

Neural correlates of adaptive cognitive control in working memory

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Abstract

Conflicts in working memory (WM) can occur when retrieval cues activate competing items, which impairs the efficiency of retrieval. It has recently been shown that WM retrieval adapts similarly to these conflicts as predicted by conflict monitoring theory for selective attention tasks. Here, we utilized event-related potentials (ERPs) to investigate whether conflict and adaptive control in WM are reflected by the same neural markers that have previously been described for selective attention tasks. In our task, participants encoded two differently colored memory lists that contained four digits each (i.e., 2 5 7 1 and 4 5 9 1), and had to recognize whether a probe item from a specific list and position was correct or incorrect. Conflict during retrieval emerged when digits at corresponding positions (e.g., 2 and 5 at the first position) were different (incongruent), but not when these digits were the same (congruent). In behavioral data, we found a congruency sequence effect, that is, responses to incongruent probe items were slower, and this effect was reduced following trials with incongruent probe items. In ERPs, this behavioral marker of adaptive control was accompanied by two effects. First, congruency affected the amplitude of an N450, and this conflict effect was reduced after incongruent trials. Second, the posterior P3 amplitude varied with the congruency of the current and the previous trial. Both results resemble those found for the Stroop task and thus highlight the similarity between conflict and adaptive control in WM and selective attention tasks.

KEYWORDS

cognitive control, conflict monitoring, event-related potentials, working memory

1 | INTRODUCTION

Working memory (WM) refers to a set of cognitive processes holding mental representations available when required for higher-level cognition (Baddeley, 2012; Goldman-Rakic, 1995; Miller et al., 2018; Miyake &

Shah, 1999; Oberauer, 2009, 2019). It has a strict capacity limitation which in turn requires WM content to be flexibly adapted to changing demands. Such an adaptation is particularly necessary when there is a conflict between WM representations that arises when several items compete for retrieval. In this case, WM content needs to be

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adapted to allow for disambiguating the to-be-retrieved item (Oberauer et al., 2013). Adaptive control processes that may serve this purpose have recently been described in a behavioral study (Hartmann et al., 2022). In these experiments, we could demonstrate that adaptive control processes in WM show a remarkable similarity with corresponding mechanisms in selective attention tasks. Here, we utilize event-related potentials (ERPs) to investigate whether this similarity extends to neural correlates of adaptive control.

Conflict monitoring theory is a popular account of adaptive cognitive control (Botvinick et al., 2004; Botvinick et al., 2001; Egner, 2008), which assumes a two-component process that regulates the recruitment of top-down control depending on the detected level of conflict. The first component—conflict monitoring—constantly registers conflict between competing representations, and has been assumed to be implemented in the dorsal anterior cingulate cortex (dACC; Botvinick et al., 2004; Carter & Van Veen, 2007). This signal in turn triggers a second component—control adjustment—that upregulates or downregulates the strength of top-down control in the subsequent trial. At least in selective attention tasks, this process is assumed to be implemented in the dorsolateral prefrontal cortex (Botvinick et al., 2004; Egner & Hirsch, 2005; Gbadeyan et al., 2016; Kerns et al., 2004). This control loop consisting of conflict monitoring and control adjustment allows top-down control to be constantly adapted to current cognitive demands (Egner, 2007, 2017). Evidence for this idea comes from selective attention tasks, such as the Stroop or flanker paradigm (Eriksen & Eriksen, 1974; MacLeod, 1991; Stroop, 1935), in which a target feature of a stimulus has to be classified while a distracting feature has to be ignored. Here, performance is impaired when the target and distractor require different responses (incongruent or conflict trials) as compared to when both require the same response (congruent or non-conflict trials) representing a so-called congruency effect. A key finding reflecting adaptive cognitive control is the congruency sequence effect which describes the finding that this congruency effect is reduced after conflict trials compared to after non-conflict trials (Egner, 2007; Gratton et al., 1992).

Studies on the cognitive control of WM suggest that the principles of conflict monitoring theory can be applied to WM processes as well. A recent study on the neural correlates of conflict in WM processes (Rac-Lubashevsky & Kessler, 2018) has demonstrated that theta activity at mid-frontal electrode sites scales with conflict in WM updating—a neural signature that has previously been found to accompany response conflict in selective attention tasks (e.g., Cavanagh & Frank, 2014). Evidence for adaptive control, however, has mainly been provided by behavioral studies. Retrieval performance has been shown to depend

on the level of maintenance demand (high- vs. low-mnemonic load, high- vs. low-distractor interference) in the previous trial (Jha & Kiyonaga, 2010). Moreover, Kiyonaga and Egner (2014) developed a novel WM Stroop task investigating conflict between WM content (“internal attention”) and a perceptual task (“external attention”), and found markers of adaptive control comparable to those produced by the Stroop task. In a recent behavioral study, we provided evidence for adaptive cognitive control in a pure WM task (Hartmann et al., 2022). Across different types of WM retrieval (recognition vs. recall), we found robust congruency sequence effects supporting the assumption that conflict between WM representations (thus conflict within internal attention) triggers trial-by-trial adaptation of control processes as well.

While these findings suggest common principles of adaptive control in selective attention tasks and WM tasks, the source of conflict and the nature of control adjustments in these two tasks are necessarily different. In selective attention tasks, conflict is caused by contradicting stimulus features and an upregulation of top-down control corresponds to a narrowing of the attentional focus (Botvinick et al., 2001). In WM tasks, however, conflict is caused when different items in WM compete for retrieval. Control adjustments might involve that additional context information needs to be activated for disambiguating WM content, which results in a change of WM content. The primary goal of the present study is to investigate whether the conflict in a WM task shows similar electrophysiological correlates as those that have previously been described for selective attention tasks, suggesting comparable mechanisms, and whether these correlates are modulated by congruency sequence effects as predicted by conflict monitoring theory.

Research using scalp EEG measures provided evidence that specific ERPs vary with the level of cognitive conflict in selective attention tasks (see Larson et al., 2014 for a review) as predicted by computational models of conflict monitoring theory (Steinhauser et al., 2012; Yeung et al., 2004). A frontocentral N2 and a frontocentral P2 are two stimulus-locked components that have been found to be increased by conflict in selective attention tasks (for the N2 see e.g. Clayson & Larson, 2011a, 2011b; Dong & Zhong, 2017; Gehring et al., 1992; Kopp et al., 1996; Yeung et al., 2004; for the P2 see e.g. Kałamała et al., 2018; Rey-Mermet et al., 2019). Whereas the N2 and P2 have primarily been found to vary with conflict in paradigms involving spatial attention (e.g., the flanker task), tasks involving semantic conflicts have been shown to produce a conflict effect in the N450 (e.g., Liotti et al., 2000; Rey-Mermet et al., 2019; West et al., 2004; West & Bailey, 2012). The conflict effects in the N2 and N450 have been shown to vary with the congruency sequence effect (Clayson &

Larson, 2011a; West & Bailey, 2012; Yeung et al., 2004), making them a particularly promising signature of adaptive cognitive control.

While neural correlates of conflict can provide indirect evidence for conflict adaptation, we also aimed to explore whether congruency sequence effects in WM are reflected in ERPs that are directly related to WM and thus could reflect control adjustments elicited by conflict. Traditionally, the centro-parietal (or posterior) P3 has been associated with attention and WM updating (Donchin & Coles, 1988; Polich, 2007), and the same component has also been shown to vary with conflict in selective attention tasks. Clayson and Larson (2011a, 2011b) showed that parietal P3 amplitudes in a flanker task were larger in current incongruent trials compared to current congruent trials and that this conflict effect was reduced following incongruent trials, thus demonstrating a congruency sequence effect. Another study showed that P3 amplitudes in a combined go/no-go flanker task were again larger in incongruent trials compared to congruent trials, but this conflict effect was maximal at fronto-central electrodes (Groom & Cragg, 2015). Finally, when comparing congruent and incongruent stimuli in a Stroop task, studies revealed the posterior P3 amplitude to be reduced for incongruent color words compared to congruent color words (Ila & Polich, 1999; Zurrón et al., 2013). These results show that the direction and localization of conflict effects in the P3 are less consistent and possibly more task-dependent than conflict effects in the fronto-central negativities discussed above.

1.1 | The present study

In the present study, we aimed to analyze electrophysiological signatures of conflict and control adjustments in a WM task to investigate whether adaptive control in WM is associated with similar mechanisms as adaptive control in selective attention tasks. To achieve this, we applied a mixed-list paradigm that has previously been used to investigate WM processes like encoding, maintenance, and retrieval (Oberauer, 2001; Oberauer et al., 2013), and in which we have already found evidence for adaptive control in behavioral data (Hartmann et al., 2022). Participants had to encode two differently colored memory lists of four digits each (e.g., a blue list comprising the digits [1 5 6 8] and a red list comprising the digits [3 5 7 8]). Each list contained two congruent items (the same digit at corresponding positions) and two incongruent items (different digits at corresponding positions). Incongruent items are supposed to evoke retrieval conflict as retrieving these digits from WM is subject to interference from the corresponding digit in the

alternative list. During probe trials, participants had to perform a recognition task, i.e., they had to judge whether a probed digit was shown at the correct position in the correct list.

First, we expected to replicate the congruency sequence effect found in the behavioral study (Hartmann et al., 2022), that is, we should obtain a performance decrement for incongruent probe items relative to congruent probe items, and this congruency effect should be reduced following incongruent trials. If conflict monitoring mediates the adjustment of WM representations, this congruency sequence effect should be mirrored in conflict-related ERP components, i.e., the N2, the P2, and the N450 during retrieval on probe trials. Amplitudes of some or all these components should be increased on incongruent trials indicating a conflict effect. Crucially, this conflict effect should be smaller following an incongruent trial as compared to following a congruent trial. Finally, we explored whether the posterior P3, a possible correlate of control adjustments in attention and WM, also varies with conflict and the congruency sequence effect. Because no consistent effects for this component have been shown in selective attention tasks, no clear prediction regarding the direction of these effects can be derived.

2 | METHOD

2.1 | Participants

In total, 30 participants were sampled from the participants' pool of the Catholic University of Eichstätt-Ingolstadt. All the participants reported normal or corrected-to-normal vision and took part for course credit or 16€. Two participants had to be excluded from the analysis because their datasets were contaminated by voltage shifts due to excessive head movements that could not be removed by filtering and artifact rejection. The final sample consisted of 28 participants (21 women, 26 right-handed, $\text{mean}_{\text{age}} = 22.68$ years, $\text{SD}_{\text{age}} = 3.61$ years). The study was approved by the ethics committee of the Catholic University of Eichstätt-Ingolstadt (no. 2018/18), and informed consent was acquired from all participants.

2.2 | Stimuli

Participants were asked to encode a memory set consisting of two lists of four items each (Figure 1) during a learning phase, and these items were later presented again in a probing phase. Four horizontally arranged rectangular frames with an edge length of 1.53° visual angle and colored in red formed one list. Four other rectangular

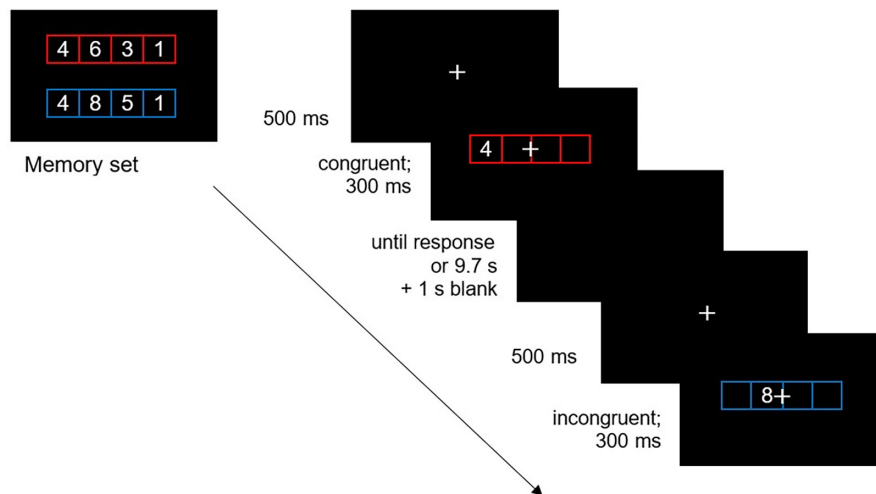


FIGURE 1 Exemplary trial sequence. At the beginning of each learning phase, the memory set (left side) consisting of two differently colored lists was presented. In the present example, the congruent items are the digits at the first and fourth position in each list. Each trial of the probing phase (right side) started with the presentation of a fixation cross. After that, a digit was presented at one of the four positions in one of the two lists, and participants had to verify whether this probe item matched the respective item in the initially learned memory set or not.

frames of the same size and colored in blue formed the other list. The two lists were presented 1.53° visual angle above or below the center of the screen during the learning phase. The items for the two lists were drawn randomly from the digits 1–9. Two of the four positions contained the same digits in both lists and were *congruent items*. The remaining two positions in each list contained different digits and were *incongruent items*. The background color was black, and the digits were presented centrally in each rectangle in white and bold Arial font. The stimuli were presented on a 21-inch monitor with a resolution of 1280×1024 pixels and a refresh rate of 60 Hz at a viewing distance of about 60 cm. During the trials of the probing phase, only one of the two lists was presented in the screen center, and only one of the positions contained a digit.

2.3 | Task and procedure

Figure 1 depicts an exemplary flow of events. The experiment started with the learning phase. Both lists were initially presented for 10 s, and afterward, participants were asked to enter the digits using the keyboard. Participants received feedback about the correctness of the entered digits. If a correct digit was entered, “ok” was presented in the respective list position. If an incorrect digit was entered, the correct digit was presented. When all digits were entered correctly three times in a row, the probing phase started. Each trial of the probing phase started with the display of a white fixation cross ($0.67^\circ \times 0.67^\circ$ visual angle) in the center of the screen. After 500 ms, one of the two lists containing a digit in one of the four rectangles

was presented, while the fixation cross remained in the center of the list. Participants had to decide whether this probe item matched the item in the initially learned list (i.e., same position and same list color) by pressing either the left or the right “ALT” key (“yes” vs. “no”; response mapping was counterbalanced across participants). The stimulus remained on the screen for 300 ms, and participants had to respond within 10 s. After a response was given or the response window expired, a blank screen was shown for 1 s until the next trial started.

Each experimental block contained 64 trials. Congruent and incongruent probe items as well as probe items requiring a “yes” response (positive probe items) and probe items requiring a “no” response (negative probe items) occurred with the same frequency. The 32 negative probe items in each block comprised four different lure conditions (see Experiment 2 in Hartmann et al., 2022): (1) 4 items from the other list but on the correct position, (2) 16 items from the same list and a different position, (3) 4 items from the other list and on a different position, (4) 8 new items not formerly learned in the list context. At the beginning of each block, the memory set was again presented for 5 s, and participants were instructed to keep their gaze on the fixation cross as long as the stimulus was presented during the block. At the end of each block, mean RT and percentage errors were displayed. Participants could take a short break between blocks and start the next block by pressing a key.

In total, the experiment comprised 16 blocks (4 practice blocks and 12 test blocks), and participants learned four different pairs of lists throughout the experiment. Each list pair had a different combination of congruent

positions. All six possible combinations appeared equally often across all participants. Before the 1st, the 5th, the 9th, and the 13th block, a new pair of lists were presented, and the learning phase started for the respective list pair. After this learning phase, participants first performed a practice block which was then followed by three test blocks until the next list pair was shown. During practice trials, the German word “Fehler” (“error”) in yellow Arial font with a visual angle of $3.06^\circ \times 0.67^\circ$ (horizontal \times vertical) was shown centrally on the screen for 500 ms after an incorrect response, followed by a black screen for 1 s. After correct responses, a black screen was shown for 1.5 s.

At the beginning of the experiment, each participant was instructed to respond as quickly and accurately as possible. At the end of the experiment, participants were thanked for taking part in the study and received either course credit or payment. The experimental session lasted approximately 2 h (1 h for experiment, and 1 h for applying and removing EEG electrodes). Individual testing took place in a sound-dim booth. The experiment was programmed using Tscope 5 (Stevens et al., 2006).

2.4 | EEG data acquisition

The EEG was recorded using a Bio-Semi ActiveTwo system (BioSemi, Amsterdam, The Netherlands) with 64 Ag-AgCl electrodes (Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, left and right mastoid). The CMS (Common Mode Sense) and DRL (Driven Right Leg) electrodes were used as reference and ground electrodes. The vertical and horizontal electrooculogram (EOG) was recorded from electrodes above and below the right eye and on the outer canthi of both eyes. EEG and EOG data were continuously recorded at a sampling rate of 512 Hz. All electrodes were offline and re-referenced to averaged mastoids.

2.5 | Data analysis

We investigated whether the congruency effect in the current trial is significantly smaller after incongruent trials compared to after congruent trials. To this end, all behavioral and EEG measures were analyzed using a 2 (previous congruency: congruent vs. incongruent) \times 2 (current congruency: congruent vs. incongruent) repeated-measures analysis of variance (ANOVA). For all analyses, the practice blocks were not analyzed. Furthermore, we

analyzed only positive probe trials as only these trials can be distinctly classified as congruent or incongruent (Hartmann et al., 2022). We further excluded: (a) the first trial of each block, (b) trials that were preceded by an error, (c) trials in which the probed position was repeated (irrespective of whether the list color was repeated or not) to exclude priming effects (Hartmann et al., 2022).

2.5.1 | Behavioral data

All behavioral data were analyzed using the afex package (Singmann et al., 2018; version 0.26–0) in R (R Core Team, 2020, version 3.6.3). Significant interactions were followed up by planned *t*-tests. If the assumption of sphericity was violated, Greenhouse–Geisser correction was applied.

Fast guesses were identified as response times (RTs) shorter than 200 ms and were removed from further analyses. For the analysis of RTs, trials with RTs deviating more than 2.5 standard deviations (*SDs*) of each participant's mean for each experimental condition (0.94% of the original data) as well as erroneous responses were removed. Error rates (ERs) were arcsine-transformed for statistical testing (Winer, 1991). Average trial numbers varied from 39.4 trials (*SD* = 7.6) in the previous incongruent/current incongruent condition to 83.1 trials (*SD* = 10.1) in the previous incongruent/current congruent condition for RT analysis, and from 42.9 trials (*SD* = 6.8) in the previous incongruent/current incongruent condition to 90.6 trials (*SD* = 8.4) in the previous congruent/current incongruent condition for ER analysis. Please note that the discrepancy in trial numbers mainly reflects that direct position repetitions were removed which can occur only in trials in which congruency is repeated.

2.5.2 | EEG data

EEG data were analyzed using custom scripts in MATLAB R2018a (The Mathworks, Natic, MA, USA) together with functions from the open-source toolbox EEGLAB v14.1.2 (Delorme & Makeig, 2004). The continuous EEG data were filtered with a 0.1–40 Hz band-pass filter. Stimulus-locked epochs were extracted ranging from 300 ms before to 1000 ms after stimulus onset. The average voltage during an interval ranging from 200 ms before stimulus onset until stimulus onset was used as a baseline. Channels were interpolated if they either met the joint probability criterion (threshold 5) or the kurtosis criterion (threshold 5) using spherical spline interpolation in EEGLAB's channel rejection routine (pop_rejchan.m). Epochs were excluded if their

amplitude exceeded $\pm 300 \mu\text{V}$ from the epoch mean and if the joint probability deviated more than 5 *SDs* from the distribution mean ($M = 53.18$, $SD = 91.27$); except in channels AF7, Fp1, Fpz, Fp2, AF8 as eye blink artifacts were corrected at a later stage. In the next step, an independent component analysis (ICA; Bell & Sejnowski, 1995) was computed and eye blink artifacts were identified and removed using the CORRMAP procedure version 1.03 (Viola et al., 2009). Finally, epochs were averaged separately for each condition and each participant. Average trial numbers varied from 36.2 trials ($SD = 8.8$) in the previous incongruent/current incongruent condition to 79.4 trials ($SD = 15.2$) in the previous incongruent/current congruent condition per participant for EEG data analysis.

We hypothesized that the retrieval conflict should be reflected in conflict-related ERP components (P2, N2, N450; Kałamała et al., 2018; Larson et al., 2014; Rey-Mermet et al., 2019). Therefore, we computed the P2 as the mean amplitude at electrode FCz in a time window ranging from 150 to 250 ms after stimulus onset (Kałamała et al., 2018; Rey-Mermet et al., 2019) and the N2 as the mean amplitude at electrode FCz in a time window ranging from 250 to 350 ms after stimulus onset (Larson et al., 2014; Rey-Mermet et al., 2019; Yeung et al., 2004). Visual inspection independent of the congruency effect revealed that the N450 amplitude was most pronounced at electrode FCz around 500 ms after stimulus onset. Therefore, we computed the N450 as the mean amplitude at electrode FCz in a time window ranging from 400 to 600 ms, which differs from previous studies (Liotti et al., 2000; Rey-Mermet et al., 2019) but can be explained by the different paradigm used in this study. Finally, we computed the posterior P3 as the mean amplitude at electrode Pz in a time window ranging from 400 to 800 ms. This time window was chosen because it is centered around the peak of the posterior P3 that occurred at around 600 ms in the present paradigm.

3 | RESULTS

3.1 | Behavioral data

The descriptive results for the analysis of RTs and ERs are displayed in Figure 2. In RTs, there was a significant effect of current congruency, $F(1, 27) = 39.82$, $p < .001$, $\eta_p^2 = .60$, but not of previous congruency, $F(1, 27) = 0.18$, $p = .671$, $\eta_p^2 = .007$. Furthermore, we found a significant congruency sequence effect as there was a significant interaction of previous and current congruency, $F(1, 27) = 6.03$, $p = .021$, $\eta_p^2 = .18$. The congruency effect was significantly reduced after incongruent trials ($M = 138$ ms, $SEM = 17$ ms, 95% CI [102 ms, 174 ms]), $t(27) = 4.70$, $p < .001$, $d = 0.88$,

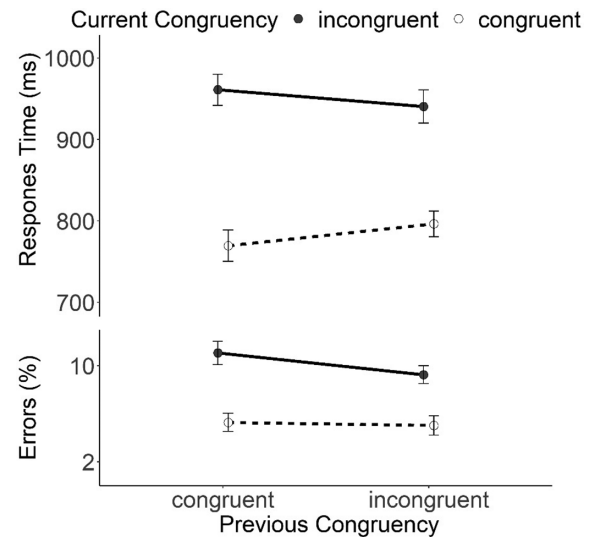


FIGURE 2 Mean response times in ms (upper panel) and mean error rates in % (lower panel) for the analysis of the congruency sequence effect. Error bars represent the within-subject standard error.

as compared to after congruent trials ($M = 198$ ms, $SEM = 17$ ms, 95% CI [158 ms, 238 ms]), $t(27) = 6.75$, $p < .001$, $d = 1.27$. The analysis of ERs revealed a significant effect of current congruency, $F(1, 27) = 33.53$, $p < .001$, $\eta_p^2 = .55$, but not of previous congruency, $F(1, 27) = 3.08$, $p = .090$, $\eta_p^2 = .10$. We found no congruency sequence effect in ERs as previous and current congruency did not interact significantly, $F(1, 27) = 1.18$, $p = .286$, $\eta_p^2 = .04$. Previous studies with selective attention tasks have shown that congruency sequence effects are smaller or even absent if stimuli or context features change across trials (for a review see, Braem et al., 2019). We therefore additionally investigated whether the congruency sequence effect was different after a list switch than after a list repetition for the behavioral as well as for the main ERP analyses. The respective analyses are included in the Materials S1.

3.2 | ERP data

Figure 3 shows ERPs for all midline electrodes from Fz to Pz to provide an illustration of the variability in ERPs across scalp positions. Shaded areas indicate the time windows and electrodes at which the specific ERPs were quantified and tested.

3.2.1 | P2

The waveform at electrode FCz (Figure 3) shows a slightly more positive P2 for current incongruent compared to current congruent trials indicating a congruency effect at

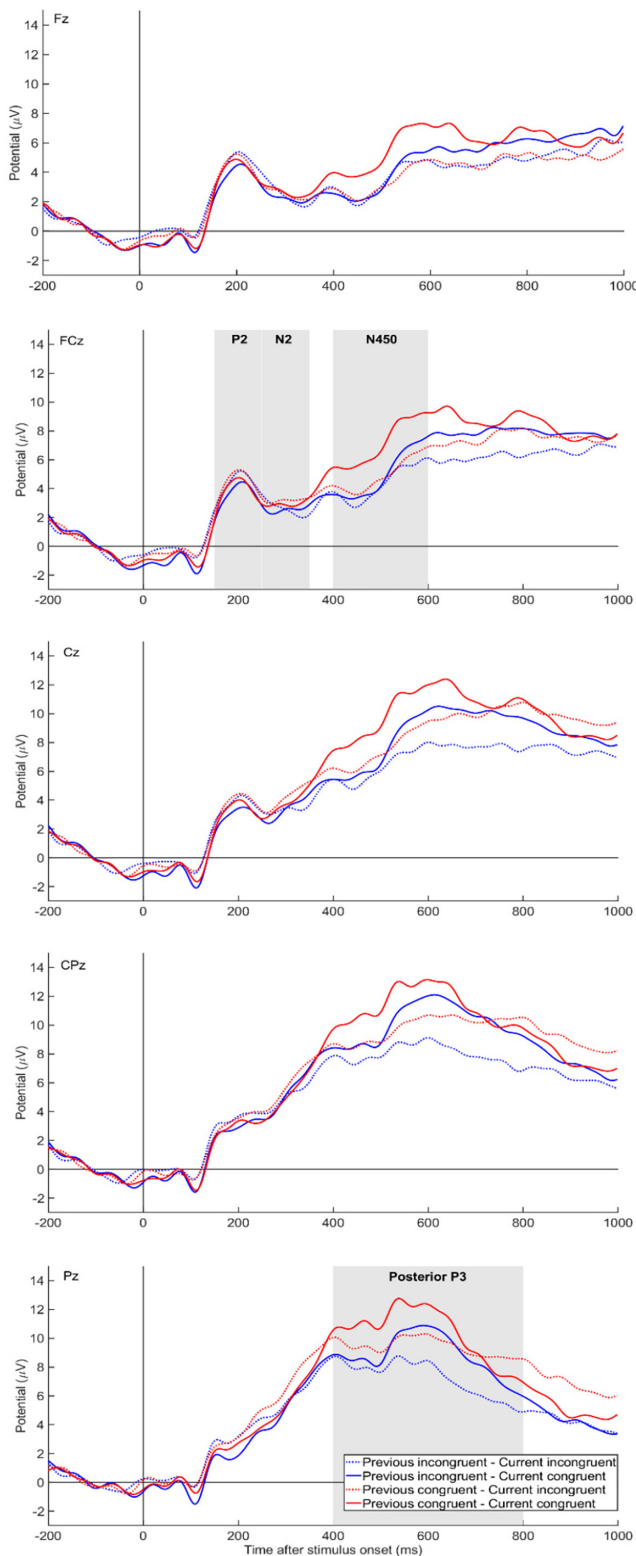


FIGURE 3 Stimulus-locked waveforms for a frontal-parietal range of midline electrodes (Fz, FCz, Cz, CPz, Pz) to visualize variability across scalp regions. Gray areas indicate the predefined time intervals for statistical testing at electrodes FCz and Pz.

frontocentral electrodes (see the corresponding topographies). However, this was not confirmed by the ANOVA: there was only a marginally significant main effect of

current congruency, $F(1, 27)=4.22$, $p=.050$, $\eta_p^2=.15$. and no significant main effect of previous congruency, $F(1, 27)=0.18$, $p=.679$, $\eta_p^2=.006$. The interaction between previous and current congruency did also not reach significance, $F(1, 27)=0.07$, $p=.787$, $\eta_p^2=.003$. Thus, there was no significantly smaller congruency effect after incongruent trials. Although it appears that the P2 varies with conflict, it has to be noted that there are already differences between current congruent and current incongruent trials in the pre-stimulus baseline at around -50 ms which could have led to the congruency effect in the P2. When setting a smaller baseline (-50 ms to 0 ms), the effect in the pre-stimulus baseline disappeared but also the significant effect in the P2, $F(1, 27)=0.46$, $p=.506$, $\eta_p^2=.02$, suggesting that the P2 conflict effect reflects noise. This receives further support from the topographies that do not show a clear frontocentral distribution of the congruency effect. We therefore conclude that conflict has no robust effect on the P2.

3.2.2 | N2

As can be seen in Figure 3, we did not find a conflict-related N2 as there was no pronounced negative deflection in the time interval ranging from 250 to 350 ms that differentiated between congruent and incongruent trials. The ANOVA showed neither a significant main effect of current congruency, $F(1, 27)=0.32$, $p=.575$, $\eta_p^2=.01$, nor of previous congruency, $F(1, 27)=1.47$, $p=.236$, $\eta_p^2=.05$, and no significant interaction, $F(1, 27)=0.13$, $p=.724$, $\eta_p^2=.005$.

3.2.3 | N450

Figure 3 shows an increased negativity for current incongruent trials in the time range of the N450 indicating a congruency effect. Moreover, this congruency effect was reduced after incongruent trials indicating a congruency sequence effect. The ANOVA showed a significant main effect of current congruency, $F(1, 27)=8.19$, $p=.008$, $\eta_p^2=.23$, and of previous congruency, $F(1, 27)=5.48$, $p=.027$, $\eta_p^2=.17$. Furthermore, we found a significant interaction of previous and current congruency, $F(1, 27)=5.08$, $p=.033$, $\eta_p^2=.16$, indicating that the congruency effect in N450 amplitudes was significantly reduced after incongruent trials ($M=0.54\mu\text{V}$, $SEM=0.47\mu\text{V}$, 95%-CI $[-1.99\mu\text{V}, 0.91\mu\text{V}]$), $t(27)=1.15$, $p=.257$, $d=0.09$, as compared to after congruent trials, ($M=2.03\mu\text{V}$, $SEM=0.47\mu\text{V}$, 95%-CI $[-3.77\mu\text{V}, -0.29\mu\text{V}]$), $t(27)=3.19$, $p=.004$, $d=0.33$. This provides evidence for conflict adaptation in WM at the level of the N450.

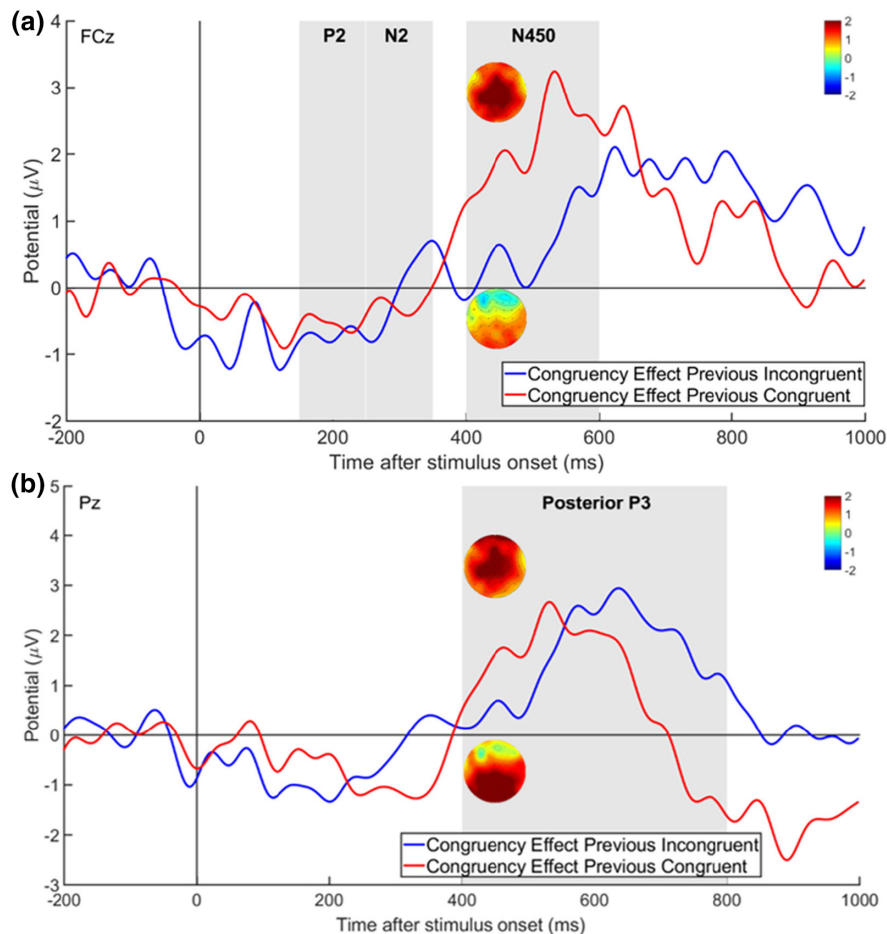


FIGURE 4 Difference waves and scalp topographies for the congruency effects as a function of previous congruency illustrating the congruency sequence effect for the N450 at electrode FCz (a) and the posterior P3 found at electrode Pz (b). Gray areas indicate the predefined time interval for statistical testing.

3.2.4 | Posterior P3

The waveforms and topographies for the posterior P3 are depicted in Figure 4. The mean voltage in the time window ranging from 400 to 800 ms was significantly more negative for current incongruent trials than for current congruent trials, $F(1, 27) = 10.97$, $p = .003$, $\eta_p^2 = .29$. Moreover, it was more negative for previous incongruent than for previous congruent trials, $F(1, 27) = 7.06$, $p = .013$, $\eta_p^2 = .21$. However, no significant interaction of previous and current congruency was revealed, $F(1, 27) = 0.40$, $p = .531$, $\eta_p^2 = .02$. Thus, while the posterior P3 varies with current and previous conflict, no congruency sequence effect was observable.

4 | DISCUSSION

The present study addressed the question of whether electrophysiological correlates of adaptive control that have previously been found for selective attention tasks (e.g., flanker, task, Stroop task) can also be found in a declarative WM task. Our approach was to measure ERPs related to conflict (P2, N2, N450) and control adjustments (posterior P3) in a mixed-list paradigm with items provoking a

high or low level of retrieval conflict. Behavioral data indicated a congruency sequence effect thus replicating our results from a behavioral study (Hartmann et al., 2022). The congruency effect in RTs was significantly reduced following incongruent trials as compared to following congruent trials. As in our previous study, we did not find such an effect in ERs. In ERPs, we found a significant conflict effect in the N450, and this conflict effect was modulated by adaptive cognitive control, i.e., it was smaller following incongruent than following congruent trials. Furthermore, for the posterior P3, both current and previous conflict led to reduced P3 amplitudes. However, these effects did not interact and thus did not show the pattern indicative of a congruency sequence effect.

So far, it has been unclear whether a retrieval conflict in WM tasks modulates the same ERP components that have been found for conflict in selective attention tasks. Our results suggest that conflict in WM retrieval is mirrored in the N450 but not in the N2 and P2 (given that the latter effects appear to reflect noise during the baseline period). This contrasts with findings from the flanker task in which the N2 rather than the N450 has been consistently found to reflect conflict and post-conflict adaptations (Dong & Zhong, 2017; Larson et al., 2014; Yeung et al., 2004). A possible explanation for why we did not

find any modulation of the N2 could be that our WM task involves attention to information in WM but not attention to stimuli in the environment and that the N2 is particularly sensitive to conflict arising from external attention rather than internal attention.

In contrast, the N450 typically indexes conflict elicited in the Stroop task (Larson et al., 2014; Liotti et al., 2000; Rey-Mermet et al., 2019; West et al., 2004; West & Bailey, 2012), although evidence for post-conflict adaptation (as reflected by the congruency sequence effect) in the N450 is mixed and mostly depends on the type of task. Whereas no effects were found using a color-word Stroop task (Larson et al., 2009, 2012) or an auditory Stroop task (Donohue et al., 2012), studies using a counting Stroop task (West et al., 2012; West & Bailey, 2012) or a confound-minimized prime-probe task using arrows (Larson et al., 2016) found that the N450 was modulated by previous conflict. Interference in the Stroop task can be attributed to semantic conflict as the color of the presented color-word stimulus interferes with the semantic meaning of the color-word (see, e.g., Burca et al., 2021; De Houwer, 2003; van Veen & Carter, 2005), and a similar reasoning can be applied to other Stroop-like paradigms (Kałamała et al., 2020). Retrieval conflict elicited during our WM task can also be seen as a form of semantic conflict, which would explain why conflict and post-conflict adaptation modulated the N450 in our task. From the perspective of WM models defining WM as a system holding information in different states of accessibility (“state-based models”; see e.g., Cowan, 2008; Oberauer, 2009), retrieval conflict arises as temporarily activated representations in long-term memory (i.e., digits at the same position in different lists) compete for internal attention. Support for this assumption comes from a WM study in which conflict could arise during WM updating based on a retro cue. Here, the N450 was enhanced in conflict trials as compared to no-conflict trials (Schneider et al., 2016).

The similarity between the present paradigm and the Stroop task is further highlighted by the results of the posterior P3. As in previous studies on the Stroop task (Ila & Polich, 1999; Zurrón et al., 2013), incongruent trials showed a reduced posterior P3 amplitude, which could indicate the enhanced difficulty associated with semantic or retrieval conflict. However, the observation that conflict in the previous trial also led to a reduced P3 in the current trial could suggest that our P3 results reflect a mechanism that is specific to the present WM task. More specifically, it is possible that the posterior P3 amplitude indicates the WM load associated with our task. In Hartmann et al. (2022), we proposed that conflict in our task leads to adjustments in WM content. Retrieving a congruent item requires only that the digit is associated with its corresponding position whereas the association

with contextual information—i.e., the list color—is not necessary. However, retrieving an incongruent item additionally requires that the item-position compound is linked to the list color to distinguish this item from the interfering item at the same position in the alternative list, leading to a strengthening of item-list bindings. This strengthening of item-list bindings could imply a higher WM load as WM content is now enriched with additional contextual information. This could explain reduced P3 amplitudes on incongruent trials as higher WM load has previously been linked to decreased P3b amplitudes (see e.g., Bailey et al., 2016; Kok, 2001; Polich, 2007). Moreover, this adjusted WM content could be carried over to the next trial which explains why conflict leads to reduced P3 amplitudes also on the subsequent trial. Crucially, these adjustments of WM content could be the basis for congruency sequence effects in our paradigm because strengthening item-list bindings should effectively reduce conflict from the irrelevant list. If this interpretation is correct, the posterior P3 in our paradigm can be viewed as an index of conflict-driven control adjustments.

Another theoretical approach accounting for the architecture of adaptive cognitive control in our task assumes a hierarchical organization of control on a rostral-caudal axis in the prefrontal cortex (Badre, 2008; Koechlin et al., 2003; Koechlin & Summerfield, 2007). The core idea of this account is that contextual information at different levels of a hierarchy constrains and guides decisions and behavior and that current goals and task demands determine which level exerts control in a given situation. From this perspective, conflict in the present paradigm implies a shift of control toward a higher level of contextual information (i.e., list identity) to disambiguate WM content and reduce conflict. This possibly provides an alternative explanation of the pattern of posterior P3 amplitudes in our task if one assumes that the posterior P3 relates to WM operations that are affected by the level of control (e.g., Rac-Lubashevsky & Frank, 2021).

Despite the differences in the level of individual components, our data suggest that adaptive control in WM involves a similar pattern of conflict-related and adjustment-related processes as adaptive control in selective attention tasks. This similarity receives further support from the additional analyses of the effects of list transition (Materials S1). These analyses revealed that congruency sequence effects in RTs as well as in the N450 were only observable in list repetition trials but not in list switch trials. This is in line with the idea that control is bound to a specific context and is retrieved when context features (here: the list) repeat (for a review, see Braem et al., 2019). For example, Kiesel et al. (2006) showed in a task-switching study that conflict resolution acts task-specific, and that conflict adaptation is only visible in task repetition

but not in task switch trials. Dignath et al. (2019) found a stronger congruency sequence effect when context repeats compared to when context alternates. They assumed that control states are bound to a specific context and are stored as trial-specific event files, which are evoked on the subsequent trial only if the context is repeated. These assumptions can be transferred to our results. Retrieval conflict implies an adjustment of the control state which is bound to the list context. Only if the list is repeated, this control state is activated leading to a congruency sequence effect. Notably, the inclusion of list transition led to a comparable pattern for the posterior P3. Whereas a congruency sequence effect was absent for this component in the main analysis, a trend towards such an effect was found for list repetitions. In contrast, list switches were even associated with a reversed congruency sequence effect. This further supports the idea that previously adjusted control states (which might correspond to WM configurations in the present case) are evoked only when the context is repeated.

Taken together, the data from this study and our previous study (Hartmann et al., 2022) support the assumption that adaptive control of selective attention and WM follow the same principles. It must be noted that alternative explanations exist, questioning the assumption that the congruency sequence effect is an index for adaptive control. Rather, it is assumed, that low-level learning processes like feature integration cause the congruency sequence effect (Braem et al., 2019; Hommel et al., 2004; Mayr et al., 2003). As we excluded all trials with position repetitions from our analysis our results cannot be explained by position priming (see a discussion of this issue in Hartmann et al., 2022). Thus, there were no complete feature repetitions in the analyzed data that could have produced a result pattern mimicking the congruency sequence effect. Nevertheless, future studies investigating conflict adaptation in WM should apply an experimental design that ensures a more stringent control of low-level learning processes which in turn allows the behavioral result pattern can be attributed to adaptive control processes (see, e.g., Braem et al., 2019).

5 | CONCLUSION

To summarize, the present study shows that adaptive control in WM follows similar principles as adaptive control in selective attention. We found that a conflict-related N450 is also found for conflict in WM retrieval and that this component shows a congruency sequence effect indicative of adaptive control. Furthermore, control adjustments might be reflected in a posterior P3 that is influenced by both current and previous conflict.

AUTHOR CONTRIBUTIONS

Eva-Maria Hartmann: Data curation; visualization; writing – original draft. **Miriam Gade:** Writing – review and editing. **Marco Steinhauser:** Conceptualization; supervision; writing – review and editing.

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DATA AVAILABILITY STATEMENT

The data and analysis scripts of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Additional analyses list transition.

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