variables. This $3 \times 3 \times 3$ design with condition, caudality, and laterality as independent variables was considered separately for the four different time windows (see previous paragraph).

3. Results

Only responses for trials with both correct prime and probe reactions were analyzed. A repeated measures analysis of variance was used for the within-subject comparisons, using the Greenhouse–Geisser epsilon estimate to compensate for sphericity violations. For both RT and ERP data, the overall F-tests yielded significant differences among the three experimental conditions. For the simplicity of presentation, we will therefore focus on direct comparisons of two levels of the condition variable (t values for the two-tailed testing are reported). For ERP data, significant interactions of condition and electrode position (caudality and/or laterality) are reported only if the effect was confirmed at an electrode cluster by post-hoc comparisons.

3.1. Behavioural data

Mean RT was longer in the negative priming than in the standard control condition, and was shortest in the repetition control condition (see Fig. 3). The negative priming and standard control conditions differed significantly ($t(14) = 3.20$, $P < 0.01$), as did the standard and repetition control conditions ($t(14) = 4.63$, $P < 0.01$). At a descriptive level, the pattern was similar in the mean error rates that were largest in the negative priming condition (8.67%), intermediate in the standard (6.45%), and lowest in the repetition control conditions (5.04%). Differences were significant between the negative priming and repetition control conditions ($t(14) = 2.37$, $P < 0.05$). Mean RTs and error rates of the prime reactions did not differ significantly between experimental conditions.

3.2. ERP data

Grand-averaged ERPs evoked by the probe sounds are depicted in Fig. 2. In line with previous ERP findings (Näätänen, Sams, Alho, & Paavilainen, 1988), auditory stimulation evoked a transient negative peak at 100 ms (N1), followed by a positivity peaking at about 180 ms (P2). At fronto-central leads, the transient components were followed by a slow negative wave extending from 200 to 800 ms post stimulus onset, including a local negative maximum between 250 and 300 ms (FN). At centro-parietal leads, the negative wave returned to baseline at about 450 ms, and was then released by a late positive component (LPC) extending up to 900 ms.

As mentioned above, the statistical analysis comprised the three pairwise comparisons of experimental conditions, separately for the temporal ERP epochs. For the N1 component, when negative priming and standard control were used as the two levels of the experimental condition variable, the latter interacted with electrode caudality ($F(2, 28) = 7.57$, $P < 0.01$). Post-hoc tests revealed a significant amplitude reduction in the negative priming condition at frontal leads ($t(14) = 2.31$, $P < 0.05$; see Fig. 3).

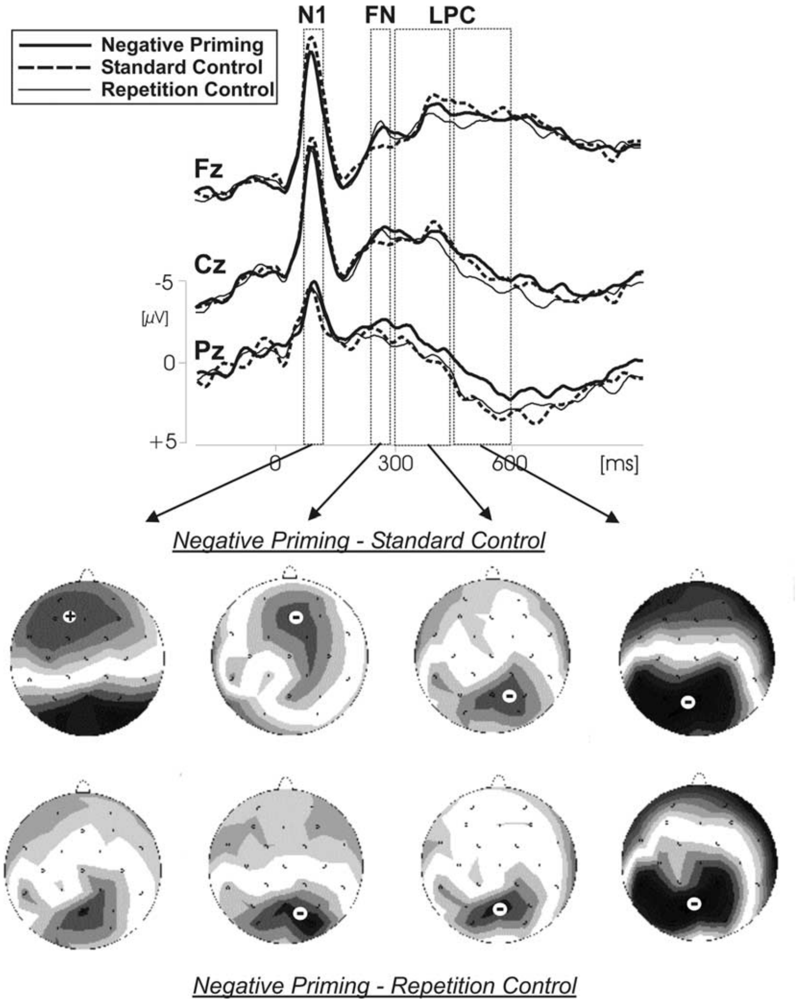

Fig. 2. Grand average ERPs ($n = 15$ subjects) evoked in the three experimental conditions (top part), and the average-referenced topographic maps referring to selected time windows (bottom part). The ERP traces recorded at frontal (Fz), central (Cz), and parietal (Pz) sites are superimposed for 'negative priming' (solid trace), and the control conditions 'standard' (dashed) and 'repetition' (dotted). Analysis focuses on the N1 component (80–130 ms), a transient frontal negativity (FN: 250–300 ms), and the early and late part of a late positive complex (LPC: early 300–450 ms; late 450–600 ms). The maps illustrate the topographical distribution of ERP effects associated with negative priming within the aforementioned time windows. The top row refers to the spatial distribution of the difference waves computed between negative priming and the standard control, and the bottom row to the corresponding difference between negative priming and the repetition control.

No effects were found when negative priming was compared to repetition control. Differences between the control conditions also depended on electrode caudality ($F(2,28) = 4.95$, $P < 0.05$), primarily reflecting a significant anterior reduction for the repetition control ($t(14) = 2.36$, $P < 0.05$). The spatial distribution of the N1 (as well as

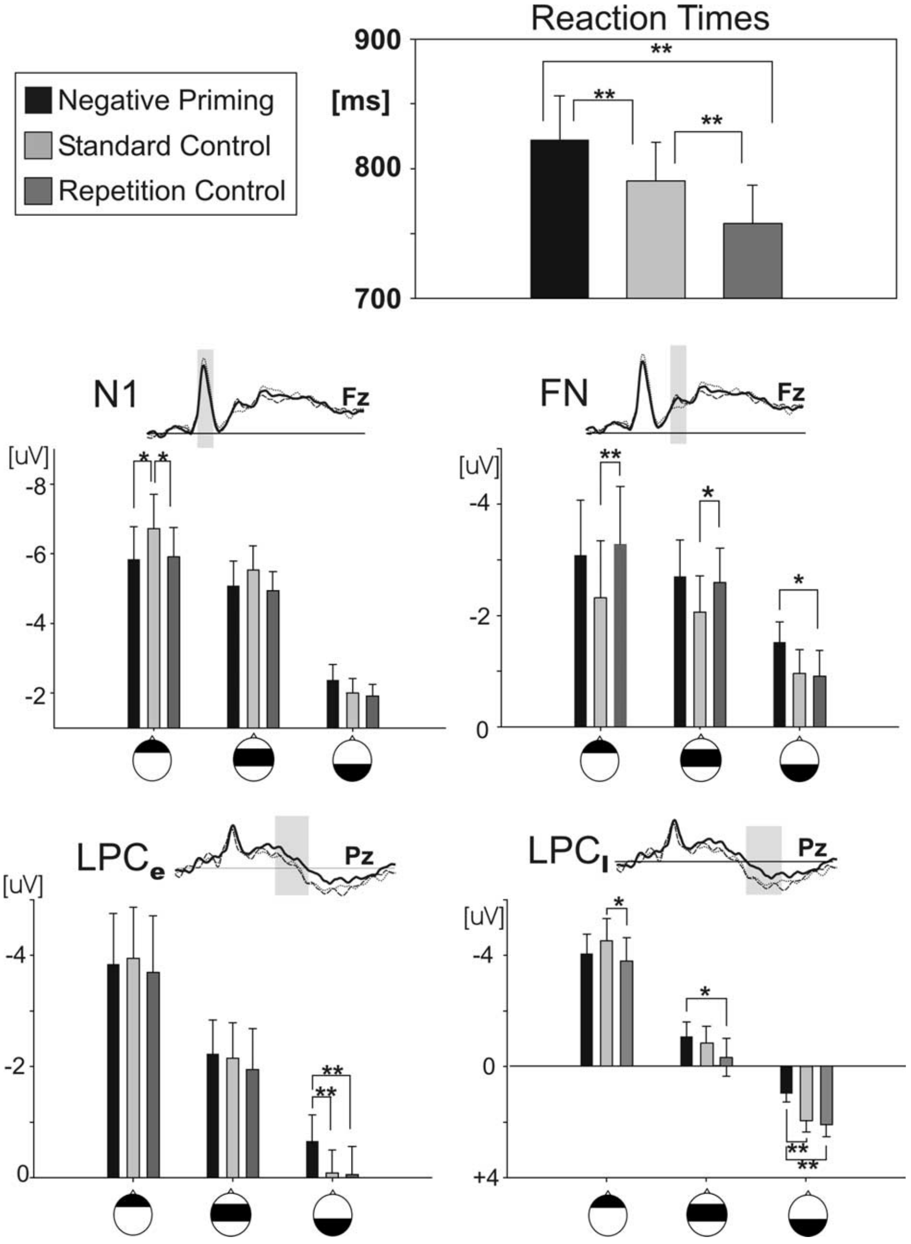

Fig. 3. Bar diagrams summarizing RT means and ERP amplitude effects. The top row diagram shows the response slowing in the negative priming as compared to the control conditions. In the middle and bottom rows, mean ERP amplitudes are separated according to the caudality of the electrode location, and significant differences between experimental conditions are indicated by an asterisk (*$P < 0.05$, **$P < 0.01$). The grey bar in the ERP sample trace indicates the time window analyzed, and icons at the *x*-axis the caudal position. Error bars in the diagram depict the standard errors of the means.

the other components) is illustrated in the average-referenced topographical maps reflecting the difference waves (*Negative Priming–Standard Control* and *Negative Priming–Repetition Control*; Fig. 2).

Within the 250–300 ms time window, negative priming ERPs were slightly enhanced but did not differ significantly from the standard control. The difference between the negative priming and repetition control conditions depended on electrode caudality ($F(2, 28) = 4.45$, $P < 0.05$). Post-hoc tests revealed an enhanced posterior negativity for negative priming ($t(14) = 2.22$, $P < 0.05$). The difference between the two control conditions also depended on electrode caudality ($F(2, 28) = 10.99$, $P < 0.01$), and was primarily due to an enhanced FN in the repetition control ($t(14) = 3.34$, $P < 0.01$) that extended to medial leads ($t(14) = 2.26$, $P < 0.05$).

The 300–600 ms LPC was bisected into $\mathrm{LPC_e}$ (late positive complex, early: 300–450 ms), and $\mathrm{LPC_l}$ (late positive complex, late: 450–600 ms). The $\mathrm{LPC_e}$ already differentiated between negative priming and the control conditions. The difference between the negative priming and standard control conditions depended on electrode caudality ($F(2, 28) = 6.66$, $P < 0.05$), indicating that the mean amplitude was more negative in the negative priming condition at posterior sites ($t(14) = 3.22$, $P < 0.01$). Similarly, the difference between the negative priming and repetition control conditions depended on electrode caudality ($F(2, 28) = 4.72$, $P < 0.05$), and was due to a greater negativity in the negative priming condition at posterior leads ($t(14) = 3.35$, $P < 0.01$). ERPs did not differ between the two control conditions.

The ERP effect that characterized the negative priming condition in the $\mathrm{LPC_e}$ was also observed in the $\mathrm{LPC_l}$. The difference between the negative priming and standard as well as the repetition control conditions depended on electrode caudality ($F(2, 28) = 12.25$, $P < 0.01$ and $F(2, 28) = 8.54$, $P < 0.01$, respectively). When compared to the standard and repetition control conditions, the negative priming condition was associated with a less positive wave at posterior leads ($t(14) = 4.35$, $P < 0.01$ and $t(14) = 3.32$, $P < 0.01$, respectively). The difference between the negative priming and repetition control conditions was also significant at medial positions ($t(14) = 2.52$, $P < 0.05$). ERP differences between the control conditions depended on caudality ($F(2, 28) = 3.70$, $P < 0.05$), and were primarily due to an enhanced FN for the standard control condition ($t(14) = 2.40$, $P < 0.05$).

4. Discussion

The present results can be summarized as follows. (1) Responses were slower when an attended sound was previously ignored, that is, a typical negative priming effect was observed. (2) Responses were faster when a distractor was previously attended. (3) Irrespective of the behavioural effect, stimulus repetition of any form (first ignored and then attended or vice versa) attenuated the auditory N1 component, and increased the FN component. (4) Electrophysiological correlates that were unique to the negative priming condition were confined to posterior electrodes, and were reflected in a diminished late positive complex starting at about 300 ms.

Auditory negative priming as reflected in an increased RT for previously ignored sounds confirms previous findings using a similar experimental paradigm (Buchner & Steffens, 2001). The decreased RTs in the repetition control have also been observed in similar negative priming studies (Kane, Hasher, Stoltzfus, Zacks, & Connelly, 1994; Lowe, 1979; Neill, 1978).

Assuming a flexible inhibition mechanism, one could expect the sensory processing of a previously ignored prime to be suppressed. Such sensory suppression has been described previously for the processing of visual motion stimuli (Valdes Sosa, Bobes, Rodriguez, & Pinilla, 1998). However, the auditory N1 component observed in the present study was attenuated in the negative priming as well as repetition control condition. This result is in line with an adaptation effect reported previously (Näätänen et al., 1988) demonstrating that the N1 is the smaller the more the consecutive auditory stimuli resemble each other. Consequently, negative priming is unlikely to be due to a process of sensory suppression.

The topography and latency of the FN are similar to those of anterior ERPs observed in other paradigms in which these ERP components were thought to be related to central inhibitory processes. Enhanced frontal activity has been elicited in NoGo or Stroop tasks (Eimer, 1993; Falkenstein et al., 2002; West & Alain, 2000) when the suppression of an inappropriate response was required. A similar ERP response accompanied the processing of auditory distractors (Schroeger, Giard, & Wolff, 2000). However, in our study neither the transient (250–300 ms) nor the sustained (300–600 ms) segment of the frontal wave was uniquely related to the negative priming condition. Negative priming shared the frontal activation pattern with the repetition control condition – in which we observed faster responding. Therefore, these data are incompatible with the assumption that negative priming is sufficiently explained in terms of a central inhibition mechanism located in the prefrontal cortex (Fuster, 1997).

The only ERP effect that was uniquely related to negative priming was a late posterior complex which shares polarity, time course, and topography of an ERP effect obtained in studies on recognition memory (Rugg & Doyle, 1994). The so-called "old/new" ERP effect denotes a more positive-going parietal ERP extending from 300 to 800 ms following the onset of an "old" compared to a "new" item. The enhancement of the positive ERP effect was found to co-vary with the quality of information retrieved from episodic memory (Wilding, 2000), and is therefore commonly related to an increase in an event's relative familiarity (Rugg & Allan, 2000; Rugg & Doyle, 1994). Greater familiarity, in turn, has been associated with more fluent processing of an event (Johnston, Dark, & Jacoby, 1985).

In our experiment, stimulus familiarity was generally high because only six different auditory stimuli were presented repeatedly throughout. Therefore, partial stimulus repetition from prime to probe – as in the repetition control or negative priming condition – was per se not expected to be sufficient to increase the baseline familiarity of the stimuli, and to induce an old/new ERP effect.

This expectation was fulfilled in the repetition control condition which did not differ from the standard control with respect to the LPC. In contrast, the repetition of a previously ignored stimulus (negative priming condition) evoked a less positive-going complex. This suggests that the processing of a previously ignored stimulus is functionally equivalent to the less fluent processing of a novel stimulus. The topographic distribution and the sustained temporal characteristics of the negative priming LPC effect might be interpreted to support a memory-based account.

However, lower-than-baseline familiarity in the negative priming condition could also be induced by other mechanisms. For example, a comparable effect might result from a persisting inhibition of the probe target being activated during the processing of this stimulus as the prime distractor. Nevertheless, it does seem that the concept of a *frontal* inhibition process is not compatible with the present data.

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