



An electrophysiological signature for proactive interference resolution in working memory[☆]

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ABSTRACT

We used event-related potentials (ERPs) to study the temporal dynamics of proactive interference in working memory. Participants performed a Sternberg item-recognition task to determine whether a probe was in a target memory set. Familiar negative probes were found to be more difficult to reject than less familiar ones. A fronto-central N2 component peaking around 300 ms post-probe-onset differentiated among target probes, familiar and less familiar non-target probes. The study identifies N2 as the ERP signature for proactive interference resolution. It also indicates that the resolution process occurs in the same time window as target/non-target discrimination and provides the first piece of electrophysiological evidence supporting a recent interference resolution model based on localization data [Jonides, J., Nee, D.E., 2006. Brain mechanisms of proactive interference in working memory. *Neuroscience* 139, 181–193].

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1. Introduction

Proactive interference (PI) occurs when memories acquired earlier impair recall or recognition of memories acquired more recently (Keppel and Underwood, 1962). It used to be a central topic in memory research, extensively studied both in short-term and long-term memory. As a determinant of working memory capacity, it is also important to higher cognitive functions that depend on working memory (Just and Carpenter, 1999).

Monsell (1978) designed a “recent-probe” paradigm to effectively measure and study proactive interference in working memory. In this paradigm, participants perform a Sternberg memory-scanning task to determine if a probe is in a set of target items they hold in mind. Critically, the probe familiarity is manipulated to be either high or low, depending on whether or not it is drawn from recent previous trials'

memory sets. PI is observed as a delayed response in rejecting familiar non-target probes, relative to less familiar non-target probes.

With this paradigm, Jonides et al. (1998) made the first attempt to examine proactive interference with modern brain imaging techniques and identified the left inferior frontal gyrus as a neural substrate for such interference resolution. This finding has been replicated in several later studies either with the same paradigm (D'Esposito et al., 1999; Bunge et al., 2001; Thompson-Schill et al., 2002; Mecklinger et al., 2003; Postle and Brush, 2004; Badre and Wagner, 2005), or with a different one involving directed-forgetting (Zhang et al., 2003a).

Recently, Jonides and Nee (2006) reviewed the current imaging evidence and proposed a biased-competition model for proactive interference resolution. In this model, a probe is classified as a target or a non-target based on evaluation of attributes associated with its representation, including familiarity codes and context codes. High familiarity non-targets elicit interference in this evaluation process due to attribute inconsistency, as familiarity codes call for a positive response but context codes for a negative response. The interference is resolved through biasing evaluation to weight more on the appropriate context codes and less on the inappropriate familiarity codes.

The present study was intended to test this model with the high temporal resolution event-related potential (ERP) technique. Specifically, we examined a central claim of the model that proactive interference is resolved in the same evaluation process that distinguishes between positive and negative probe items. To support this claim, one would

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predict the electrophysiological correlate of proactive interference to occur in the same time window when the positive and negative probes are differentiated. It would be difficult, if not impossible, to test such a prediction with function MRI at its present temporal resolution.

Our task followed that in Zhang et al. (2003a) where participants held an initial set of four letters in mind and were then instructed to ignore two of them and remember the remaining two as the target set. Later, they judged whether or not a probe was in the target set. The probe was in the memory set for the *Yes* trials (requiring a positive response), but not in the set for the *No* or *Lure* trials (both requiring a negative response). The *Lure* condition, with probes drawn from recently ignored letters, resembles the “high-familiarity recent-negative” condition in Jonides et al. (1998). For the *No* condition, the probes did not appear in the initial memory set, making this condition resemble their “low-familiarity non-recent negative” condition. Proactive interference was indexed as delayed response to probes in the *Lure* condition than in the *No* condition, as shown in Zhang et al. (2003a).

Several ERP studies using variants of the Sternberg task showed that there are at least two components sensitive to the distinction between *Yes* and *No* trials. Kramer et al. (1991) reported a delayed and smaller parietal P3 for negative probes relative to positive probes, as well as a larger frontal negativity (N340). The same effect on P3 amplitude was also found in our previous study (Zhou et al., 2004) which, in addition, documented without further analysis an enhanced anterior N2 for the negative trials relative to positive trials. This negative deflection seems to resemble a N270 component that Wang and colleagues found to be associated with mismatch detection under a variety of task settings (Wang et al., 2004; Zhang et al., 2003b).

It is more difficult to identify a priori the ERP component that would be sensitive to proactive interference in working memory as the present study seems to be the first one of its kind. In long-term memory research, we have only found two ERP studies on proactive interference, which used the paired-association paradigm and reported a more pronounced positive deflection in the P3 latency range for the interference condition, relative to the control condition (Uhl et al., 1990; Rößner et al., 1999).

2. Methods

2.1. Participants

Eighteen college students (mean age=23.2 years, 8 male) from Beijing Normal University (Beijing, China) were recruited. All were right-handed with normal or corrected-to-normal vision. None of them reported any neurological or psychiatric diseases. Informed consent was obtained in accordance with guidelines from the Institute of Psychology, the Chinese Academy of Sciences, Beijing. Data from four participants were discarded because of excessive number of trials contaminated by eye blinks and other artifacts.

2.2. Stimuli and procedure

Participants were seated in a dimly lit and sound-attenuated room. All visual stimuli were in black with a white background, presented on a computer monitor that was about 1 m away, subtending a visual angle of $7.7^\circ \times 7.2^\circ$. Participants were instructed to remain relaxed and to minimize motion-related artifacts throughout the experiment.

All participants completed 7 blocks, each with 40 trials. The first block served for practice and was excluded from data analysis. The procedure mainly followed that of Zhang et al. (2003a). As in Fig. 1, each trial started with a 2000-ms preparation screen with a small central square dot, followed by a study display presented for 1000 ms. A 500-ms fixation cross display was then shown, followed by a 500-ms cue display. There was another 1500-ms fixation display

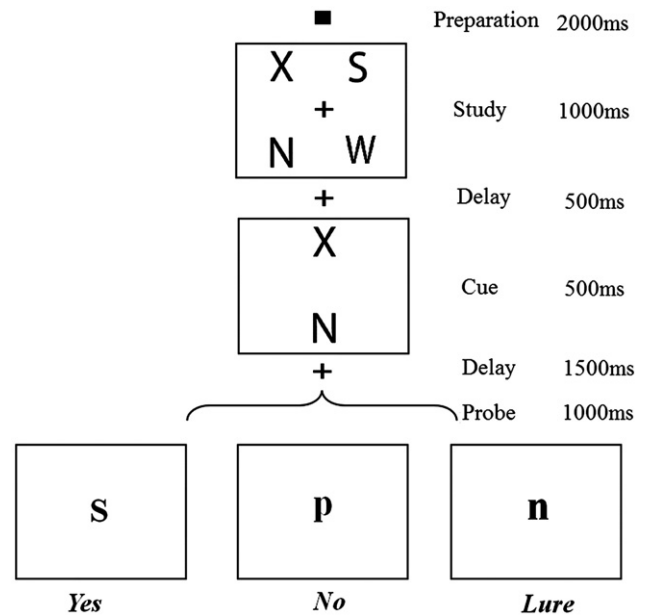


Fig. 1. Illustration of the task and conditions with a sample trial. Participants saw four consonant letters ('X N S W') in the study display and were then cued to ignore two of them ('X N') and focus on remembering the rest two ('S W') as the memory set. They responded to a probe by deciding whether it was a member of the memory set. In the *Yes* condition, the probe ('s') was in the memory set, in the *No* condition, it ('p') was not. In the *Lure* condition, the probe ('n') was not in the memory set but drawn from the recently ignored cue letters.

after cue offset and before probe onset. The probe letter would be turned off as soon as participants responded or at the end of a 1000-ms response window. Following probe offset, a fixation cross was displayed for 1000 ms before the next trial started.

Participants were told to remember the four letters in the study display (e.g., 'X N S W') before they saw the two cue letters (e.g., 'X N'), which were always the same as either the left or the right two study letters with equal probability. Upon cue onset, they were to ignore the cue letters and hold only the remaining two letters (e.g., 'S W') as the final memory set. They then judged if the probe letter (e.g., 'n') was in the final memory set or not. Both response speed and accuracy were emphasized. Each participant used one thumb to press a button indicating a *Yes* response and a different thumb to press a different button indicating a *No* response. The mapping between *Yes/No* responses was counterbalanced across subjects.

Drawn from a pool of 21 consonants, all letters were presented in upper-case except the probe letter which was in lower-case. For *Yes* trials, the probe was randomly picked from the two letters in the final memory set. For *No* trials, the probe was not among the four study letter. For *Lure* trials, the probe was randomly picked from the cue letters. All letters in any trial would not repeat in the immediately preceding or following trials. There were 20 *Yes* trials, 10 *No* trials and 10 *Lure* trials in each block, randomly intermixed.

2.3. Recording system and data analysis

EEG was recorded from the scalp through 64 non-polarizable Ag/AgCl sintered electrodes in pre-configured caps, with a 500 Hz sampling rate using the Neuroscan EEG system. The sites of electrodes followed the extended 10–20 convention. Mean of both mastoids was used as reference and AFz as ground. Bandwidth ranged from 0.05 to 40 Hz. The horizontal EOG was recorded at the outer canthi of both eyes and the vertical EOG recorded between supraorbit and suborbit of the left eye. Impedance in all electrodes was below 8 k Ω . Data inspection and artifact rejection were performed offline. Eye movement artifacts were removed using regression-based weighting

coefficients. Epochs with amplitudes exceeding $\pm 80 \mu\text{V}$ in any channel were excluded with an automated procedure. Only waveforms from behaviorally correct trials were analyzed. ERPs were calculated offline and separately for each of the three types of trials with 1600 ms epochs starting 200 ms before probe onset. Mean reaction time (RT) and error rate were analyzed using a repeated-measure one-way ANOVA with trial type as the factor. Only correct trials were included in RT analysis.

3. Results

3.1. Behavioral data

The mean RTs averaged over all fourteen valid participants were 588 ms (SD=3.8), 612 ms (SD=5.3), and 659 ms (SD=5.4) for the *Yes*, *No*, and *Lure* conditions, respectively. The corresponding error rates were 7.3% (SD=0.5), 2.5% (SD=0.8), and 5.0% (SD=0.8). ANOVA on RT revealed a significant main effect of trial condition ($F(2, 26)=35.72$, $p<0.0001$). Post-hoc comparisons indicated that *No* trials were slower than *Yes* trials (612 vs. 588 ms, $t(13)=3.16$, $p<0.005$), and *Lure* trials were slower than *No* trials (659 vs. 612 ms, $t(13)=5.80$, $p<0.0001$). For error rates, there was a significant main effect of trial condition ($F(2, 26)=12.81$, $p<0.01$), with *Yes* trials being less accurate than *No* trials (7.3% vs. 2.5%, $t(13)=5.0$, $p<0.0001$) and *Lure* trials being less accurate than *No* trials (5.0% vs. 2.5%, $t(13)=2.27$, $p<0.05$).

3.2. Electrophysiological data

Grand average potentials over fourteen participants, as depicted in Fig. 2, revealed in most electrode sites a sequence of positive and negative deflections, which we identified as the N1, P2, N2, and P3 components. As modulations of these components by trial condition, central to our interest, were mostly seen in the fronto-central regions, we conducted ANOVA on representative electrodes in these regions (except for P3, see below). Note the anterior N1 and P2 components seen here may be different from those observed in occipital regions in the literature.

Repeated-measure ANOVAs with Greenhouse–Geisser correction were performed on the amplitudes of N1, P2, and N2, with trial type

(*Yes*, *Lure*, and *No*), laterality (left hemisphere, midline, and right hemisphere), and gradient (frontal: F3, Fz, F4; fronto-central: FC3, FCz, FC4; and central: C3, Cz, C4) as factors. Results related to the laterality factor were omitted as it did not interact with the *No* vs. *Lure* comparison that defined proactive interference as our central interest. For P3, both the laterality and gradient factors were omitted. Examining only the trial type factor, repeated-measure one-way ANOVAs were conducted on P3 amplitude and latency using six parietal electrodes (Pz, P3/4, CPz, and CP3/4) where this component is known to be most evident. All amplitudes were measured relative to the pre-stimulus baseline.

3.3. N1

The mean amplitude of N1 was measured in the 80–120 ms time window. There were only two main effects on trial type and gradient ($F(2, 26)=6.60$, $p<0.01$; $F(2, 26)=12.53$, $p<0.001$) but not any interaction effects ($F_s<1$). Post-hoc comparisons showed reduced N1 in *Lure* trials relative to *No* trials (-0.51 vs. $-1.56 \mu\text{V}$, $t(13)=4.28$, $p<0.001$) but no difference between *Yes* and *Lure* trials (-1.01 vs. $-0.51 \mu\text{V}$, $t(13)=1.48$, $p>0.1$), between *Yes* and *No* trials (-1.01 vs. $-1.56 \mu\text{V}$, $t(13)=2.08$, $p=0.06$).

3.4. P2

The positively going waveform following N1 was identified as P2 whose mean amplitude was measured from the 150–200 ms time window. There was a main effect for trial type ($F(2, 26)=4.83$, $p<0.05$) and for gradient ($F(2, 26)=9.1$, $p<0.005$) but the two did not interact ($F<1$). *Lure* trials showed a larger amplitude than did *Yes* trials and *No* trials (5.61 vs. 4.89 μV , $t(13)=2.51$, $p<0.05$; 5.61 vs. 4.55 μV , $t(13)=3.16$, $p<0.01$), but there was no difference between *Yes* and *No* trials (4.89 vs. 4.55 μV , $t(13)=0.84$, $p>0.1$).

3.5. N2

N2 was identified as the most negatively going peak in the latency range of 250–300 ms with mean amplitude averaged over the 200–350 ms time window. There was a main effect for trial type

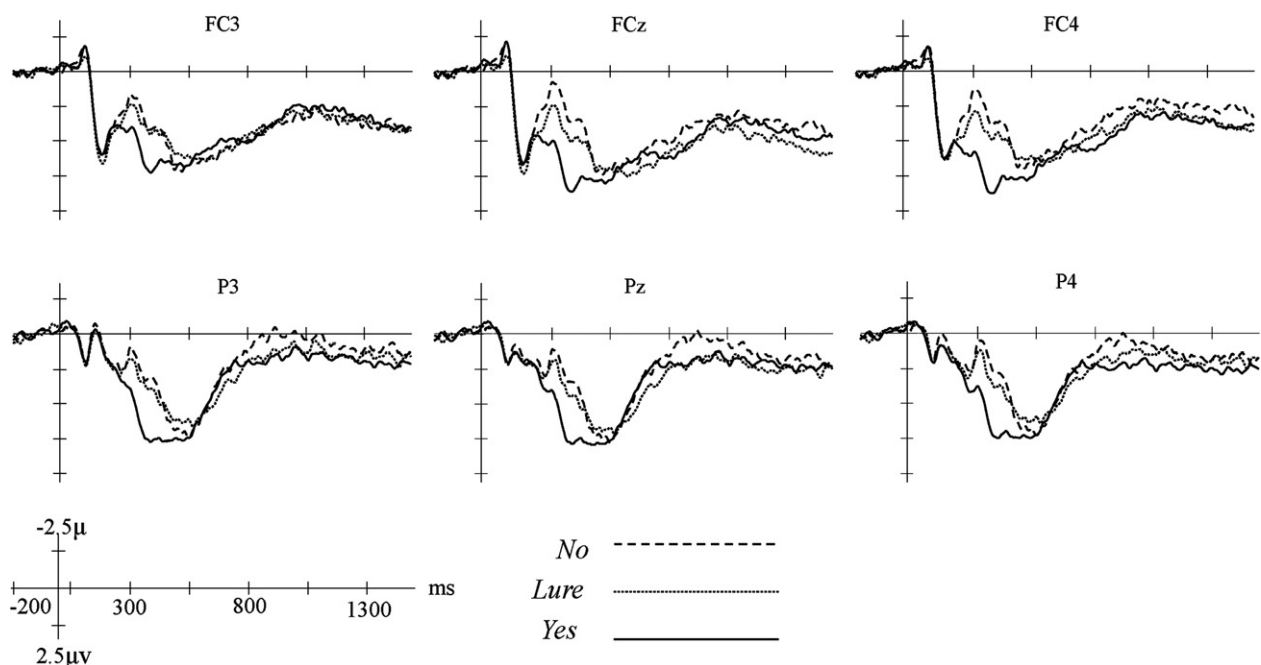


Fig. 2. Grand average of ERPs associated with response to the probes in the *Yes*, *No*, and *Lure* conditions at six representative electrode sites in fronto-central and parietal regions.

($F(2, 26)=11.03, p<0.0001$) but not for gradient or their interaction ($F_s<1$). N2 showed a larger negative shift for *No* trials than for *Lure* and *Yes* trials (2.31 vs. 3.64 μV , $t(13)=3.40, p<0.005$; 2.31 vs. 4.70 μV , $t(13)=3.73, p<0.005$). Difference between N2 amplitude for *Lure* and *Yes* trials also reached significance (3.64 vs. 4.70 μV , $t(13)=2.28, p<0.05$).

3.6. P3

P3 peak was defined as the maximum positive point in the waveform during the 300–600 ms period and its mean amplitude was averaged over a 120-ms time window centered at the peak. The trial type effect was significant on P3 latency ($F(2, 26)=10.63, p<0.001$) but not on P3 amplitude ($F(2, 26)=1.63, p>0.1$). The latency was significantly shorter for *Yes* trials than for both *No* (407 vs. 503 ms, $t(13)=3.98, p<0.005$) and *Lure* trials (407 vs. 482 ms, $t(13)=3.33, p=0.005$).

4. Discussion

The behavioral results replicated the Zhang et al. (2003a) study in finding a clear proactive interference effect, i.e., response to probes in the *Lure* condition was significantly slower than in the *No* condition (659 vs. 612 ms). Error rate effect showed a consistent pattern (5.0% vs. 2.5%). That the *Yes* responses were significantly faster than the *No* responses (588 vs. 612 ms) is typical in the Sternberg task literature, often explained with a serial memory scanning process (Sternberg, 1966). The higher error rate for the *Yes* trials relative to the *No* trials (7.3% vs. 2.5%) may result from confusion between the study set and the cue set caused by retroactive interference. Such confusion, however, would have had little effect on the *No* trials where the probe was out of either set.

The ERP data shows that, shortly after the probe onset, the brain already differentiated between the *No* and the *Lure* trials, with an amplitude reduction in N1 around 100 ms and an amplitude increase in P2 around 175 ms. Such a positive shift of the N1–P2 complex may be related to attentional suppression of *Lure* probes that were actively ignored just recently and became no-longer relevant, as found in some previous studies (Alho et al., 1987; Filipović et al., 2000). That there was no significant difference between the high-familiarity *Yes* and the low-familiarity *No* trials suggests an absence of familiarity effect at this early stage. This interpretation needs confirmation in future research as it implies that the *Lure* trials should differ from the *Yes* trials as well. However, this was statistically true only for P2 but not for N1.

As expected, both N2 and P3 showed differentiation between the *Yes* and the *No* trials, and are thus interpreted to be involved in classifying probes as target or non-target. The N2 component, prominent in fronto-central areas, showed a significantly larger amplitude for the *No* condition than for the *Yes* condition, as in Kramer et al. (1991), Wang et al. (2004), and Zhou et al. (2004) described in the introduction. Its latency was 300 ms, in the same range of the N270, N350 reported in these studies.

The P3 component, prominent in parietal area where it is typically observed, peaked significantly later in the *No* condition than in the *Yes* condition. This P3 effect was only on latency, therefore similar but not identical to those in other studies. While Kramer et al. (1991) found P3 both smaller and delayed for negative trials, Zhou et al. (2004) only found an amplitude effect. It remains to see which factors are important for a latency effect and which for an amplitude effect. One such factor may be task complexity. The Zhou et al. (2004) study, although not focusing on *Yes/No* differences, adopted a Sternberg task highly comparable to the present one. Both used letter sets presented visually and simultaneously. Both used a memory set of two letters and a target-probe delay interval around 1500 ms. Therefore, the different effects observed may be due to the introduction of *Lure* probes in the present experiment which could have affected processing of the *No* probes and produced a processing delay.

The novel and more critical result is that the N2 amplitude was significantly smaller for the *Lure* trials than for the *No* trials. This suggests that the N2 component was sensitive to the distinction between these two types of negative trials and therefore related to proactive interference. The ERP waveforms for the *Lure* and the *No* trials converged totally in P3, indicating that PI was fully resolved within the time window of N2. Examination of the stimulus-locked Lateralized Readiness Potential (LRP) results did not reveal any significant differences in onset time (an index for response competition) between these two conditions, excluding the possibility that PI arose at the level of response selection.

Briefly, N2, while sensitive to target/non-target discrimination, was also indicative of PI resolution. This pattern of results supports the biased-competition model (Jonides and Nee, 2006) described in the introduction which predicts that the PI resolution involves the same pre-response evaluation process for target/non-target discrimination.

The model also accounts for the result that the N2 amplitude for the *Lure* trials was in between that of the *No* and *Yes* trials. According to the model, the probe was evaluated based on two memory attributes, familiarity and context codes. The *Yes* probes, eliciting a smaller N2, were associated with high familiarity and appropriate context codes, and the *No* probes, eliciting a larger N2, were associated with low familiarity and inappropriate context codes. The *Lure* probes, being half like the *Yes* probes (high familiarity) and half like the *No* probes (appropriate context codes), was evaluated under the influence of the two attributes towards opposite directions and therefore elicited a compromised N2 with intermediate amplitude. As times went on and the evaluation process was biased to weight more on the correct context codes, the waveform of the *Lure* trials eventually merged with that of the *No* trials, indicating complete disregard of influence from familiarity and the resolution of PI.

Although we explain the results with the evaluation process to resolve code incompatibility, the N2 effect is also predicted by the degree of mismatch. That is, the N2 amplitude gets increasingly larger from the *Yes* probes matching on both code recency (i.e., familiarity) and context relevance, the *Lure* probes matching on recency but not context, to the *No* probes matching on neither. This suggests that our N2 may be functionally identified with the anterior N270 reported by Wang and colleagues (Wang et al., 2004; Zhang et al., 2003b), which is elicited by non-targets and considered to reflect mismatch detection. In contrast, our N2 should be distinguished from a 'N2c' component in other studies (e.g., Ritter et al., 1979; Hillyard and Münte, 1984) which has posterior scalp distribution and is primarily elicited by targets or target features (see Folstein and Van Petten, 2008 for a detailed discussion).

One issue to be addressed in future research is to examine how to relate the present interpretation of N2 to another account of N2 as index for inhibition (Heil et al., 2000; Ramautar et al., 2006) or conflict-monitoring (Nieuwenhuis et al., 2003; Yeung and Matthew, 2004). In those contexts, a larger N2 is typically observed for conditions involving inhibition or conflict. Such a condition in the present study, the *Lure* condition, however, elicited a smaller N2. Another issue is to examine whether our results are specific to verbal materials as proactive interference can be modality-dependent (Leung and Zhang, 2004).

5. Conclusion

The present ERP study examined the temporal profile of proactive interference in working memory using a Sternberg item-recognition task and identified a fronto-central N2 component as its electrophysiological correlate. With similar scalp distribution and eliciting conditions, this component resembles a previously reported N270 component considered to reflect mismatch detection. The data show that proactive interference occurs in the same time window where targets and non-targets are discriminated and its resolution seems to

involve biased-competition between two kinds of memory attributes. Such results are consistent with and therefore provide the first piece of ERP evidence for a model of proactive interference resolution (Jonides and Nee, 2006) that has been primarily developed from brain imaging data focusing on functional localization.

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