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The dynamics of cognitive control: Evidence for within-trial conflict adaptation from frequency-tagged EEG

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Abstract

A central topic in the cognitive sciences is how cognitive control is adapted flexibly to changing task demands. Conflict monitoring theory originally proposed conflict triggered adjustments of cognitive control after a conflict trial to improve *subsequent* performance. In the present study, we tested the hypothesis that readjustments of cognitive control occur continuously *within* a conflict trial itself. Using frequency tagged electroencephalogram in a flanker task, we traced the allocation of attention to target and distracter stimuli. We found evidence for a conflict-triggered within-trial contrast enhancement dissociating target and distracters. This contrast enhancement vanished for consecutive trials with constant tagging frequencies, indicating that trial-to-trial conflict adaptation effects may, at least partly, be the product of interacting processes serving conflict resolution within trials.

Descriptors: Conflict monitoring, EEG, Frequency tagging, Executive functions, Cognitive control, Dynamics

Cognitive control comprises the ability to focus on relevant information and to protect our intentions in an environment full of distractions. Despite its importance for goal oriented behavior, the mechanisms of cognitive control, and in particular how and when it is recruited, are still under debate. In the laboratory, cognitive control has been studied by tasks inducing response conflicts such as the so-called flanker task (Eriksen & Eriksen, 1974). Participants are instructed to respond to a central target letter and to ignore distracter letters surrounding the target. The basic finding with this task is a congruency effect in response times (RT): Responses are faster for congruent trials, on which target and distracters are mapped to the same response, compared to incongruent trials, on which target and distracters are mapped to different responses. This congruency effect is typically reduced for consecutive incongruent trials. These sequential conflict adaptation effects have been interpreted as evidence for an enhanced recruitment of cognitive control following high conflict in order to promote goal pursuit in the face of conflicting input (Gratton, Coles, & Donchin, 1992; Ullsperger, Bylsma, & Botvinick, 2005; but see Mayr, Awh, & Laurey, 2003).

To date, the most influential account of sequential conflict adaptation effects is conflict monitoring theory (Botvinick, Braver, Barch, Carter, & Cohen, 2001). According to this theory, the detection of conflict in an incongruent trial $N-1$ is assumed to be mediated by the anterior cingulate cortex (ACC; Botvinick, Cohen, & Carter, 2004). Detected conflict then triggers adaptation processes in the dorsolateral prefrontal cortext (dlPFC; Kerns et al., 2004), leading to enhanced cognitive control in the next trial N to prepare for subsequent conflicting input. Based on this proposition, conflict monitoring theory inspired a considerable amount of research (for a review, see Egner, 2007), which has led to several modifications to account for further data (Brown, Reynolds, & Braver, 2007; Davelaar, 2008; Verguts & Notebaert, 2008).

However, in the process of this research, two interpretations emerged about how conflict adaptation proceeds exactly. The first interpretation assumes that the conflict adaptation process is independent of the conflict resolution process within a conflict trial: Conflict in trial $N-1$ is detected by the ACC and is relayed over time to the dlPFC, leading to conflict adaptation *in the next trial N* (for typical examples, see, e.g., Kerns et al., 2004; Verguts & Notebaert, 2008; for a critical review of this interpretation, see Mansouri, Tanaka, & Buckley, 2009). This interpretation could be drawn directly from the original work on conflict monitoring (Botvinick et al., 2001), where the content of the conflict detection module is read out at the end of each trial and, hence, is, in principle, independent of the conflict resolution process within the conflict trial $N-1$. This conflict adaptation *across* trials is also similar to other suppression theories (e.g., Stürmer, Leuthold, Soetens, Schroter, & Sommer, 2002).

The second interpretation assumes that processes of conflict resolution and subsequent conflict adaptation are not that clearly separable and might instead reflect reactive conflict adaptation *within* the conflict trial $N-1$ itself (Braver, Gray, & Burgess, 2007; e.g., Brown et al., 2007; Davelaar, 2008; Goschke & Dreisbach, 2008). In this conception, the ACC still detects the

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PSYCHOPHYSIOLOGY

conflict in trial $N-1$, leading to control readjustment by the dlPFC, solving the conflict in trial $N-1$ directly (e.g., by increasing attention to goal-relevant information and/or suppressing conflicting information). That is, control readjustments occur online within the conflict trial $N-1$. Importantly, subsequent sequential conflict adaptation effects on trial N might by due to a mere carryover of the adjusted control settings from the previous trial $N-1$. In this view, the ACC is still necessary to signal conflict to the PFC, yet it loses its role in maintaining the conflict information across time for an independent adaptation process following the conflict in trial $N-1$. This second interpretation is supported by several findings in the recent literature. For example, it has been found that conflict in a primary task impaired the detection of prospective memory cues if this cue lies on the distracting but conflict eliciting dimension. This has been interpreted as a conflict-triggered inhibition of the distracting stimulus dimensions within the conflict trial itself (Goschke & Dreisbach, 2008). Also consistent with the idea that conflict adaptation may reflect a carryover of within-trial control adjustments from the previous trial $N-1$, it has been found that switching between different tasks produced higher switch costs in trial N following high compared to low conflict trials $N-1$. This is exactly what one would expect if the conflict on the previous trial $N-1$ already induced an inhibition of the competing and distracting task set (Brown et al., 2007; Goschke, 2000). Taken together, conflict adaptation effects in trial N might at least partly reflect a carryover of conflict-triggered readjustments for target selection in the conflict trial $N-1$ rather than preparatory recruitment of enhanced control.

Unfortunately, both theoretical views, adaptation *across trials* and adaptation as a carryover of *within-trial* readjustments, make very similar predictions with respect to sequential trial-to-trial effects of a conflict. Thus, support for the within-trial readjustment view necessitates tracing the respective readjustment processes *within* a trial. Hence, previous studies using functional magnetic resonance imaging and response times (e.g., Egner & Hirsch, 2005) and even studies using event-related potentials (ERP; e.g., Freitas, Banai, & Clark, 2009; Larson, Kaufman, & Perlstein, 2009; Van Veen & Carter, 2002) and electromyographic measures (EMG; e.g., Burle, Possamaï, Vidal, Bonnet, & Hasbroucq, 2002) could not or only indirectly distinguish between these alternative hypotheses.

In the present study, we took a novel approach to distinguish empirically between conflict adaptation *across* trials versus readjustment *within* trials by using frequency tagging in combination with electroencephalogram (EEG) measurements. This technique allows us to trace the continuous allocation of attention to targets and distracters by tagging them with different flicker frequencies (Fuchs, Andersen, Gruber, & Müller, 2008; Müller, Andersen, & Keil, 2007; Müller, Teder-Sälejärvi, & Hillyard, 1998). The flicker elicits steady-state, visually evoked potentials (SSVEPs) in the EEG, a signal oscillating at the stimulus flicker frequency. Increased amplitudes of the respective signal for target or distracters, extracted from the EEG with time–frequency methods, have been shown to indicate enhanced allocation of attention to the respective stimulus in divided attention tasks (e.g., Toffanin, de Jong, Johnson, & Martens, 2009). Hence, this method offers two major advantages: First, it enables us to extract the time course of attentional deployment within a trial (Müller et al., 1998). Second, by using different tagging frequencies for target and distracter stimuli within the same trial, we can separately extract the time course of attention deployed to targets and distracters.

We applied this method to a number flanker task, where participants had to respond to a centrally presented target number surrounded by distracting numbers. The target number and the distracter numbers were tagged with different temporal flicker frequencies (9 and 12 Hz). From our within-trial readjustment hypothesis, two predictions were derived. First, the amplitude of the target-related signal should be enhanced and the amplitude of the distracter-related signal should be attenuated within incongruent trials N in contrast to congruent trials N (see Figure 1b). Second, we expected these within-trial readjustment effects to vanish on incongruent (high conflict) trials N preceded by incongruent trials $N-1$ (compared to incongruent trials preceded by congruent trials), as has been shown previously in experiments across trials (e.g., Egner & Hirsch, 2005). The second prediction follows from the assumption that the within-trial readjustment on an incongruent trial $N-1$ puts the cognitive system in a state where it is optimally configured for coping with the conflict in trial N (i.e., attention is enhanced for the target and attenuated for the distracters). If this state persists until trial N, less online readjustment should be required for selecting the correct response, leading to the behavioral effect of sequential conflict adaptation. Although this second prediction of changes *across* trials would also be in accordance with conflict monitoring theory, in combination with the first prediction of *within*-trial readjustments, it also serves to validate our new methodological approach that has—to our knowledge—not been applied to conflict adaptation processes before.

To provide further validation for this new methodological approach, we also analyzed surrogate EEG data. These data were created by simulating SSVEPs either in accordance with the hypothesis of within-trial readjustments or in accordance with the hypothesis that there are no within-trial changes, but only conflict adaptation processes across trials. Hence, by comparing empirical data with results from the two simulation models we attempted to further validate our method.

Methods

Participants

Twenty-two university students (10 female, mean age 24.52 years, age range 21–30) with normal or corrected-to-normal vision participated in the study. Data of 3 participants had to be discarded because of high error rates ($>10\%$, median error rate: 3.5%). Participants gave informed consent according to the Declaration of Helsinki and received class credit points or 5€ per hour.

Apparatus and Stimuli

Participants were seated in an electrically shielded and dark EEG recording cabin, the head resting on a chin rest at a distance of 1.5 m from a 17-in. screen. The experiment was controlled by Presentation software (Neurobehavioral Systems), running on a Windows XP SP2 personal computer.

The target stimulus (randomly selected from the numbers 2, 5, 6, and 9) was presented at the screen center, surrounded by four identical distracter stimuli (either a number from the same set 2, 5, 6, and 9 or the letter H) that were arranged horizontally and vertically around the target stimulus (see Figure 1a). All stimuli were shown in white, surrounded by a gray circle on a black background. They had a width of 0.6° at 1.5 m distance on a 17-in. screen running at a resultion of 1024×768 pixels. The

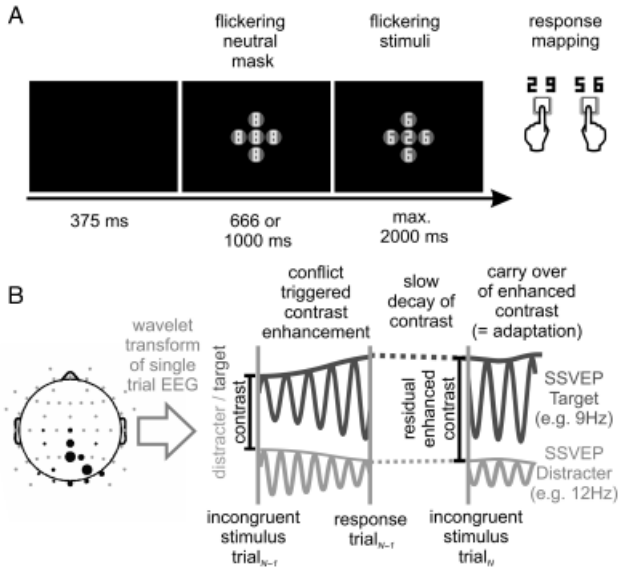

Figure 1. Experimental setup (A) and hypothesized SSVEP waveforms (B) in the occurrence of conflict, showing conflict adaptation in the amplitude modulation. Black electrode markers indicate used electrodes; the size of the markers indicates the frequency of electrode inclusion into data analysis.

gray circles extented 1.41°, and the whole number display had a 4.5° visual angle. Screen refresh frequency was 72 Hz. Distracter and target stimuli flickered with different frequencies of 9 or 12 Hz (50% of cycle time on, 50% cycle time off; frequency balanced over trials; see below) to produce the different SSVEPs.

Participants were instructed to press the left key with the index finger of the left hand for the numbers 2 and 9 and the right key with the index finger of the right hand for the numbers 5 and 6 (or vice versa, counterbalanced over participants) on a standard computer keyboard. Because numbers were presented in a digital format (see Figure 1A), this response mapping balanced the perceptual features between stimuli and the two responses (2 is similar to 5 and 6 is similar to 9). To ensure that stimuli in distracter positions were processed, we included no-go trials (letter H as a distractor) in which participants had to refrain from responding (cf., e.g., Fischer & Schubert, 2008).

Design

The combinations of target and distracter numbers resulted in 20 possible trials: 8 × response *congruent* trials (e.g., 5 5 5 or 2 9 2), 8 × response *incongruent* (e.g., 2 5 2 or 6 9 6) trials, and 4 × *no-go* trials (e.g., H 2 H). This resulted in a 20 (trial $N-1$) × 20 (trial N) transition matrix, resulting in a completely balanced block of trial transitions with 400 trials. Complete repetitions (20 trials) were excluded to avoid effects of repetition priming (Mayr et al., 2003).

The experiment consisted of three blocks of 380 transition balanced trials with short breaks between blocks. Furthermore, each block began with 10 additional random trials (excluded from the analyses) to allow for accommodation after each break. The flicker frequency of the target and distracter stimuli and the mask duration were also balanced over all trials of the experiment. Because it has been shown previously that flicker frequency might have an effect on behavioral results (e.g., Müller & Hübner, 2002), we included switches in flicker frequencies of target and distracter between trials as an independent variable in our analyses, coded as frequency *switch* (target and distracter switch frequency from trial $N-1$ to trial N) and *no-switch* (target and distracter keep frequency from trial $N-1$ to trial N) trials.

Overall, this design yielded a design matrix including the factors congruency N (*congruent*/*incongruent*), congruency $N-1$ (*congruent*/*incongruent*), and frequency switch (*switch*/*no-switch*). Because no-go trials were excluded from the analysis, we had 768 trials for analysis with this matrix ($16 \times 16 = 256$ trials per block).

Procedure

Each trial started with a black screen for 375 ms. Next, the number 8 was presented as a neutral mask at the positions of target and distracters, for a duration of either 666 or 1000 ms. Mask items were already tagged with the flicker frequency of the following target and distracters, respectively. This served to accommodate SSVEP amplitude to the flicker (Keil, Moratti, Stolarova, Bradley, & Lang, 2003). Subsequently, the stimuli were presented until response execution (maximum of 2000 ms). No feedback was provided (see Figure 1A).

Prior to the experiment, participants were instructed to respond as fast and accurately as possible to the targets while ignoring distracters and avoiding responses in case of no-go trials. To improve EEG data quality, participants were advised to maintain a central fixation and keep relaxed while not moving within a trial. Prior to the experiment, participants performed 40 practice trials to get familiarized with the procedure (20 trials with feedback and 20 trials without feedback as in the experiment).

Data Acquisition and Analysis

EEG was recorded with a modified 10–20 setup containing 62 electrodes referenced to the left mastoid. Two electrodes were placed below the left and right eyes as electrooculograms to monitor vertical eye movements and blinks. Impedance was kept below 5 kΩ. Data were recorded with 1000 Hz sampling frequency, a time constant of 10 s, and a 250 Hz low-pass filter.

Data were analyzed using EEGLAB (Delorme & Makeig, 2004) and MATLAB 2006a (The Mathworks) on Windows XP SP2. For analysis, data were bandpass filtered (1.5–90 Hz, two-way least-squares FIR filtering with zero-phase distortion, 10 Hz lowpass transition band width) and downsampled to 250 Hz after recording. Data were then epoched (− 500 ms to 1500 ms relative to stimulus onset). Because eye blinks and eye movements would cause an interruption of the continuous flicker stream, individual trials containing this kind of artifacts within the critical window from the onset of the imperative stimulus to the trial's response were rejected by semiautomatic threshold detection. To minimize the loss of trials, muscular artifacts and remaining eyeblink and eye movement artifacts were removed by independent component analysis (Jung et al., 2000) and data driven component clustering (Scherbaum, 2006). On average, this procedure yielded 73 trials per condition per subject.[1]

[1]The average number of trials per condition ranged from 67 to 79 trials. For 1 participant, the remaining number of trials ranged from 12 to 29 trials per condition. For all the other participants, the minimum was 33 trials and the maximum was 105 trials. Because removing the subject did not change the results (it even slightly increased the F statistics), we decided to keep it in the analysis.

We used the following procedure to extract SSVEP amplitude for target and distracter stimuli (for a validation of this method on surrogate data, see the Simulation section):

Step 1: To improve the signal-to-noise ratio, we chose a best electrode approach, as it is often used in the field (e.g., Fuchs et al., 2008). For this, we identified the posterior electrode with the maximum energy over all conditions and trials for the frequency of interest, individually for each participant. We then identified the best neighboring electrode (for mean topographies, see Figure 5, below). The signals of both electrodes were then extracted as described below and averaged.

Step 2: Data were bandpass filtered (9 and 12 ± 1.5 Hz) to avoid frequency crosstalk due to the wide frequency bands of the wavelets used in the next step (Müller, 2008; Rodriguez et al., 1999).

Step 3: We extracted the instantaneous energy as a measurement of continuous signal amplitude for the specific tagging frequencies. We performed wavelet analysis using complex Morlet's wavelets[2] with a constant ratio f_0/σ_f of 7 (cf., e.g., Tallon-Baudry et al., 1997) and extracted continuous energy for each trial and for both tagging frequencies.

Step 4: To allow averaging across different frequencies with different temporal properties and different baseline energy levels, we normalized the energy signal to its baseline (-375 ms to -125 ms before stimulus onset) by first subtracting baseline mean and then standardizing to the baseline standard deviation (see Rodriguez et al., 1999, for a similar normalization procedure).

Step 5: The resulting energy signal was time normalized to 100 equal time slices between stimulus onset and response. In this way, we created for every trial an energy signal of equal length (cf. McKinstry, Dale, & Spivey, 2008, for a similar approach on mouse trajectories) locked to both stimulus and response of the trial. This normalization was performed for the following reason. If within-trial readjustments mirror conflict resolution between target and distracter information by continuous signal augmentation (target) and/or inhibition (distracter), we expect this process to bind the stimulus and the response events together. The conflict, elicited by the stimulus, triggers the conflict resolution process that, after being finished, initiates the response. Therefore, the process under investigation is neither purely stimulus locked nor purely response locked but requires a stimulus–response locked analysis. Luckily, in contrast to ERP components that strongly depend on absolute phase, SSVEP amplitude is a phase independent signal, enabling us to normalize each trial and investigate the process of interest in the necessary stimulus–response-locked manner. Because we expect within-trial readjustments to reach their maximum at the end of each trial, a response-locked analysis would also be possible. However, this bears the cost of a loss of signal change due to smearing at the signal onset, because response-locked analysis is based on the assumption of a response-locked process (see the supplementary material for a simulation of these effects). Hence, at best, this would reduce statistical power for effects over time. The same holds for stimulus-locked analysis, with smearing occurring at the end of the trial, especially because in this paradigm, stimuli flickered until response only.

Step 6: We averaged the resulting signals over trials and frequencies for each condition in the design matrix. Data were then grand averaged across participants.

For analysis of behavioral data and SSVEP data, we excluded all error trials and trials following an error (2%). Trials not matching the outlier criterion (RT > 3.5 *SD*, applied for each participant) were also discarded (0.5%).

Results

Response Times

A repeated measures analysis of variance (ANOVA) showed a significant main effect for congruency N, $F(1,19) = 32.79$, $p < .01$. Congruent trials (685 ms) were faster than incongruent trials (711 ms). There was no significant effect for congruency $N-1$, $F(1,19) = 0.79$, $p = .38$, and a marginal effect for frequency switch, $F(1,19) = 3.43$, $p = .08$, with no-switch trials being slightly faster (695 ms) than switch trials (701 ms). There was no interaction between congruency N and congruency $N-1$, but there was a significant three-way interaction of Congruency N × Congruency $N-1$ × frequency switch, $F(1,19) = 5.96$, $p < .05$, indicating that conflict adaptation effects depended on the frequency switch. Accordingly, subsequent ANOVAs confirmed a reliable effect of conflict adaptation in the condition of no frequency switch, Congruency N × Congruency $N-1$, $F(1,19) = 6.31$, $p < .05$, and a reversed conflict adaptation effect in the condition of frequency switch, Congruency N × Congruency $N-1$, $F(1,19) = 7.04$, $p < .05$ (see Figure 2).

SSVEP Amplitudes

We calculated contrasts for congruency N (incongruent − congruent) separately for the target and the distracter signals and separately for congruency $N-1$ and frequency switch. This yielded eight contrast signals shown in Figure 3, indicating within-trial readjustments by a rising target contrast and a decreasing distracter contrast. As should be expected from the analysis of RT data and the reliable interaction of conflict adaptation with frequency switch, a contrast enhancement between target and distracters was found for incongruent trials following congruent trials if no frequency switch occurred between trial N and trial $N-1$. Also as expected, this contrast enhancement could also be found for incongruent trials following incongruent trials if a frequency switch occurred between trial N and trial $N-1$.

For statistical analysis of these effects, we subtracted the respective target and distracter signals to obtain an overall measure of contrast enhancement. The resulting contrast was divided into three equal time windows, each averaging across 33 time slices, reducing the time factor levels for the subsequent ANOVA from 100 to 3. An ANOVA of these contrasts with the factors congruency $N-1$, frequency switch, and time yielded a significant

[2]The used wavelet family was defined as

$$w(t, f_0) = (\sigma_t\sqrt{\pi})^{-1/2} \exp(-t^2/2\sigma_t^2) \exp(2i\pi f_0 t)$$

with $\sigma_f = 1/2\pi\sigma_t$.

σ_f and σ_t denote the length of the wavelet in the frequency and time domains, t denotes time, and f_0 denotes the frequency of interest (9/12 Hz here). The wavelet has a Gaussian shape around its center frequency. The ratio f_0/σ_f should be chosen greater than 5 (Grossmann, Kronland-Martinet, & Morlet, 1989) and was set to 7 (e.g., Rodriguez et al., 1999; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997). At 9 Hz, this leads to σ_t of 124 ms and to a σ_f of 1.29 Hz. At 12 Hz, this leads to σ_t of 90 ms and to a σ_f of 1.71 Hz. The wavelet duration was 3 σ_t.

After convolution of the filtered signal with the wavelet, the instantaneous energy is defined as $E_n(f, t) = \lfloor F_n(f, t)\rfloor^2$. $F_n(f, t)$ denotes the spectrum (in this case the complex result of the convolution) of the signal. Energy was extracted for every time bin and for $f = 9$ Hz and 12 Hz, according to the tagging frequencies.

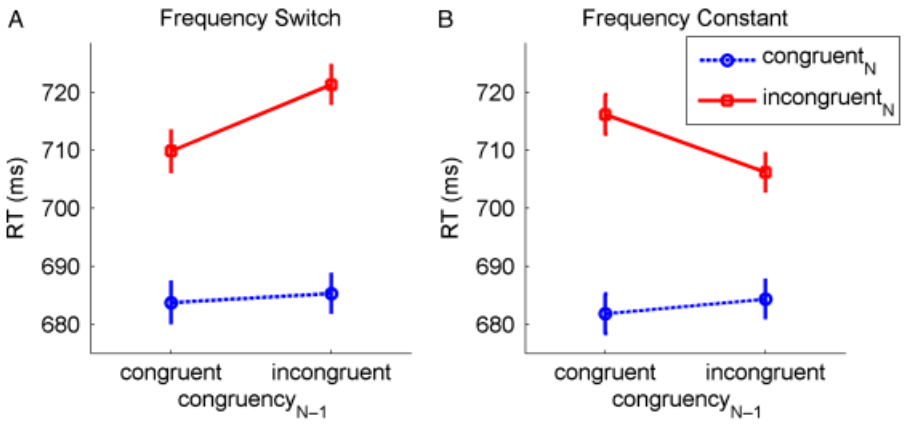

Figure 2. Response times for frequency switch (A) and no-switch (B) trials as a function of congruency in the current trial (N) and the previous trial ($N-1$). Error bars show standard errors.

interaction of Congruency $N-1$ × Frequency Switch, $F(1,19) = 10.8$, $p < .05$, and a significant interaction of Time × Congruency $N-1$ × Frequency Switch, $F(2,38) = 3.47$, $p < .05$, mirroring the interaction found in the RT data.

A subsequent ANOVA, performed only for no-switch trials, revealed a reliable effect of congruency $N-1$, $F(1,19) = 6.46$, $p < .05$, and a marginal Time × Congruency $N-1$ interaction, $F(2,38) = 2.64$, $p = .08$, supporting the expected contrast enhancement. The analogous ANOVA performed only for switch trials also revealed a reliable (but reversed) effect of congruency $N-1$, $F(1,19) = 6.46$, $p < .05$, but no reliable interaction of Time × Congruency $N-1$, $F(2,38) = 2.12$, $p = .13$.

Overall, these results are consistent with the RT data and, most importantly, indicate a contrast enhancement developing over time within trials for incongruent no-switch trials N preceded by a congruent trial $N-1$, as well as for incongruent switch trials N preceded by a another incongruent trial $N-1$.

Simulation

Although the results were consistent with our hypotheses, we are aware that the chosen novel approach of single-trial wavelet-based SSVEP amplitude analysis holds several uncertainties. First, the chosen bandpass filter and wavelet parameters could have a decisive influence on the results. Although we chose these parameters according to previous studies (Fuchs et al., 2008; Rodriguez et al., 1999; Tallon-Baudry et al., 1997), they have not been applied in combination to the analysis of single-trial SSVEP amplitude before. Second, the procedure of averaging across

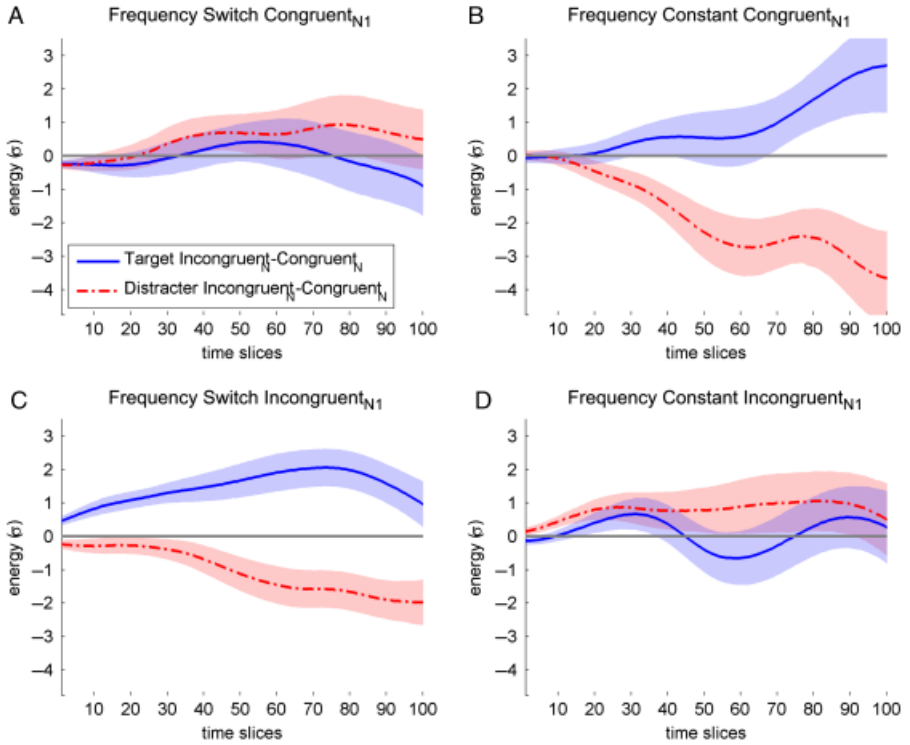

Figure 3. SSVEP amplitude contrasts (congruent – incongruent in current trial N), split up by frequency switch (A, C) and no-switch (B, D) and for congruency in the previous trial $N-1$ (congruent: A, B; incongruent C, D). Shaded areas show standard errors.

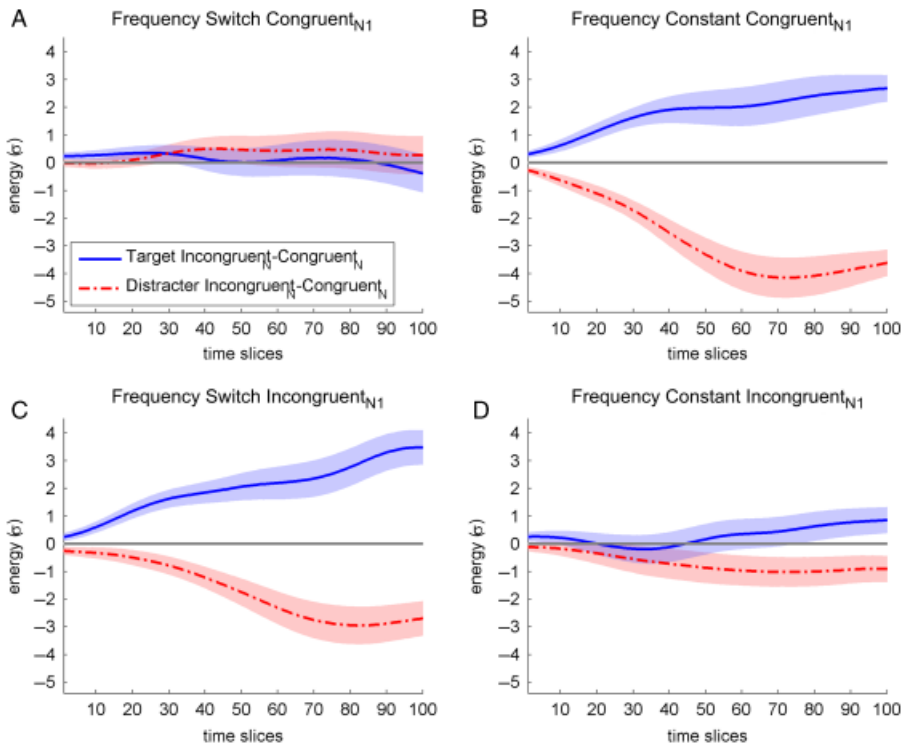

Figure 4. SSVEP amplitude contrasts of simulated surrogate data (congruent – incongruent in the current trial *N*), split up by frequency switch (A, C) and no-switch (B, D) and for congruency in the previous trial $N-1$ (congruent: A, B; incongruent C, D). Shaded areas show standard errors.

different frequencies could influence the results, because the extracted signals contain different temporal properties and baseline energy levels. By our standardization procedure, we tried to minimize theses influences (cf. Rodriguez et al., 1999, for a similar approach for synchronization values).

To minimize the possibility that these uncertainties decisively influenced our results, we chose to validate our methodological approach by surrogate data analysis. We modeled the expected EEG dat, by simulating SSVEP signals according to the properties of every single trial (i.e., congruency *N*, congruency $N-1$, flicker frequency of target and distracter, and frequency switch) of every participant. We created two sets of data: One set modeled the data under the hypothesis of within-trial readjustments (readjustment set). The other set modeled the data under the hypothesis of no readjustments within a trial (null set). We then analyzed the created surrogate data sets with the same procedure as the real data (see Figure 4).

Comparing the statistical contrast measures of real and surrogate data should reveal a high correlation for the readjustment set and a low correlation for the null set if our methodological approach was valid.

The modeling of data included the following steps. First, we modeled the respective amplifying and attenuating signals for the readjustment set as a linear response function, defined by the parameters start signal level, response time, and response signal level decay. These parameters were chosen in dependency on congruency *N*, congruency $N-1$, and frequency switch, according to our hypotheses and the behavioral findings (for parameter values, please see the supplementary material). For the null set, the signal levels followed the same parameters but stayed constant over time.

Second, the resulting signal was used to modulate sine waves of 9 and 12 Hz, according to the frequencies of the modeled trial. The overall amplitude of the sine waves was chosen to match previous SSVEP amplitude findings (Toffanin et al., 2009) for different frequencies. Similary, target/distractor signal strength was also set differently to account for the different size on the screen.

Third, this simulated SSVEP signal was mixed with random noise typical for EEG data (cf. Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007).

The resulting simulated data of the readjustment set for one participant are shown in Figure 5C,D). The grand averaged real contrast data and grand averaged surrogate contrast data revealed similar temporal profiles (see Figure 4) and show a high correlation, $r(10) = 0.95$, $p < .05$, for the readjustment set. In contrast, the real contrast data and surrogate contrast data for the null set showed no significant correlation, $r(10) = 0.28$, $p = .38$. Taken together, this strongly supports the validity of our method.

Discussion

The aim of the present study was to investigate if sequential conflict adaptation effects in a conflict trial *N* could represent a carryover of conflict-triggered attentional readjustments serving conflict resolution in the previous conflict trial $N-1$. To investigate the underlying within-trial dynamics of attentional readjustments, we used flicker frequency tagged stimuli in a modified version of the Eriksen flanker paradigm. The flickering stimuli elicited steady-state, visually evoked potentials in the EEG, serving as a continuous marker of the deployment of visual attention.

Behaviorally, we found reliable effects of conflict and across-trial conflict adaptation (sequential modulation of the flanker effect). As predicted, EEG data showed continuous within-trial

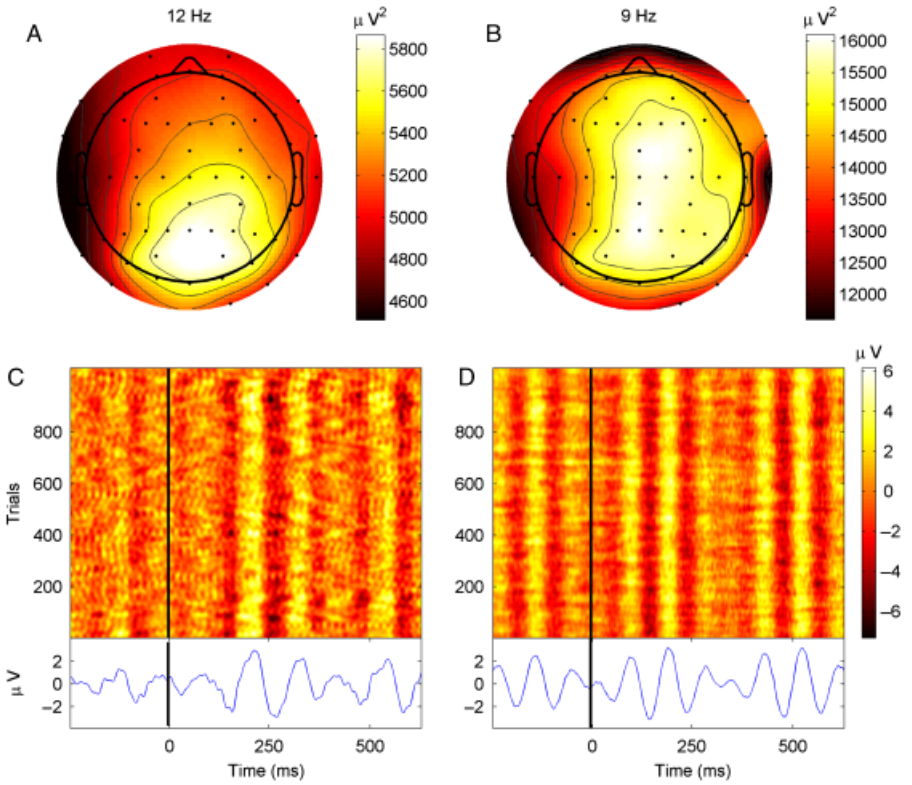

Figure 5. Grand average SSVEP topographies for 12 Hz (A) and 9 Hz (B). Below, the ERP image and ERP of one participant (C) in comparison to the simulated surrogate data for the same participant (D).

readjustments of control in the occurrence of conflict, as indicated by target- and distracter-specific changes of SSVEP amplitude within trials. The dynamics of these within-trial readjustments depended on previously experienced conflict, indicating a carryover of previous readjustments to the next trial as an effect of conflict adaptation. Hence, to our knowledge, our study is the first one to reveal the dynamics of conflict resolution and conflict adaptation in terms of continuous readjustments within trials carried over from trial to trial.

Importantly, the carryover of previous readjustments strongly depended on the repetition or switch of flicker frequencies tagging the target and distracter stimuli. On the one hand, for flicker frequency repetitions, we found conflict-triggered readjustments in incongruent trials N only if the previous trial $N-1$ had been congruent, and, therefore, no readjustments had occurred before the incongruent trial N. On the other hand, for flicker frequency switches, we found conflict-triggered readjustments for incongruent trials N only if the previous trial $N-1$ was incongruent, and, therefore, previous readjustments had been presumably directed at the wrong signal. Interestingly, this pattern of findings indicates that the seemingly task-irrelevant flicker frequency systematically modulated conflict-triggered readjustment processes.

At least two interpretations seem feasible to account for the finding of reliable conflict adaptation effects for flicker frequency repetitions but not for switches, both strengthening our preferred interpretation of conflict adaptation as a carryover effect. The first interpretation is in line with recent proposals of context-dependent conflict adaptation. In particular, many studies demonstrated that sequential modulations of interference effects critically depend on similarities between previous and current task requirements, leading to proposals of context-specific control adjustments (e.g., Fischer, Plessow, Kunde, & Kiesel, 2010; Kiesel, Kunde, & Hoffmann, 2006; Notebaert & Verguts, 2008; Spapé & Hommel, 2008). For example, sequential modulations of interference effects were eliminated when significant changes between trials occurred in irrelevant task features (Spapé & Hommel, 2008) or in global task parameters, such as single- or dual-task contexts (Fischer et al., 2010). Flicker frequency seems to be an important aspect of task context, even though flicker frequency was completely irrelevant to the task itself. Therefore, changing the frequencies that are associated with either the target stimulus or the distracter stimulus might provide a significant context change that eliminates the carryover of control settings and, thus, the sequential trial-to-trial effects. Importantly, from this retrieval-based view, assumptions of context-specific control adjustments and/or the retrieval of previous control settings do not challenge the assumption of sequential modulation effects reflecting carried over "control settings" that were necessary to resolve the conflict in trial $N-1$ (Spapé & Hommel, 2008), but just represent a different view on the processes underlying the phenomenon.

The second explanation can be derived from previous studies in the area of task switching (Brown et al., 2007; Goschke, 2000). For example, participants performing magnitude judgments (Task A) and parity judgments (Task B) on numbers are faced with congruent (numbers require the same response in both tasks) and incongruent trials (numbers require different responses in each task). Goschke found that switching between tasks produced slower RTs and increased switch costs if a task switch occurred between two incongruent trials. This has been interpreted as increased focusing on relevant information of Task A in the incongruent trial $N-1$.

Because, in case of a task switch, this Task A relevant information becomes now irrelevant for Task B, it interferes even more strongly with processing Task B in trial N. This stronger interference after task switch is due to the shift in attention to task-relevant features of the previous incongruent trial that are now irrelevant in the current incongruent trial.

Therefore, if conflict adaptation was a carryover of readjustments serving target selection under the occurrence of conflict, these results can be explained by a shift in attention to a feature of the currently active task. Under the assumption that flicker frequency might have captured participants' attention, although there was no explicit instruction to attend to it, a similar pattern of results could be expected. This interpretation is supported by three findings. First, different flicker frequencies activate different neural networks in the brain (Skrandies, 2007; Srinivasan, Bibi, & Nunez, 2006). If specific neural assemblies are activated more strongly when the information processed by these assemblies is in the focus of attention, this could explain this involuntary capture of attention. Second, the finding of slower reaction times in frequency switch trials compared to no-switch trials also mimics the pattern of RT in task switching, also supporting our assumption. Third, the context dependency of conflict adaptation on irrelevant contextual features described above also supports this interpretation (Spapé & Hommel, 2008). Our data even go one step further by showing a complete reversal of the adaptation effect in the RT data for incongruent trials as well as a reversal of the SSVEP amplitude readjustment effect after frequency switches.

Summarizing both interpretations, the effect of frequency switches provides even stronger support for our main hypothesis of carryover within trial readjustments and indicates one way control parameters can be carried over from one trial to another, dependent on task context information (Spapé, 2009).

Our results also add a new perspective to previous suggestions that conflict resolution is implemented as a process selectively inhibiting the wrong response (e.g., Ridderinkhof, 2002): According to our findings, within-trial readjustments of control contribute to conflict resolution by increasing the signal ratio between target and distracter in the case of conflict. Although this seems to contradict response-based conflict resolution at first sight, from a view based on a strong mutual connection between perception and action (e.g., Humphreys & Riddoch, 2003) one could naturally expect conflict-driven adjustments to interact at all stages in the processing stream. However, there is an important difference between the approach based on response inhibition and our approach based on readjustments of control by contrast enhancement. The selectively inhibited wrong response in trial $N-1$ would be carried over to trial N as an advantage for repetitions of the correct response in trial $N-1$. But only readjustments of control expressed as contrast enhancement could be carried over to trial N as an advantage for relevant information. Hence, only the latter one can provide the basis for conflict adaptation by a carryover from trial $N-1$.

Although most models based on conflict monitoring theory follow an interpretation assuming the conflict signal to be read out at the end of a trial to trigger adaptation for the next trial (e.g., Botvinick et al., 2001; Verguts & Notebaert, 2008), there is already some indirect evidence suggesting within-trial readjustments (Braver et al., 2007; e.g., Burle et al., 2002; Ridderinkhof, 2002). However, to the best of our knowledge, our study provides the first direct evidence for (a) the continuous adjustments of cognitive control within a trial and (b) the assumption that these control adjustments might be carried over to the subsequent trial, leading to typical conflict-adaptation effects.

It should be noted, though, that our results do not exclude the possibility of proactive control processes working in between trials as previously proposed by Braver et al. (2007). Our results indicate that conflict resolution within trials and conflict adaptation across trials are not necessarily independent processes. Alhough this, in particular, contrasts with the original work on conflict adaptation (Botvinick et al., 2001) it provides the possibility to specify more precisely the relationship between reactive and proactive modes of control (Braver et al., 2007). Conflict resolution as a result of reactive adjustments and conflict adaptation are interwoven processes at different time scales influencing each other continuously.

Based on the accumulating evidence of within-trial readjustments, it is tempting to question the role of the ACC as a trigger module that signals conflict for future control adaptation. A different and in our view more parsimonious explanation can be provided by the assumption of carryover mechanisms (e.g., Gilbert & Shallice, 2002). In a carryover model, conflict could be resolved by continuous competition between conflicting input (cf. Eriksen & Schultz, 1979; Usher & McClelland, 2001) under the influence of PFC activation patterns representing task instructions and interacting reciprocally with the input. In the case of conflict, these interactions lead—as a by-product of conflict resolution within the conflict trial—to amplification of the relevant goal and processing pathway and/or to suppression of the irrelevant goal and processing pathway. Assuming that this amplification/suppression needs time to decay and thus persists until the next trial (Gilbert & Shallice, 2002), it could account not only for task-switching effects but also for sequential conflict-adaptation effects in terms of a passive by-product of conflict resolution on the previous trial. Hence, instead of an explicit subsystem, monitoring and transferring information about conflict, this model provides a simpler explanation: Conflict adaptation across trials could be the result of the network interaction dynamics necessary for conflict resolution within a conflict trial (see also Mayr & Awh, 2009). Although it is beyond the scope of a single paper to decide between these alternative explanations, it is noteworthy that this model would be consistent with accumulating evidence suggesting that the ACC as an alleged conflict-monitoring system is not necessary for all instances of conflict adaptation (Mansouri et al., 2009). Moreover, the model would also be consistent with the effects of flicker frequency switches we obtained: If different networks activated by different flicker frequencies (Skrandies, 2007; Srinivasan et al., 2006) are part of the relevant/irrelevant pathways, their amplification or suppression in one trial should indeed have the effect that more time is required to readapt after a frequency switch.

In conclusion, to our knowledge our study is the first one to directly trace the dynamics of conflict adaptation within trials by studying a continuous marker of the deployment of visual attention. Because our approach represents a novel combination of several techniques, we used the analysis of computationally simulated surrogate EEG data to confirm the validity of the chosen methods and parameters. Although further studies will be required to examine the generalizability of our findings across additional experimental variations (e.g., holding flicker frequencies constant over blocks of trials), this study provides a first step to continuously trace the dynamics of cognitive control and provides evidence for a model of conflict adaptation in terms of within-trial readjustments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Model formulas for calculating EEG surrogate data.

Table S1: Hypothesized adaptation per condition.

Table S2: Parameter values for modelling the surrogate EEG data.

Appendix S2: Model for stimulus-response locked EEG analysis.

Figure S1: 200 simulated trials, sorted by RT and arranged for stimulus-locked, response-locked and stimulus-response locked analysis.

Figure S2: Averaged signals for different methods ('ERPs') and average signal changes within a trial for these methods.

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