



Neural cascade of conflict processing: Not just time-on-task



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ARTICLE INFO

Keywords:

Conflict processing
Task difficulty
Cognitive control
Time-on-task
EEG

ABSTRACT

In visual conflict tasks (e.g., Stroop or flanker), response times (RTs) are generally longer on incongruent trials relative to congruent ones. Two event-related-potential (ERP) components classically associated with the processing of stimulus conflict are the fronto-central, incongruency-related negativity (N_{inc}) and the posterior late-positive complex (LPC), which are derived from the ERP difference waves for incongruent minus congruent trials. It has been questioned, however, whether these effects, or other neural measures of incongruency (e.g., fMRI responses in the anterior cingulate), reflect true conflict processing, or whether such effects derive mainly from differential time-on-task. To address this question, we leveraged high-temporal-resolution ERP measures of brain activity during two behavioral tasks. The first task, a modified Eriksen flanker paradigm (with congruent and incongruent trials), was used to evoke the classic RT and ERP effects associated with conflict. The second was a non-conflict control task in which, participants visually discriminated a single stimulus (with easy and hard discrimination conditions). Behaviorally, the parameters were titrated to yield similar RT effects of conflict and difficulty (27 ms). Neurally, both within-task contrasts showed an initial fronto-central negative-polarity wave (N2-latency effect), but they then diverged. In the difficulty difference wave, the initial negativity led directly into the posterior LPC, whereas in the incongruency contrast the initial negativity was followed by a second fronto-central negative peak (N_{inc}), which was then followed by a considerably longer-latency LPC. These results provide clear evidence that the longer processing for incongruent stimulus inputs do not just reflect time-on-task or difficulty, but include a true conflict-processing component.

1. Introduction

In our daily life, we are constantly exposed to a wide variety of activities requiring actions contrary to habitual or automatic responses. Such goal-oriented behaviors require adaptive cognitive control processes to overcome situational interference and select the correct behavior, and are critical for the successful navigation of our complex environments.

In experimental settings, paradigms employing conflicting stimulus inputs have been used extensively as a tool to investigate the cognitive control mechanisms that are marshaled to address such conflict and choose the correct responses (Botvinick et al., 2001). Some classic conflict experimental paradigms (e.g., Stroop, flanker; see below) have consistently shown that conflicting (or incongruent) stimulus inputs (relative to nonconflicting or congruent ones) lead to decrements in behavioral performance, as reflected by slower response times (RTs) and lower accuracy. From a neural standpoint, studies using these

tasks while recording various measures of brain activity, such as functional MRI (fMRI) and event-related potentials (ERPs), have found differential brain activity for conflicting versus nonconflicting inputs. It has proven difficult, however, to demonstrate whether the neural effects of conflict, as gauged by differences between the processing of conflicting and nonconflicting stimulus inputs, are truly specific to the processing of conflict, or whether they result mainly from differential time-on-task (longer for the incongruent trials), perhaps just due to greater difficulty (Carp et al., 2010). The goal of the present study was to directly examine this question, leveraging the high temporal resolution of ERPs.

Stimulus conflict occurs due to the presence of task-irrelevant perceptual information that interferes with the processing of task-relevant information (Kornblum, 1994). For example, in the classic Stroop conflict paradigm (Stroop, 1935; for a review see MacLeod, 1991), subjects are asked to name the font color of a displayed color word. RTs are slower when the font color and color word are not the

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<http://dx.doi.org/10.1016/j.neuropsychologia.2016.12.022>

Received 7 February 2016; Received in revised form 18 December 2016; Accepted 21 December 2016

Available online 23 December 2016

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same (incongruent – e.g., the word RED shown in blue font) than when the two colors match (congruent – e.g., RED shown in red font). It is postulated that this observed behavioral effect is due to the strongly automatic response of word reading interfering with the task goal of identifying and responding correctly to the font color. In the flanker conflict task, originally developed by Eriksen and Eriksen (1974), subjects are instructed to identify the central item (e.g., one of two possible letters) in a multi-item array. Here, instead of the irrelevant color word providing conflict, the surrounding items can induce conflict when they do not match the central one (e.g., ‘SSHSS’), due to the competing representations of the more numerous “flankers” needing to be ignored. This results in slower RTs in response to incongruent arrays as compared to congruent arrays (e.g., ‘SSSS’).

Neurally, ERP studies have revealed several hallmark brain-activation effects derived from the incongruent versus congruent contrast, which have generally been interpreted as reflecting the processing of the conflicting input present in the incongruent trials. One widely cited neural marker of conflict processing is the incongruency negativity (“N_{inc},” sometimes referred to as the N450), which peaks around 450 ms post-stimulus over midline central scalp locations (Appelbaum et al., 2014; Badzakova-Trajkov et al., 2009; Coderre et al., 2011; Liotti et al., 2000; Rebai et al., 1997; Tillman and Wiens, 2011; West and Alain, 2000). This negative-polarity ERP effect, most associated with the Stroop task, is thought to arise in part from activation of the anterior cingulate cortex (ACC) in the prefrontal cortex (Carter and van Veen, 2007; Liotti et al., 2000), a brain region that has correspondingly been found with fMRI to activate in response to incongruent trials relative to congruent trials in conflict paradigms (Larson et al., 2009; Szűcs and Soltész, 2012; West et al., 2004).

The flanker task also produces a conflict-related negative-polarity effect that is commonly isolated by contrasting the incongruent minus congruent conditions. This effect typically also has a midline-central scalp distribution, but can occur somewhat earlier (250–400 ms), especially with simpler stimuli (e.g., arrows), partially overlapping the N2 deflection of the ERP (Bartholow et al., 2005; Danielmeier et al., 2009; Folstein and Van Petten, 2008; Frühholz et al., 2011; Heil et al., 2000; Tillman and Wiens, 2011). Using modified Eriksen flanker stimuli, previous work has shown a positive relationship between the N2-latency effect and increasing stimulus incompatibility (Forster et al., 2011), suggesting that this effect specifically indexes spatial conflict processing. Moreover, the N2-latency effect has been demonstrated to index conflict adaptation, with its amplitude decreasing during the second of two consecutive incongruent trials (Forster et al., 2011; Larson et al., 2012; Larson and Clayson, 2011), while the N_{inc} typically has not, suggesting differential cognitive functions associated with these components (Larson et al., 2014). Nevertheless, it remains unclear whether the N_{inc} and N2-latency conflict effects reflect the same cognitive process occurring at distinct temporal stages of conflict processing, due to task-specific conflict manipulations, or their mechanisms are fundamentally different, potentially due to the recruitment of different subregions of ACC or nearby cortical areas.

An additional ERP component of interest associated with the temporal cascade of conflict processing is a posteriorly-distributed positive wave known as the late positive complex (LPC, also termed “conflict slow potential”). This hallmark activation is characterized by a long-duration positive-polarity wave that is larger for incongruent relative to congruent trials, with the differential processing onset at around 500 ms post-stimulus (Appelbaum et al., 2009; Coderre et al., 2011). The LPC has been evoked particularly robustly in EEG studies of the Stroop task (Appelbaum et al., 2009; Coderre et al., 2011; Liotti et al., 2000; West and Alain, 2000) and is believed to reflect either processing of semantic meaning of words, due to its oft-observed greater magnitude over left hemisphere (Liotti et al., 2000; West and Alain, 2000), or processes important for trial-by-trial conflict adaptation (Donohue et al., 2012; Larson et al., 2009). Previous studies using the Eriksen flanker task have reported more varied LPC effects, in

terms of both amplitude and latency (Appelbaum et al., 2011; Donohue et al., 2012).

Previous experiments using fMRI have suggested that controlling for RT differences eliminated the effects of response conflict on the fMRI measures of brain activity (Carp et al., 2012, 2010), meaning that such conflict effects may really just be due to differential time-on-task, namely due to processes not specifically related to conflict, such as autonomic arousal or cognitive effort. Similarly, there has been controversy over the role of medial prefrontal cortex (mPFC) in conflict processing. For instance, Grinband et al. (2011a) reported correlations between dorsal medial frontal cortex (dmFC) activity and time-on-task during incongruent trials, rather than with conflict more generally. These findings from Grinband et al. suggest that the previously described role of dorsal prefrontal and anterior cingulate cortex, namely detection of conflict and signaling for increased cognitive control (Botvinick et al., 2001), might be insufficient for explaining conflict processing effects. The results from Grinband et al. (2011a) were not without controversy, however, as Yeung et al. (2011) questioned the validity of their simulations of dmFC activity and argued that the reported results are predicted by, rather than in direct conflict with, the conflict monitoring theory (for the response from Grinband and colleagues, see also Grinband et al., 2011b). To account for these and other experimental findings from fMRI and monkey neurophysiology, it has been alternatively theorized that mPFC performs the cognitive functions of predicting the outcomes of all possible actions, comparing these predictions against the actual outcomes, and updating outcome predictions based on discrepancies between previous predictions and their outcomes (Alexander and Brown, 2010; Brown, 2011).

Moreover, there has been little study as to whether the ERP effects elicited in conflict tasks, specifically the midline central negative-polarity effect and the LPC, reflect conflict detection per se or instead may reflect differential time-on-task, due to the slower RTs observed for trials consisting of conflicting stimulus inputs. However, it would be necessary to understand the influence of RT on brain activation, in the absence of conflict, to properly elucidate the cognitive control mechanisms responsible for the negative-polarity and LPC effects observed in these earlier studies. A meta-analysis of positron emission tomography (PET) research concluded that task difficulty is an important factor in modulating activity in the ACC, citing possible interactions with response modification and working memory demands (Paus et al., 1998). In terms of ERPs, the negative-polarity conflict effect often appears as a relative negative deflection partially encompassing the P3 (P300) raw ERP wave (Liotti et al., 2000; West and Alain, 2000), and the latency of the P3 has been associated with variations in RTs in the presence of stimulus incongruency (Doucet and Stelmack, 1999). Additionally, several studies have reported positive correlations between RTs and P3 amplitudes resulting from task difficulty (Verleger et al., 2014) and response compatibility (Doucet and Stelmack, 1999), suggesting a possible overlap in brain activation due to the similar effects of both difficulty and conflict on RTs. Accordingly, it remains possible that independent manipulations of conflict and difficulty might evoke similar neural activity effects, which would suggest that much of the putative effects of conflict are actually just the result of time-on-task arising simply from difficulty differences.

In the present study we aimed to determine whether the neural effects associated with conflict manipulation do indeed reflect processes specific for conflict detection and processing in response to incongruent stimuli, rather than resulting from just time-on-task or difficulty. For the measures of brain activity, we focused on the midline central negative-polarity effect and the posteriorly-distributed LPC, classic neural markers that have been associated with stimulus conflict processing. We utilized two behavioral tasks, a version of the Eriksen flanker task (with incongruent and congruent trials) and a visual discrimination task (with difficult versus easy discrimination levels). We titrated the parameters within these conditions so that the RT

differences for the conditions within each task (incongruent versus congruent and difficult versus easy) were similar. This titration approach helped ensure that our ERP results would reflect the specific effects of incongruency and of discrimination difficulty, rather than differences in time-on-task unique to each condition or an interaction between task and condition. We predicted that the within-task incongruent versus congruent contrast and the hard versus easy contrast would elicit some similar ERP components, as well as some unique ones, lending credence to the notion that the associated neural mechanisms are not just due to differential time-on-task or difficulty.

2. Methods

2.1. Subjects

A total of 35 healthy subjects (ages 18–35 years, mean 24 years, SD: 5.0 years; 19 female; 2 left-handed) participated while their EEG was recorded. All participants gave written informed consent as reviewed in accordance with the Duke Medical Center Institutional Review Board, and were paid a compensation of 15 dollars per hour for their time. Data from two subjects were excluded from further analysis due to technical errors during the EEG recording session and high levels of noise in the EEG data. Data from 13 of the remaining participants were excluded from ERP analysis as the result of the RT titration process (see Section 2.6 “RT titration process” below for more details).

2.2. Stimuli and task

The experimental design consisted of two behavioral tasks (Fig. 1) to independently manipulate the effects of conflict and task difficulty. The flanker task was used to induce conflict (incongruent versus congruent trials), while the difficulty task was a control for time-on-task (difficult discrimination versus easy discrimination). For each task, subjects were instructed to respond based on which gap (upper versus lower) in the presented target circle was perceived to be larger. The two gaps were each a set width in the flanker task, but the two circles flanking the middle attended target circle on each side either matched the center circle (congruent) or were flipped to be opposite from the configuration of the center circle (incongruent). In the difficulty task, only one circle was presented but the large gaps varied in size, relative to the smaller gap, from trial to trial to create easy and difficult conditions. The stimuli were adapted from a prior study investigating the effects of spatial attention on reward processing (Krebs et al., 2012). For both tasks, the target was presented just below the fixation

cross in the middle of the screen, with equal trial-by-trial probability for the larger gap being on the top or bottom for each trial. There was a 50–50 distribution of congruent and incongruent trials in the congruency flanker task and of easy and hard trials in the difficulty discrimination task. In both tasks, participants responded by pressing buttons on the back of a game controller with the right hand, using their index finger to press the top button and their middle finger to press the bottom button.

2.3. Procedure

All stimuli were presented on a 24 in. computer monitor (1920 × 1080 resolution, 120 Hz refresh rate) in a dimly lit room. Subjects were seated at a viewing distance of 57 cm and fixated on a visual cross in the center of the screen throughout the task. The behavioral paradigm consisted of two blocks for each task (presented in ABAB order, with the first presented task counterbalanced across subjects), for a total of four blocks in an hour. Participants performed 30 practice trials prior to beginning each of the four blocks, during which brain activation was not recorded. An accuracy rate of at least 90% on the practice was required to advance to the experimental block; otherwise the practice trials were repeated. The four EEG blocks consisted of 400 trials each. During each block, participants were presented with brief breaks (5 s duration) every 15 trials, with longer breaks (20 s duration) every 150 trials.

2.4. Data acquisition and analysis

The brain electrophysiological activity of each participant was recorded via a custom-designed, extended-coverage 64-channel electrode cap furnished with active electrodes (ActiCap, Brain Products, Gilching, Germany). An online bandpass filter of 0.01–250 Hz was used on a BrainAmp MR-Plus amplifier (Brain Products) with a sample rate of 500 Hz per channel. Impedances of all channels were kept below 15 k Ω (which was easily sufficient due to the active nature of the electrodes), and fixation on the central cross was monitored with both horizontal and vertical EOG recordings. Data were referenced to the right mastoid during recording, but were re-referenced offline to the algebraic average of the left and right mastoids.

Offline data analyses were performed using EEGLAB (Delorme and Makeig, 2004). EEG data were epoched from 500 ms prior to 1000 ms after the onset of each stimulus. Trials containing a correct response between 200 and 1000 ms following stimulus onset were time-locked averaged, re-sampled at 250 Hz, and filtered using a 0.1–60 Hz bandpass causal FIR filter, with a 6 dB roll-off. Independent component analysis (ICA) was conducted in EEGLAB to remove eyeblink artifacts from the epochs. Additional ERP analyses were performed using the FieldTrip toolbox for EEG/MEG analysis (Oostenveld et al., 2011). Difference wave contrasts for each task were computed by subtracting the average response for each condition (i.e., hard minus easy and incongruent minus congruent). Finally, the ERP averages were baseline corrected from –200 to 0 ms.

Additionally, artifact rejection with an amplitude threshold titrated for each subject was used to reject epochs containing non-blink artifacts (eye movements, muscle tension, and channel drift). Artifact rejection thresholds (mean: 86 μ V, SD: 9 μ V) were chosen based on visual inspection of the EEG data, but applied blind to both trial type and behavioral performance, to maximize the number of included trials while minimizing artifacts. On average, 16% of correct trials were rejected in each condition due to artifacts, which did not differ between conditions (difficulty vs. congruency; $F(1,32)=0.269$, $p=0.605$, $\eta_p^2 < 0.001$, condition (e.g., easy/congruent vs. hard/incongruent; $F(1,32)=0.031$, $p=0.862$, $\eta_p^2 < 0.001$), or an interaction of task and condition ($F(1,32)=0.015$, $p=0.901$, $\eta_p^2 < 0.001$).

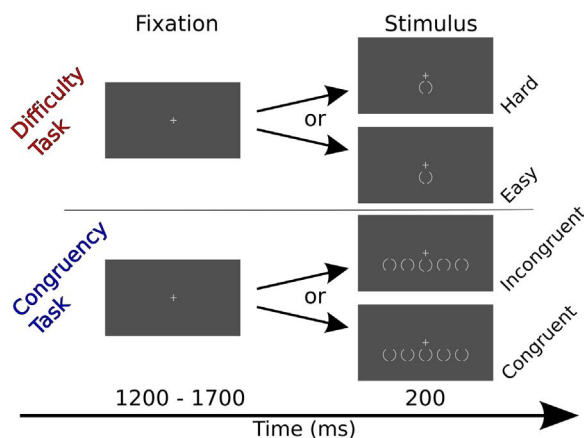


Fig. 1. Visual representation of the two task paradigms. On top is a sample trial for the difficulty task (with either an easy or hard gap discrimination required on each trial) and on the bottom is a sample trial for the flanker task (with either a congruent or incongruent stimulus array in each trial). Each task was presented in a blocked format with two blocks per task (ABAB format), randomized across subjects.

2.5. Statistical analyses

Behavioral data were analyzed and plotted using the statistical programming package R (R Core Team, 2014). A factorial 2×2 repeated-measures analysis of variance (rANOVA), within subject design, was conducted on the RT and accuracy effects of two factors: task (difficulty vs. congruency) and within-task condition (easy/congruent vs. hard/incongruent). In addition, after performing behavioral analysis to exclude incorrect trials and EEG preprocessing to remove artifacts from our data, we verified that the number of trials included in the ERP analysis did not differ with respect to task or condition (see section “Analysis of possible signal-to-noise differences due to artifact rejection” of the [Supplementary Material](#)).

We also performed sequential analyses for each task (Gratton et al., 1992) to examine the interaction between previous and current trial type (see “Sequential analyses” section and [Supplementary Figure 1 of the Supplementary Material](#)).

ERP data were analyzed to test for significant effects in two *a priori* regions of interest (ROIs). The fronto-central ROI consisted of four electrode sensors: midline sensors Cz and FCz and more lateral sensors C1a and C2a, just anterior to C1 and C2, respectively. These fronto-central electrode sensors have been shown to be the site of the topographic maximum of the N_{inc} in earlier studies (Appelbaum et al., 2011; Donohue et al., 2016). The four sensors in the centroparietal ROI included sensor Pz, the previously-reported topographic maximum of the LPC (Appelbaum et al., 2011), and three other nearby electrode sensors: CPz, CP3a, and CP4a. We assessed the onset and duration of ERP effects within our two ROIs using cluster-based permutation statistics. This approach was chosen to limit potential biases and to account for multiple comparisons (Maris and Oostenveld, 2007). Cluster-based analysis consists of converting the data for each ROI separately to t -values, then neighboring time-points that reached a critical t -value (of which $p < 0.05$) were clustered and the corresponding t -values summed to reach a cluster statistic. Subsequent statistical significance was determined by means of permutation. In the permutation approach, data labels for the conditions to be compared (e.g., hard vs. easy in the difficulty task) were shuffled and permuted 10,000 times, calculating a t -statistic for each permutation and giving rise to a null-distribution to which the cluster-statistic of the real labels could be compared. We report all clusters that reached a significance level of $\alpha = 0.05$.

2.6. RT titration process

Data from subjects who did not exhibit a robust behavioral effect in either task (i.e., RT slowing for incongruent versus congruent trials or difficult trials versus easy trials) were excluded from additional behavioral or ERP analyses. This selection was performed to ensure well-matched behavioral effects between the two behavioral tasks,

preventing significant differences between the RT effects in the two tasks from influencing or biasing the analyzed ERP results. The criteria for this exclusion, blind to individual subjects’ performance, were defined as having a very small incongruency or difficulty RT effect (< 5 ms between the average incongruent and congruent conditions or average hard and easy conditions, respectively) and/or greatly varying RT effects between the two tasks (> 30 ms difference between the two RT effects). Based on these criteria for exclusion, 13 of the original 33 participants were excluded from further analyses. Of the 13 participants excluded in this RT titration process, 3 were excluded for not displaying a behavioral effect of congruency (< 5 ms), 4 were excluded for showing a large difference in behavioral effects between the two tasks (> 30 ms), and 6 were excluded for exhibiting both a small effect of congruency and a large difference in the two behavioral effects. No participants needed to be excluded for not displaying a behavioral effect of difficulty. To verify the validity of this procedure by ensuring unintended effects were not introduced through this RT titration process, we also analyzed the behavioral and ERP results both from the subjects who met the standard for inclusion as well as for the original 33 subjects (see [Supplementary Figures 2 and 3](#)).

3. Results

3.1. Behavioral performance

The subjects in the post-RT titration group ($N=20$) had slower RTs for the incongruent condition relative to the congruent condition in the flanker task (**Incongruent $M=473$ ms** (± 56), **Congruent $M=447$ ms** (± 52)), as well as slower RTs for the hard condition relative to the easy condition in the difficulty task (**Hard $M=465$ ms** (± 57), **Easy $M=437$ ms** (± 50)). The RT difference for the two within-task conditions was approximately 27 ms ([Fig. 2](#), left), with a significant main effect of condition (easy/congruent vs. hard/incongruent) when collapsing across the two tasks ($F(1,19)=5.15$, $p=0.026$, $\eta_p^2=0.060$). We also noted slightly slower RTs overall in the flanker task relative to the difficulty task, but this effect of task on RTs was not significant ($F(1,19)=0.59$, $p=0.44$, $\eta_p^2=0.008$). Furthermore, as expected due to the RT titration process, the interaction of task and condition was also not significant ($F(1,19)=0.0019$, $p=0.97$, $\eta_p^2 < 0.001$).

We also investigated these effects prior to the RT titration process. For all subjects ($N=33$), the effect of condition (easy/congruent vs. hard/incongruent) on RT was significant ($F(1,32)=4.85$, $p=0.029$, $\eta_p^2=0.037$), but the effects of task ($F(1,32)=0.012$, $p=0.91$, $\eta_p^2 < 0.001$) and the interaction of condition and task ($F(1,32)=0.48$, $p=0.49$, $\eta_p^2 < 0.001$) were not significant, reflecting the same findings we observed in the post-RT-titration group for the subsequent ERP analyses ([Supplementary Figure 2](#), left panel).

Post-RT titration participants had an average error rate of 5.3%

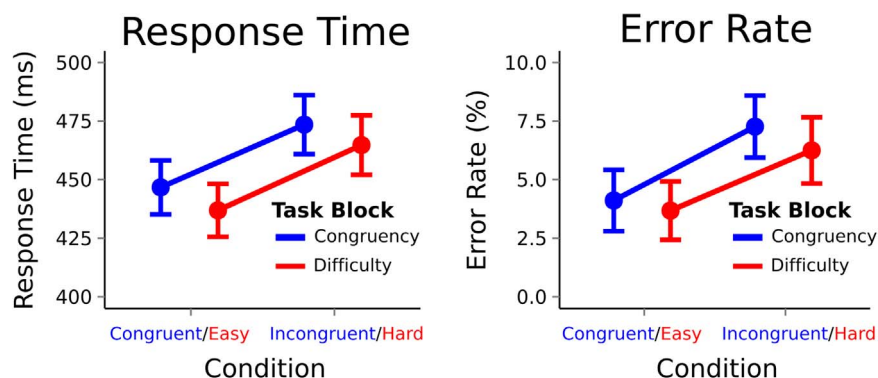


Fig. 2. Behavioral results. Subjects were slower to respond in the incongruent (versus congruent) condition and in the hard (versus easy) condition (left panel). Subjects made fewer errors when responding to congruent (versus incongruent) and easy (versus hard) trials (right panel). Error bars represent the SEM.

collapsed across the four behavioral conditions (Fig. 2, right). As expected, more errors were committed in the incongruent condition relative to the congruent condition (**Incongruent $M=7.3\%$** (± 5.9), **Congruent $M=4.1\%$** (± 5.8)), and during hard trials relative to easy trials (**Hard $M=6.2\%$** (± 6.3), **Easy $M=3.7\%$** (± 5.6)). The main effect of condition (easy/congruent vs. hard/incongruent) was significant ($F(1,19)=4.68$, $p=0.034$, $\eta_p^2=0.058$), but neither the effect of task (difficulty task vs. congruency task) nor the interaction of task and condition were significant ($F(1,19)=0.30$, $p=0.59$, $\eta_p^2=0.004$; $F(1,19)=0.049$, $p=0.83$, $\eta_p^2 < 0.001$). Again, additional analysis confirmed that the RT titration process did not skew these effects (Supplementary Figure 2, right panel). More specifically, when all subjects were included ($N=33$), only the within-task effect of condition on accuracy was significant ($F(1,32)=5.43$, $p=0.021$, $\eta_p^2=0.040$), whereas the effects of task ($F(1,32)=0.38$, $p=0.54$, $\eta_p^2=0.003$) and the interaction of task and condition ($F(1,32)=0.066$, $p=0.80$, $\eta_p^2 < 0.001$) remained not significant.

3.2. ERPs

For both the difficulty and congruency tasks, we derived ERP difference waves between the two conditions within each task, namely for the hard minus easy trials and for incongruent minus congruent trials, respectively (Fig. 3). Utilizing difference wave contrasts allows for direct comparison between the two tasks because the raw sensory differences subtract out, thus isolating the effects of the congruency and difficulty manipulations. A permutation approach was used to identify significant ERP effects in these difference waves by comparing the two constituent raw waves (see Section 2.5 “Statistical analyses” above), and by comparing these two difference waves to each other to highlight differences in processing between the two tasks.

In the difficulty task, the first electrophysiological difference for hard minus easy trials was notable for its negative-polarity deflection in the fronto-central channels (Fig. 3, right). This negativity occurred from around 296–356 ms after target stimulus onset (mean amplitude: $-0.92 \mu\text{V}$, SD: $0.15 \mu\text{V}$; $p=0.040$). Following this negativity, the activity transitioned to a posteriorly-distributed positive slow wave (larger

positivity for hard as compared to easy trials), lasting from 416 to 652 ms (mean amplitude: $+1.55 \mu\text{V}$, SD: $0.43 \mu\text{V}$; $p < 0.001$).

In contrast, the incongruent minus congruent difference wave from the flanker task showed a longer-duration negativity encompassing two peaks of activity, the first more fronto-central, and the second more centro-parietal. Notably, the early part of this conflict-derived effect had a similar onset and similar time course as the negativity derived from the hard minus easy difference wave, but then clearly diverged as it continued on to the second negativity (Fig. 3, right). The first negativity in the incongruency contrast peaked between 300 and 388 ms (mean amplitude: $-0.93 \mu\text{V}$, SD: $0.25 \mu\text{V}$; $p=0.005$) and the second between 416 and 488 ms (mean amplitude: $-0.91 \mu\text{V}$, SD: $0.19 \mu\text{V}$; $p=0.019$). Over parietal channels, there was a single positivity in the conflict-derived difference waves, from 576 to 756 ms (mean amplitude: $+1.72 \mu\text{V}$, SD: $0.36 \mu\text{V}$; $p < 0.001$), occurring later as compared to the positivity in the difficulty contrast.

Similar to our behavioral results, our ERP findings were relatively unaffected by our RT titration process. Analysis of all 33 subjects shows similar latencies and durations for these ERP components relative to our findings from the 20 participants in the post-RT titration group, with a more posterior distribution of the difficulty N2-latency effect and a more continuous effect in the congruency difference wave across the latency of the two-peak N2/N_{inc} complex (Supplementary Figure 3).

The topographic plots of the of the hard minus easy difference wave (Fig. 4, top row) reveal the shift from the roughly 300–360 ms frontal negativity to the large posterior positivity from about 420–660 ms. The longer-lasting negativity in the incongruent minus congruent difference wave topographic plots (Fig. 4, bottom row) gives way to a topographic shift, moving more posterior and changing polarity beginning around 580 ms after stimulus onset. Additionally, the significant positivity in parietal channels beginning around 580 ms has a much later onset compared to the positivity in the difficulty difference wave. The similar distributions of the early fronto-central negative components lend further evidence to shared cognitive processes being recruited in that time window by both tasks. Additionally, these topographic plots also show the more posterior distribution of the late positivities, even though they occur at different latencies in the two difference waves.

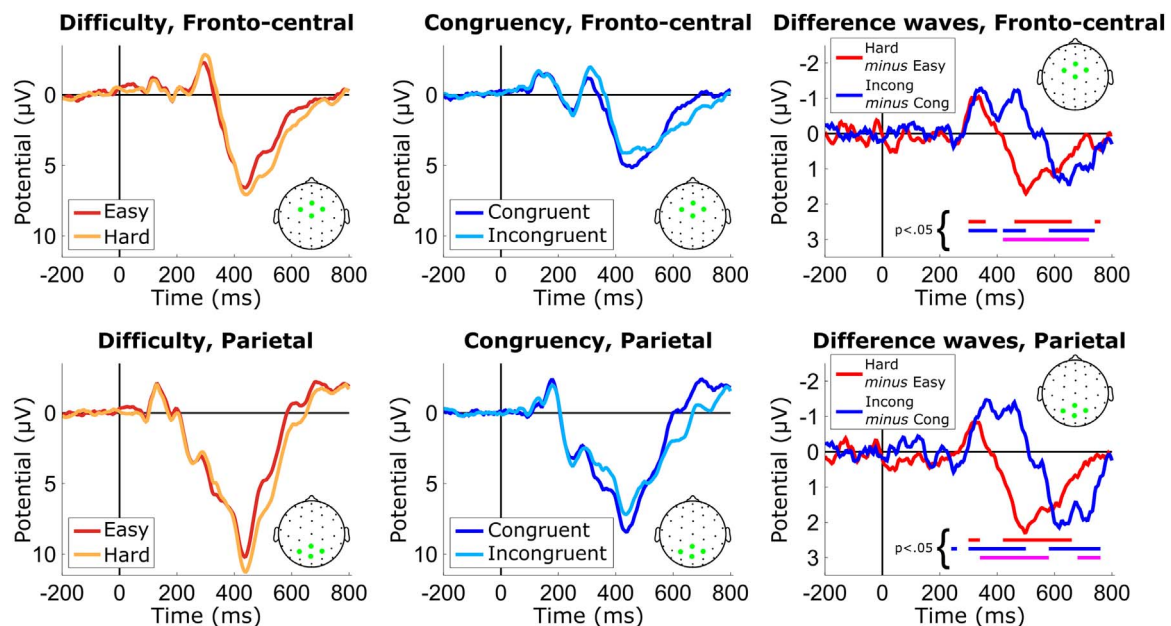


Fig. 3. ERP raw waves (left and middle panels) and difference waves (right panel) for each task. The difficulty task is shown on the left and the congruency task in the middle. Fronto-central channels are shown in the top row and parietal channels are shown in the bottom row of each of the columns (traces are averaged ERPs within each of our two *a priori* ROIs, as shown in the green colored channels highlighted next to each panel). For the difference waves, horizontal lines below the difference waves indicate time ranges identified in our permutation tests where the differences between constituent raw waves were significant ($p < 0.05$) for the difficulty difference wave (red), the congruency difference wave (blue), and the difference between the two difference waves (magenta). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

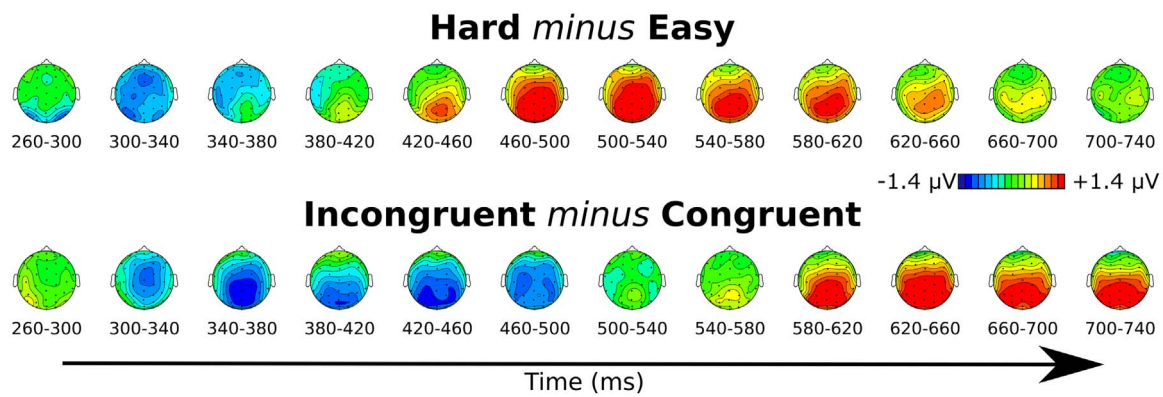


Fig. 4. Difference wave topographic plots for the difficulty task (top) and congruency task (bottom). The difference waves are plotted in 40 ms bins, from 260 to 740 ms post-stimulus.

4. Discussion

The current study examined whether the neural effects associated with conflict result solely from conflict-specific processing, or rather from the effects of differential time-on-task due to enhanced difficulty, as measured by longer RTs for incongruent trials. We created conflict and difficulty tasks, with similar target stimuli, using a variant of the Eriksen flanker task and a visual discrimination task, respectively. RT effects were well matched between the conflict and difficulty tasks after excluding participants who did not exhibit robust behavioral effects in either task.

The observed patterns of brain activation in the ERP difference waves for each task both included early fronto-central negativities (early N2-latency effect), with onsets around 300 ms post-stimulus, followed by a longer-latency, posterior positive slow wave (LPC). However, in the incongruency difference wave we also observed a sustained second negative peak that was consistent with the N_{inc} between these two other neural effects. The temporal differences and spatial similarities between the components in each difference wave supports the notion that there are some overlapping and some dissociable cognitive mechanisms underlying conflict processing and difficulty processing.

4.1. Behavioral results

As expected, subjects were slower to respond on the hard and the incongruent trials relative to the easy and the congruent trials, respectively. After excluding data from subjects who did not exhibit robust behavioral effects in either task, we obtained well-matched RT effects between the congruency and difficulty tasks, effectively eliminating time-on-task as a potential confounding variable from subsequent ERP analyses.

4.2. Electrophysiological results

4.2.1. Differential cascade of neural activity for conflict and difficulty

This fronto-central negativity in both the difficulty and congruency difference waves, beginning around 300 ms post-stimulus, was the first significant neural marker of differential processing between the hard and easy trials and between the incongruent and congruent trials. Particularly striking was the close correspondence of the time course of this early negativity for the two contrasts over fronto-central scalp, which then diverged dramatically at around 350–390 ms for the two tasks. More specifically, the divergence of the two difference waves was characterized by the difficulty contrast proceeding to an early, robust, posteriorly distributed LPC, whereas the incongruency contrast transitioned to a second negativity that was somewhat more posterior (central-parietal) than the first, and then to a posterior LPC that was elicited considerably later in time.

4.2.2. Early N2 effect in common for the two tasks

The presence of a similar early N2-latency effect in both of the difference waves suggests it reflects a process that has some commonality between the two tasks. Behaviorally, the more difficult perceptual discrimination in the difficult trials and the presence of distracting flankers in the incongruent trials both led to slower RTs and higher error rates. Thus, this early negative-polarity effect may reflect detection of a more cognitively demanding, more difficult condition in a given trial, or perhaps some supplemental allocation of attentional resources for such a condition (Tillman and Wiens, 2011). This idea of allocating attentional resources is consistent with several fMRI studies showing increased activation of medial prefrontal cortex with greater time-on-task in tasks both with and without manipulations of conflict (Grinband et al., 2011a; Weissman and Carp, 2013). Although anterior N2-latency effects have been reported separately in EEG studies of both visual-discrimination difficulty and conflict processing, this effect was observed in response to both due to our use of nearly-identical target stimuli for both tasks, under circumstances where the RT effects were matched. This negativity in the difficulty difference wave is consistent with the N2b component, which has previously been demonstrated to be amplitude modulated by the difficulty in both visual discrimination (Senkowski and Herrmann, 2002) and auditory detection tasks (Guo et al., 2010). On the other hand, the timing of this earlier negativity is in line with previously-reported conflict effects in the flanker task observed in the N2 latency range (see Folstein and Van Petten, 2008 and Larson et al., 2014 for reviews). However, these previously-reported negativities which were derived from the incongruent-minus-congruent different waves may have included both conflict and difficulty effects that overlapped in time (or bridged together) under the specific stimulus parameters of those experiments.

4.2.3. Incongruency negativity (N_{inc}) for the incongruency contrast

As the early negativity subsided in the difficulty difference wave and proceeded to an LPC, a second negative peak was observed in the congruency difference wave, likely reflecting the main part of the N_{inc} (Appelbaum et al., 2011; Larson et al., 2009). In the present study, this negative deflection appeared as a continuation of the N2 effect in the congruency difference wave with an onset of 416 ms and fronto-central distribution. The fact that this second negative peak was observed only in the incongruency difference wave, and not in the difficulty difference wave, suggests that this later ERP component is reflective of processes specifically involved in conflict processing – such as processing response conflict between the flankers and central target – rather than a cognitive process common to both tasks. Furthermore, this result allows us to rule out the contribution of differential time-on-task to this difference wave, because the RT titration process matched the congruency and difficulty RT effects to 27 ms in each contrast, so these RT effects alone would not have been sufficient to elicit the N_{inc} .

Previous literature has indicated that negative-polarity effects in the

200–500 latency range can be elicited by conflict both in Stroop tasks (where it has often been called the N450) and in flanker tasks (e.g., Appelbaum et al., 2011; Donohue et al., 2016), with an earlier, sometimes distinct, N2-latency effect often also seen in flanker tasks (in the present study and in Donohue et al., 2016). Larson et al. (2014) reported that the flanker N2-latency effect tends to be sensitive to conflict adaptation effects and between-trial cognitive control adjustments, while the Stroop N450/ N_{inc} generally is not. In the present study, we were unable to address the possibility of differential conflict adaptation effects between our earlier and later negativities due to insufficient number of trials for the required sequence sub-bins. Rather, we explicitly focused on using difficulty vs. incongruency manipulations to differentiate between these two components. More specifically, our comparison between a congruency task and a difficulty task, with the RT effects matched through a titration process, represents a strength of the current study as it has allowed us to better disentangle the neural cascades of processing underlying both conflict processing and time-on-task/difficulty. Furthermore, the results indicate that the congruency difference wave can include reflections of distinct stages in the neural cascade of conflict processing, with the early N2-latency effect in the present study mainly indexing the initial detection of difficulty or an allocation of attentional resources, and the later negativity (which we called a N_{inc} here) reflecting conflict-specific processes, such as dealing with the response-mapping conflict in order to be able to respond appropriately.

Although our experimental design utilized modified Eriksen flanker stimuli to elicit spatial conflict effects, it should also be noted that several previous studies using flanker stimuli have reported a single negativity spanning the observed latencies of the N2-latency and N_{inc} effects observed here (e.g., Appelbaum et al., 2011) or a single negativity in the N2 latency range (e.g., Danielmeier et al., 2009; Freitas et al., 2009). Several aspects of experimental design may explain these varying results. First, variants of the Eriksen flanker task have traditionally utilized arrows (Kopp et al., 1996), letters or numbers (Fuentes, 1999; Yeung and Nieuwenhuis, 2009), or colored shapes (Diedrichsen et al., 2000; Henik et al., 1999). In the current study, our stimuli were circles with gaps, modified from Krebs et al. (2012). Although these stimuli diverged from a more typical flanker stimulus design, this selection allowed us to better establish consistency in stimuli and task instructions between the two tasks, while also allowing us to obtain some distinguishing separation between the difficulty and conflict-processing effects. Nevertheless, future work will be needed to fully tease apart the role of stimulus complexity on conflict-related ERP components. We also note that several recent studies have presented flankers as early as 100 ms prior to the central target (Forster et al., 2011; Larson et al., 2012), which could also cause separate N2 and N_{inc} effects to merge together into a single negativity in some cases by shifting the conflict-specific effect to occur somewhat earlier.

4.2.4. Late positive complex (LPC) in common for the two effects

Robust posterior positive-complex effects with similar amplitudes were observed in the conditional difference waves for the two tasks, but at very different latencies. In the difficulty difference wave, the peak latency of the LPC (~500 ms) occurred soon after the mean RTs for hard (465 ms) and easy (437 ms) trials. This trend was not observed in the incongruency LPC, which exhibited considerably later onset and peak latencies, occurring only after the longer-duration N_{inc} negativity and after the mean RTs of both the incongruent (473 ms) and congruent (447 ms) trials. These differences in timing of the LPC for the condition contrasts, despite the closely matched RT differences for those contrasts, suggest a dissociation between the behavioral output and the neural activations underlying this component. Furthermore, the LPC observed in the difficulty difference wave is consistent with earlier work describing the correlation between difficulty of perceptual discrimination and the amplitude of the LPC (Guo et al., 2010).

4.3. General discussion

The results of this study suggest there are both some common and some unique cognitive mechanisms in the cascade of processing evoked by difficulty versus by incongruency. Keeping the RT effects well-matched in each task, we observed in both task ERP difference waves an early negativity in the N2 time range, reflecting an initial detection of difficulty and recruitment of cognitive resources, followed by a divergence of processing unique to each task. In the conflict task, the early fronto-central negativity was followed by a longer-duration, somewhat more central-parietal negativity (N_{inc}), presumably to address the response-mapping conflict and respond appropriately, which was then followed a hallmark posterior positivity consistent with the classic LPC. In sharp contrast, in the difficulty task the early N2-latency effect led immediately to a posterior positivity consistent with the LPC, possibly for better sensory processing in the visual discrimination. Thus, while difficulty and incongruency seemed to evoke some common brain wave activation patterns initially, they then clearly elicited some unique ones, even when RTs are matched, meaning the neural processing effects associated with conflict processing are not simply due to time-on-task or task difficulty.

5. Conclusions

In summary, the present study sheds light on the relationship between the processing of conflict and difficulty, while keeping RT effects similar. Both the incongruent and hard conditions resulted in slower responses relative to the congruent and easy conditions, respectively. Both stimulus conflict and increased difficulty elicited short-latency fronto-central negativities (early N2-latency effect) with similar onsets and early time courses, suggesting a common process of difficulty detection or recruitment of additional cognitive resources in both tasks. In the conflict difference wave only, however, this negativity was followed by a second negativity of extended duration, consistent with the conflict-related N_{inc} . These results indicate the neural activations that are elicited during the processing of conflicting (incongruent) stimulus inputs are not simply reflective of increased time-on-task or difficulty, but are indeed reflective of processes specific for the processing of conflict. Additionally, the LPC was much later for conflict than for difficulty, again despite matched RT differences, underscoring the dissociation between this late activity and behavioral output, as well as the different cascade of processing required to resolve conflicting information. These findings therefore demonstrate that conflict processing and difficulty processing have partly shared and partly unique neural underpinnings.

Acknowledgements

This work was supported by NIH grant R01-NS051048 to M.G.W.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://doi:10.1016/j.neuropsychologia.2016.12.022>.

References

- Alexander, W.H., Brown, J.W., 2010. Computational models of performance monitoring and cognitive control. *Top. Cogn. Sci.* 2 (4), 658–677. <http://dx.doi.org/10.1111/j.1756-8765.2010.01085.x>.
- Appelbaum, L.G., Boehler, C.N., Davis, L.A., Won, R.J., Woldorff, M.G., 2014. The dynamics of Proactive and reactive cognitive control processes in the human brain. *J. Cogn. Neurosci.* 26, 1021–1038. <http://dx.doi.org/10.1162/jocn>.
- Appelbaum, L.G., Meyerhoff, K.L., Woldorff, M.G., 2009. Priming and backward influences in the human brain: Processing interactions during the stroop interference effect. *Cereb. Cortex* 19, 2508–2521. <http://dx.doi.org/10.1093/cercor/bhp036>.
- Appelbaum, L.G., Smith, D.V., Boehler, C.N., Chen, W.D., Woldorff, M.G., 2011. Rapid

- modulation of sensory processing induced by stimulus conflict. *J. Cogn. Neurosci.* 23, 2620–2628. <http://dx.doi.org/10.1162/jocn.2010.21575>.
- Badzakova-Trajkov, G., Barnett, K.J., Waldie, K.E., Kirk, I.J., 2009. An ERP investigation of the Stroop task: the role of the cingulate in attentional allocation and conflict resolution. *Brain Res.* 1253, 139–148. <http://dx.doi.org/10.1016/j.brainres.2008.11.069>.
- Bartholow, B.D., Pearson, M.A., Dickter, C.L., Sher, K.J., Fabiani, M., Gratton, G., 2005. Strategic control and medial frontal negativity: beyond errors and response conflict. *Psychophysiology* 42 (1), 33–42. <http://dx.doi.org/10.1111/j.1469-8986.2005.00258.x>.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652. <http://dx.doi.org/10.1037/0033-295X.108.3.624>.
- Brown, J.W., 2011. Medial prefrontal cortex activity correlates with time-on-task: what does this tell us about theories of cognitive control? *NeuroImage*.
- Carp, J., Fitzgerald, K.D., Taylor, S.F., Weissman, D.H., 2012. Removing the effect of response time on brain activity reveals developmental differences in conflict processing in the posterior medial prefrontal cortex. *NeuroImage* 59 (1), 853–860. <http://dx.doi.org/10.1016/j.neuroimage.2011.07.064>.
- Carp, J., Kim, K., Taylor, S.F., Fitzgerald, K.D., Weissman, D.H., 2010. Conditional differences in mean reaction time explain effects of response Congruency, but not accuracy, on posterior medial frontal cortex activity. *Front. Hum. Neurosci.* 4 (December), 231. <http://dx.doi.org/10.3389/fnhum.2010.00231>.
- Carter, C.S., van Veen, V., 2007. Anterior cingulate cortex and conflict detection: an update of theory and data. *Cogn. Affect. Behav. Neurosci.* 7, 367–379. <http://dx.doi.org/10.3758/cabn.7.4.367>.
- Coderre, E., Conklin, K., Van Heuven, W.J.B., 2011. Electrophysiological measures of conflict detection and resolution in the Stroop task. *Brain Res.* 1413, 51–59. <http://dx.doi.org/10.1016/j.brainres.2011.07.017>.
- Danielmeier, C., Wessel, J.R., Steinhilber, M., Ullsperger, M., 2009. Modulation of the error-related negativity by response conflict. *Psychophysiology* 46 (6), 1288–1298. <http://dx.doi.org/10.1111/j.1469-8986.2009.00860.x>.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134 (1), 9–21. <http://dx.doi.org/10.1016/j.jneumeth.2003.10.009>.
- Diedrichsen, J., Ivry, R.B., Cohen, A., Danziger, S., 2000. Asymmetries in a unilateral flanker task depend on the direction of the response: the role of attentional shift and perceptual grouping. *J. Exp. Psychol. Hum. Percept. Perform.* 26 (1), 113–126. <http://dx.doi.org/10.1037/0096-1523.26.1.113>.
- Donohue, S.E., Appelbaum, L.G., McKay, C.C., Woldorff, M.G., 2016. The neural dynamics of stimulus and response conflict processing as a function of response complexity and task demands. *Neuropsychologia* 84, 14–28. <http://dx.doi.org/10.1016/j.neuropsychologia.2016.01.035>.
- Donohue, S.E., Liotti, M., Perez, R., Woldorff, M.G., 2012. Is conflict monitoring supramodal? Spatiotemporal dynamics of cognitive control processes in an auditory Stroop task. *Cogn. Affect. Behav. Neurosci.* <http://dx.doi.org/10.3758/s13415-011-0060-z>.
- Doucet, C., Stelmack, R.M., 1999. The effect of response execution on P3 latency, reaction time, and movement time. *Psychophysiology* 36 (3), 351–363.
- Eriksen, B.A., Eriksen, C.W., 1974. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys.* 16 (1), 143–149. <http://dx.doi.org/10.3758/BF03203267>.
- Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology* 45, 152–170. <http://dx.doi.org/10.1111/j.1469-8986.2007.00602.x>.
- Forster, S.E., Carter, C.S., Cohen, J.D., Cho, R.Y., 2011. Parametric manipulation of the conflict signal and control-state adaptation. *J. Cogn. Neurosci.* 23 (4), 923–935.
- Freitas, A.L., Banai, R., Clark, S.L., 2009. When cognitive control is calibrated: event-related potential correlates of adapting to information-processing conflict despite erroneous response preparation. *Psychophysiology* 46 (6), 1226–1233. <http://dx.doi.org/10.1111/j.1469-8986.2009.00864.x>.
- Frühholz, S., Godde, B., Finke, M., Herrmann, M., 2011. Spatio-temporal brain dynamics in a combined stimulus-stimulus and stimulus-response conflict task. *NeuroImage* 54 (1), 622–634. <http://dx.doi.org/10.1016/j.neuroimage.2010.07.071>.
- Fuentes, L.J., 1999. Inhibitory tagging of stimulus properties in inhibition of return: effects on semantic priming and flanker interference. *Q. J. Exp. Psychol. Sect. A.* <http://dx.doi.org/10.1080/713755797>.
- Gratton, G., Coles, M.G., Donchin, E., 1992. Optimizing the use of information: strategic control of activation of responses. *J. Exp. Psychol. Gen.* 121 (4), 480–506.
- Grinband, J., Savitskaya, J., Wager, T.D., Teichert, T., Ferrera, V.P., Hirsch, J., 2011a. Conflict, error likelihood, and RT: Response to Brown & Yeung et al. *NeuroImage* 57 (2), 320–322. <http://dx.doi.org/10.1016/j.neuroimage.2011.04.027>.
- Grinband, J., Savitskaya, J., Wager, T.D., Teichert, T., Ferrera, V.P., Hirsch, J., 2011b. The dorsal medial frontal cortex is sensitive to time on task, not response conflict or error likelihood. *NeuroImage* 57 (2), 303–311.
- Guo, J., Gao, S., Hong, B., 2010. An auditory brain-computer interface using active mental response. *IEEE Trans. Neural Syst. Rehabil. Eng.* 18, 230–235. <http://dx.doi.org/10.1109/TNSRE.2010.2047604>.
- Heil, M., Osman, A., Wiegmann, J., Rolke, B., Hennighausen, E., 2000. N200 in the Eriksen-task: Inhibitory executive processes? *J. Psychophysiol.* 14, 218–225. <http://dx.doi.org/10.1027/0269-8803.14.4.218>.
- Henik, A., Ro, T., Merrill, D., Rafal, R., Safadi, Z., 1999. Interactions between color and word processing in a flanker task. *J. Exp. Psychol. Hum. Percept. Perform.* 25 (1), 198–209. <http://dx.doi.org/10.1037/0096-1523.25.1.198>.
- Kopp, B., Rist, F., Mattler, U., 1996. N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology* 33, 282–294. <http://dx.doi.org/10.1111/j.1469-8986.1996.tb00425.x>.
- Kornblum, S., 1994. The way irrelevant dimensions are processed depends on what they overlap with: the case of Stroop- and. *Psychol. Res.* 56, 130–135. <http://dx.doi.org/10.1007/BF00419699>.
- Krebs, R.M., Boehler, C.N., Roberts, K.C., Song, A.W., Woldorff, M.G., 2012. The involvement of the dopaminergic midbrain and cortico-striatal-thalamic circuits in integrating reward prospect and task demands. *Cereb. Cortex.* 22 (3), 607–615. <http://dx.doi.org/10.1093/cercor/bhr134>.
- Larson, M.J., Clayson, P.E., 2011. The relationship between cognitive performance and electrophysiological indices of performance monitoring. *Cogn. Affect. Behav. Neurosci.* 11 (2), 159–171.
- Larson, M.J., Clayson, P.E., Baldwin, S.A., 2012. Performance monitoring following conflict: internal adjustments in cognitive control? *Neuropsychologia* 50 (3), 426–433.
- Larson, M.J., Clayson, P.E., Clawson, A., 2014. Making sense of all the conflict: a theoretical review and critique of conflict-related ERPs. *Int. J. Psychophysiol.*
- Larson, M.J., Kaufman, D.A.S., Perlstein, W.M., 2009. Neural time course of conflict adaptation effects on the Stroop task. *Neuropsychologia* 47 (3), 663–670. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.11.013>.
- Liotti, M., Woldorff, M.G., Perez, R., Mayberg, H.S., 2000. An ERP study of the temporal course of the Stroop color-word interference effect. *Neuropsychologia* 38, 701–711. [http://dx.doi.org/10.1016/S0028-3932\(99\)00106-2](http://dx.doi.org/10.1016/S0028-3932(99)00106-2).
- MacLeod, C.M., 1991. Half a century of research on the Stroop effect: an integrative review. *Psychol. Bull.* 109, 163–203. <http://dx.doi.org/10.1037/0033-2909.109.2.163>.
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164 (1), 177–190. <http://dx.doi.org/10.1016/j.jneumeth.2007.03.024>.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.*, 2011. <http://dx.doi.org/10.1155/2011/156869>.
- Paus, T., Koski, L., Caramanos, Z., Westbury, C., 1998. Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: a review of 107 PET activation studies. *Neuroreport* 9, R37–R47.
- Core Team, R., 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org/>.
- Rebai, M., Bernard, C., Lannou, J., 1997. The Stroop's test evokes a negative brain potential, the N400. *Int. J. Neurosci.* 91 (1–2), 85–94. <http://dx.doi.org/10.3109/00207459708986367>.
- Senkowski, D., Herrmann, C.S., 2002. Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task. *Clin. Neurophysiol.* 113, 1742–1753. [http://dx.doi.org/10.1016/S1388-2457\(02\)00266-3](http://dx.doi.org/10.1016/S1388-2457(02)00266-3).
- Stroop, J.R., 1935. Studies of interference in serial verbal reactions. *J. Exp. Psychol.* 18 (6), 643–662. <http://dx.doi.org/10.1037/h0054651>.
- Szűcs, D., Soltész, F., 2012. Functional definition of the N450 event-related brain potential marker of conflict processing: a numerical Stroop study. *BMC Neurosci.* 13, 35. <http://dx.doi.org/10.1186/1471-2202-13-35>.
- Tillman, C.M., Wiens, S., 2011. Behavioral and ERP indices of response conflict in Stroop and flanker tasks. *Psychophysiology* 48, 1405–1411. <http://dx.doi.org/10.1111/j.1469-8986.2011.01203.x>.
- Verleger, R., Baur, N., Metzner, M.F., Smigajewicz, K., 2014. The hard oddball: effects of difficult response selection on stimulus-related P3 and on response-related negative potentials. *Psychophysiology*. <http://dx.doi.org/10.1111/psyp.12262>.
- Weissman, D.H., Carp, J., 2013. The Congruency Effect in the posterior medial frontal cortex Is More consistent with time on task than with response conflict. *PLoS ONE* 8 (4).
- West, R., Alain, C., 2000. Effects of task context and fluctuations of attention on neural activity supporting performance of the Stroop task. *Brain Res.* 873, 102–111. [http://dx.doi.org/10.1016/S0006-8993\(00\)02530-0](http://dx.doi.org/10.1016/S0006-8993(00)02530-0).
- West, R., Bowry, R., McConville, C., 2004. Sensitivity of medial frontal cortex to response and nonresponse conflict. *Psychophysiology* 41 (5), 739–748. <http://dx.doi.org/10.1111/j.1469-8986.2004.00205.x>.
- Yeung, N., Cohen, J.D., Botvinick, M.M., 2011. Errors of interpretation and modeling: a reply to Grinband et al. *NeuroImage*.
- Yeung, N., Nieuwenhuis, S., 2009. Dissociating response conflict and error likelihood in anterior cingulate cortex. *J. Neurosci.* 29 (46), 14506–14510. <http://dx.doi.org/10.1523/JNEUROSCI.3615-09.2009>.