

It's the Other Way Around! Early Modulation of Sensory Distractor Processing Induced by Late Response Conflict

Bernhard Pastötter and Christian Frings

Abstract

■ Understanding the neural processes that maintain goal-directed behavior is a major challenge for the study of attentional control. Although much of the previous work on the issue has focused on prefrontal brain areas, little is known about the contribution of sensory brain processes to the regulation of attentional control. The present EEG study examined brain oscillatory activities invoked in the processing of response conflict in a lateralized Eriksen single-flanker task, in which target letters were presented at fixation and single distractor letters were presented either left or right to the targets. Distractors were response compatible, response incompatible, or neutral in relation to the responses associated with the targets. The behavioral results showed that responses to targets in incompatible trials were slower and more error prone than responses in compatible trials. The electrophysiological results revealed an early sensory lateral-

ization effect in (both evoked and induced) theta power (3–6 Hz) that was more pronounced in incompatible than compatible trials. The sensory lateralization effect preceded in time a mid-frontal conflict effect that was indexed by an increase of (induced) theta power (6–9 Hz) in incompatible compared with compatible trials. The findings indicate an early modulation of sensory distractor processing induced by response conflict. Theoretical implications of the findings, in particular with respect to the theory of event coding and theories relating to stimulus–response binding [Henson, R. N., Eckstein, D., Waszak, F., Frings, C., & Horner, A. Stimulus-response bindings in priming. *Trends in Cognitive Sciences*, 18, 376–384, 2014; Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24, 849–878, 2001], are discussed. ■

INTRODUCTION

Our brain is constantly bombarded with information from the different senses while at the same time only a small subset of the current information is actually relevant for our goals. To make this situation even worse, humans typically have several goals activated at a time (e.g., overarching goals like “avoiding danger” that should be always active and very specific goals like “searching for your keys”). The different stimulus information must be matched to our current goals to promote goal-directed behavior. Obviously, there might be conflict between the processing of currently relevant and, for the task at hand, irrelevant information, which can arise either at the perceptual level or the level of response selection. Stimulus conflict arises at the perceptual level when the relevant information is perceptually different from the irrelevant information, whereas response conflict arises at the level of response selection when distracting stimuli suggest interfering actions. Although it is clear that human behavior outside the laboratory is quite complex—as we can juggle several goals with different priorities at a time with ease and evaluate and process stimuli accordingly—it

is nevertheless important to pinpoint aspects of this complex behavior and investigate the tools with which humans achieve efficient behavior. Controlling stimulus and response conflict is one process with which humans act, although it is clear that there is much more to action regulation than just controlling stimulus information (e.g., behavioral routines due to binding, self-monitoring, tasks sets, attentional and intentional weighting, prioritization due to self-relevance, and so on).

Accordingly, research in the cognitive sciences has developed several experimental paradigms to pinpoint the control processes with which humans can handle these conflicts and successfully achieve goal-directed behavior. One task in particular, the Eriksen flanker task, is well suited to independently measure conflicts at the level of perception and the level of response selection (Eriksen & Eriksen, 1974; see Eriksen, 1995, for a review). In the visual variant of this task, flanker or distractor stimuli are presented adjacent to a target stimulus. Stimulus conflict is measured by comparing trials in which the flankers are identical to the target (i.e., they are stimulus congruent and response compatible) with trials in which the flankers are perceptually different from the target but still suggest the same response (i.e., they are stimulus incongruent but response compatible). In contrast,

University of Trier

response conflict is measured by comparing trials in which the flankers are perceptually different from the targets but suggest the same response (i.e., they are stimulus incongruent and response compatible) and trials in which the flankers are also perceptually different from the target but, in addition, suggest a different response (i.e., they are stimulus incongruent and response incompatible). Typically, both stimulus and response conflict lead to cost effects in the Eriksen flanker, indexed by slower RTs and more errors in conflict than non-conflict trials. The costs are typically explained by attentional control processes. One idea is that the internal representation of the flanker stimuli may be inhibited or actively suppressed at the perceptual level and also at the level of response selection, yet inhibition of interfering information needs attentional resources, which leads to the observed cost effects (e.g., Frings, Wentura, & Wühr, 2012; Lamers & Roelofs, 2011; Wühr & Frings, 2008; Heil, Osman, Wiegmann, Rolke, & Hennighausen, 2000; of course, there are other interpretations of the flanker effect in terms of response biases or response competition or in terms of an attentional gradient, e.g., White, Ratcliff, & Starns, 2011). The effects are not restricted to visual stimuli. Both stimulus and response conflicts in the flanker task (or variants thereof) have been well documented in the literature to arise across the senses, in vision (Eriksen & Eriksen, 1974), in audition (Chan, Merrifield, & Spence, 2005), in touch (Evans & Craig, 1992), and even cross-modally (Frings & Spence, 2010).

Understanding the neural processes that maintain goal-directed behavior is a major challenge for the study of attentional control. Much of the previous work on the issue has focused on prefrontal brain areas, in particular the ACC and associated regions of the medial frontal wall, which are believed to play a vital role in the detection of conflict and the regulation of attentional control. It is a prominent idea that ACC functions as a conflict monitor that detects conflicts between concurrently activated relevant and irrelevant information (Botvinick, Cohen, & Carter, 2004; Van Veen & Carter, 2002a). Corresponding evidence arose from fMRI studies showing that ACC is more activated on conflict than nonconflict trials in conflict tasks, including the Stroop task (MacDonald, Cohen, Stenger, & Carter, 2000), the Simon task (Peterson et al., 2002), and the Eriksen flanker task (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). In addition, EEG studies have demonstrated that conflicting stimuli or responses can elicit larger negative deflections in early ERP components (e.g., N200 and N400) over midfrontal electrodes, likely originating from ACC (e.g., Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011; Hanslmayr et al., 2008; Van Veen & Carter, 2002b; Liotti, Woldorff, Perez, & Mayberg, 2000). Consistently, both EEG and MEG studies on brain oscillatory activity have shown that midfrontal theta oscillations (4–8 Hz) typically show a power increase in conflict compared with nonconflict trials, an effect that has been source-localized to ACC (e.g., Pastötter, Berchtold,

& Bäuml, 2012; Nigbur, Ivanova, & Stürmer, 2011; Pastötter, Hanslmayr, & Bäuml, 2010; Hanslmayr et al., 2008; see Cavanagh & Frank, 2014, for a review). Thereby, it has been shown that mainly induced (i.e., not phase-locked) but less evoked (i.e., phase-locked) theta oscillations are related to the processing of (response) conflict (Cohen & Donner, 2013; Cavanagh, Zambrano-Vazquez, & Allen, 2012). Although there is evidence that ACC responds to both stimulus and response conflict, ACC conflict effects seem to be strongest for conflict arising at the level of response selection (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001).

In addition to ACC, other brain regions are involved in conflict processing and attentional control, including the dorsolateral prefrontal cortex (DLPFC), inferior frontal gyrus, posterior parietal cortex, anterior insula, and visual cortex, with the different structures being differentially related to stimulus and response conflict (see Nee, Wager, & Jonides, 2007, for a review). Importantly, both fMRI and EEG studies employing the flanker task (or variants thereof) have shown that early sensory distractor processing in visual brain areas can be modulated by conflicting stimuli (Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Donohue, Todisco, & Woldorff, 2013; Appelbaum et al., 2011; Kelley & Lavie, 2011). In the study by Appelbaum et al. (2011), stimulus and response conflict were varied nonorthogonally. Occipital brain activity was contrasted between conditions with conflicting and (partially) nonconflicting flankers in a lateralized version of the visual Eriksen flanker task, in which the distractors were presented left and right to the targets. In no-conflict trials, all distractors were nonconflicting (stimulus congruent and response compatible); in conflict trials, all distractors were conflicting (stimulus incongruent and response incompatible). In a third condition, the distractors were conflicting in one hemifield but nonconflicting in the other hemifield. In these partial-conflict trials, the results showed a sensory lateralization effect over occipital electrode sites, with more positive ERPs contralateral than ipsilateral to the conflicting distractor side, that emerged simultaneously in time with a midfrontal N200 conflict effect. The sensory lateralization effect was suggested to indicate attentional distraction caused by the conflicting flankers. The findings by Appelbaum et al. (2011), together with the findings from other fMRI and EEG work (e.g., Marini et al., 2016; Donohue et al., 2013; Kelley & Lavie, 2011), support the view that occipital brain activity in general and sensory lateralization in particular are modulated by stimulus conflict arising at the perceptual level. However, because of the nonorthogonal manipulation of stimulus and response conflict in the earlier work, in principle, both stimulus and response conflict could have contributed to the modulation of the sensory lateralization effect.

This study examined whether (lateralized) occipital brain activity is modulated by response conflict arising at the level of response selection; that is, we propose the

counterintuitive idea that response conflict arising at later processing stages can influence early sensory processing. Yet, with respect to the literature on action control in the last decade, one can make a clear argument for this idea. In particular, it has been established that the links between perception and action are much closer and more intertwined than previously assumed. A theory that has been widely used to investigate action control is the theory of event coding (TEC; Hommel, Müsseler, Aschersleben, & Prinz, 2001), which provides a framework for understanding the linkages between perception and action. Based on the ideomotor principle (see Shin, Proctor, & Capaldi, 2010; Stock & Stock, 2004, for reviews), TEC assumes that actions are represented by codes of their perceptual consequences and further that perceived events and produced actions may share the same representations (Hommel, 2004, 2009). TEC has been used to explain a range of phenomena, including stimulus–response (S-R) effects in general and priming effects in particular (for reviews, see Henson, Eckstein, Waszak, Frings, & Horner, 2014; Henson, 2009). For our purpose here, it is relevant that TEC assumes that, even after a single pairing of a stimulus and a response, the S-R episode is bound into a memory (or event file) and upon repetition of any part of this episode is again reinstated. Indeed, corresponding evidence arose from fMRI and EEG studies, showing that the repetition of a stimulus directly retrieves the response that was previously associated to it, thereby suggesting that—after an initial pairing—reencountering a stimulus makes the previous response instantly accessible (Horner & Henson, 2012; Dobbins, Schnyer, Verfaellie, & Schacter, 2004).

Concerning our study, we therefore assume that, in a typical response conflict task with fixed S-R mappings, reencountering a stimulus after a few trials directly retrieves the particular response. Given that research on action control yields ample evidence that also flanker stimuli can directly activate responses due to S-R bindings (e.g., Frings & Rothermund, 2011; Frings, Rothermund, & Wentura, 2007; Mayr & Buchner, 2006), we hypothesized that reencountering a flanker might instantly activate the associated response, and because of S-R bindings, interference due to response conflict might influence the processing of flankers at very early levels of sensory information processing. Of course, such view is in contrast to established sequential information processing models from research on the psychological refractory period (see Pashler, 1994).

This study examined the behavioral and electrophysiological effects of response conflict in a lateralized single-flanker version of the Eriksen task. This version was chosen because previous imaging work has shown that it can produce reliable distractor competition effects in early visual cortex (Kelley & Lavie, 2011). Targets were presented at central fixation, and single flanking distractors were presented either left or right to the targets. Distractors were always stimulus incongruent, that is,

perceptually different from the targets. Response conflict effects were examined by comparing behavioral and EEG data between response-incompatible (INC), response-compatible (COM), and neutral (NEU) conditions. Regarding the electrophysiological effects of response conflict, oscillatory brain activities and lateralized readiness potentials (LRPs) were examined. With regard to LRPs, onset times of stimulus-locked and response-locked potentials (S-LRP and LRP-R, respectively) were analyzed as chronometric markers for the duration of premotor (S-LRP) and motor processing stages (LRP-R), respectively (see Eder, Leuthold, Rothermund, & Schweinberger, 2012). With regard to oscillatory activities, both stimulus-related and response-related power changes across EEG frequencies from 1 to 30 Hz were computed and compared between experimental conditions. Both evoked and induced parts of the oscillatory signal were calculated. Evoked oscillations are phase-locked to stimulus or response onset (as is the ERP), whereas induced oscillations are not (see Tallon-Baudry & Bertrand, 1999). Both nonlateralized and lateralized (to distractor presentation side) effects of response conflict were examined.

Several expectations arose. Behaviorally, response conflict effects were expected for both RT and response accuracy, reflected in slower and more error-prone responses on incompatible than compatible (and neutral) trials. At the electrophysiological level, with respect to LRP onsets, we expected a response conflict effect on S-LRP onset, due to later S-LRP onset on incompatible than compatible and neutral trials, but no conflict effect on LRP-R onset (e.g., Kopp, Rist, & Mattler, 1996; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). With regard to nonlateralized EEG activity, we expected an increase of induced (but not evoked) theta power over midfrontal electrodes on incompatible compared with compatible (and neutral) trials (e.g., Cohen & Donner, 2013; Cavanagh et al., 2012). Most important, with regard to lateralized EEG activity, we expected a modulation of sensory distractor processing induced by response conflict. The hypothesis was based on the finding that sensory distractor processing can be modulated by the processing of conflicting information (e.g., Appelbaum et al., 2011) and current theories on action control and S-R binding, which suggest a close link between perception and action, and the processing of stimulus and response conflict, respectively (Henson et al., 2014; Hommel, 2004, 2009; Hommel et al., 2001). Because mainly low-frequency oscillations in the theta (around 5 Hz) and alpha band (around 10 Hz) have been linked to lateralized control of visuospatial attention (theta: e.g., Van der Lubbe, Bundt, & Abrahamse, 2014; Green & McDonald, 2008; alpha: e.g., Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000), we expected to find a sensory lateralization effect in theta or alpha power over occipital electrode sites. As argued above, theories from action control research would predict that the flanker stimuli directly activate the associated responses in parallel with the sensory processing. Thus, interference

due to response conflict might already impact visual processing of the irrelevant distractors, leading to enhanced sensory lateralization during the processing of response incompatible distractors.

METHODS

Participants

Thirty-four students from the University of Trier, Germany, were included in the study (29 women, 6 left-handed, mean age = 20.7 years, $SD = 2.2$ years). Six additional participants were tested but eliminated from analysis because of excess physiological noise in the EEG data (four participants) or not following task instructions (two participants). All participants reported normal or corrected-to-normal vision; no participant reported any history of neurological disease. All participants gave written informed consent before examination and received course credit for participation. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics review committee at the University of Trier.

Stimuli and Task

Participants performed a lateralized Eriksen single-flanker task, in which target letters were presented at central fixation and flanking distractor letters were presented either left or right to the targets. In each trial, only a single distractor letter was shown. Three experimental conditions were included in this study (Figure 1). In all conditions, target stimuli were the letters D, F, J, and K. In the COM

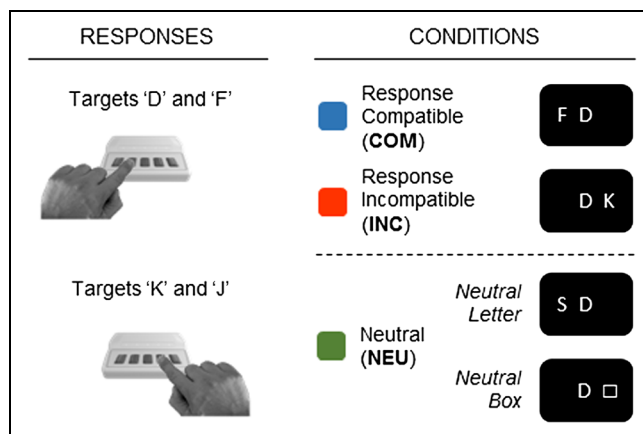


Figure 1. Experimental task. Participants performed a lateralized Eriksen single-flanker task, in which target letters were presented at central fixation and flanking distractor letters were presented at either left or right to the targets. Participants responded to target letters with their left and right index fingers. In the COM condition, targets and distractors were mapped to the same response, whereas in the INC condition, targets and distractors were mapped to different responses. In addition, an NEU condition with two neutral-trial types was included, in which the distractors were not mapped to any responses. Letters were used as distractors in neutral-letter trials; a box was presented as distractor in neutral-box trials.

and INC conditions, distractor stimuli were also the letters D, F, J, and K. The letters “D” and “F” were mapped to a left-hand response, the letters “J” and “K” were mapped to a right-hand response. In the COM condition, the distractors were response compatible to the targets, that is, targets and distractors were mapped to the same response (e.g., target “D” and distractor “F”). Importantly, distractors never matched the targets, that is, distractors were always stimulus incongruent to the targets at the perceptual level. In the INC condition, distractors were response incompatible to the targets, that is, targets and distractors were mapped to different responses (e.g., target “D” and distractor “K”). The assignment of the single distractor letters to the target letters was chosen to be one-to-one and kept constant for all participants (“D”–“K” and “J”–“F”), as it naturally was in the COM condition (“D”–“F” and “J”–“K”). Response (in)compatibility effects were examined by comparing data between compatible and incompatible trials in the COM and INC conditions, respectively. In addition, a NEU condition with two neutral trial types was included in the study. In neutral-letter trials, the distractors were the letters “S,” “G,” “L,” and “H,” which were not mapped to any response; the assignment of the single distractor letters to the target letters was chosen to be one-to-one and kept constant for all participants (“D”–“S,” “F”–“G,” “J”–“L,” and “K”–“H”). In neutral-box trials, a box was presented as distractor (□); the box was not mapped to any response.

All stimuli were shown in white on black background, at viewing distance of 65 cm. Stimuli were approximately 1.2° in size. Letters were written in Arial font. Targets were presented in the center of the screen. Distractors were centered 3.5° to the left or right of the targets. Between displays, a fixation cross was shown in the center of the screen, which was 0.5° in size. Two response buttons were marked on a Chronos response box (Psychology Software Tools). Participants were instructed to place their left index finger on the left button and their right index finger on the right button of the Chronos response box (see Figure 1). They were asked to press the left button in response to the target letters “D” and “F,” and the right button in response to the target letters “J” and “K.” Participants were asked to respond as quickly and accurately as possible to the targets and to ignore the flankers. They were asked to maintain fixation on the center of the screen at all times and to not move the eyes.

An experimental session consisted of 320 single trials, presented in 10 blocks of 32 trials each. Within each block, all predefined combinations of target and distractor stimuli, with the same number of left- and right-hemifield distractor presentations, were realized in a counter-balanced manner. Order of compatible, incompatible, neutral-letter, and neutral-box trials was randomized with the constraints that no trial type, target letter, or distractor hemifield was repeated more than three trials in a row. Each single trial began with a fixation cross, which was shown in the center of the screen for an interval of variable

duration of 2–2.5 sec. If a participant did not fixate the cross at the end of this interval, the duration of the interval was prolonged until fixation. Eye gaze was controlled by simultaneous eye tracking (Eyegaze System, LC Technologies; calibration was done before the experiment). Maximum permissible gaze deviation was set to 1.75° radius from the fixation cross. After presentation of the fixation cross, the target letter was shown together with one single distractor letter. The target was shown in the middle of the screen, and the distractor was shown either left or right to the target. Target and distractor stimuli remained on the screen until a response was made by the participant. No feedback was provided. After the response, the next single trial started with presentation of the fixation cross. To familiarize participants with the procedure, they were given one block of 32 practice trials before the experiment. Presentation and recording of behavioral responses was done with E-Prime software (v2.0, Psychology Software Tools).

Analysis of Behavioral Data

Both mean RT and error rate were analyzed. For each participant, trials with RT greater or less than 2.5 standard deviations from the individual mean RT were excluded from further analysis. For RT analysis, only trials were included for which responses on both the current trial and the previous trial were correct. Mean numbers of trials included in the final analysis were 74.9 compatible trials ($SD = 4.1$, Min = 65, Max = 80), 74.3 incompatible trials ($SD = 4.4$, Min = 61, Max = 80), 75.0 neutral-letter trials ($SD = 3.5$, Min = 63, Max = 80), and 74.7 neutral-box trials ($SD = 4.0$, Min = 66, Max = 80).

Behavioral data were analyzed with repeated-measures ANOVAs with the factor of Experimental condition (COM, INC, NEU). Greenhouse–Geisser correction was applied where appropriate. Post hoc comparisons were conducted using Tukey honestly significant difference (HSD) testing, which accounts for the problem of multiple testing and maintains the significance threshold at 5% ($HSD_{.05}$). Note that, a priori, the behavioral (and EEG) data in the NEU condition were contrasted between neutral-letter and neutral-box trials. As it turned out, there were no significant differences between the two neutral trial types, neither in the behavioral data nor in the EEG data. Therefore, the present results were based on a single NEU condition, including both neutral-letter and neutral-box trials.

Recording of EEG Data

Electrophysiological data were recorded from 65 Ag/AgCl electrodes, which were positioned according to the 10–10 electrode system with reference to FCz (EC80, Montage No. 1, EasyCap). The ground was placed at location AFz. The EOG was recorded from four bipolar channels, positioned on the inferior and superior regions of the left eye and the outer canthi of both eyes, to monitor the vertical

and horizontal EOG. Electrode-skin impedance was kept below 5 k Ω for all electrodes. Signals were digitalized with a sampling rate of 500 Hz and amplified between 0.016 and 250 Hz (BrainAmp, BrainVision Recorder, v1.20, Brain Products).

Preprocessing of EEG Data

EEG recordings were re-referenced offline against average reference and EOG corrected by using calibration data and generating individual EOG artifact coefficients, as implemented in BESA Research (v6.1, BESA Software; see Ille, Berg, & Scherg, 2002). Remaining artifacts were marked by careful visual inspection. EEG data were segmented into epochs ranging from –2.5 to 2.5 sec around the onsets of stimuli and responses. To avoid filter artifacts at the edges of the segments, further analyses were restricted to intervals ranging from –1.5 to 1.5 sec around stimulus and response onsets. Segments containing artifacts and segments with response errors either on the current or the previous trial were discarded from further analysis.

LRP Analysis

The EEG data were averaged time-locked to stimulus onset for S-LRP analysis and response onset for LRP-R analysis. For each participant and experimental condition, the ERP at the recording site over the motor cortex ipsilateral to the response hand was subtracted from the ERP at the homologous contralateral recording site (C4 minus C3 for left-hand responses, C3 minus C4 for right-hand responses). The LRP was calculated by averaging the resulting difference waveforms across hands, separately for conditions. Negative deviations of the resulting LRP indicate stronger activation of the correct response hand than of the incorrect response hand at the level of the motor activation.

LRP onsets were measured after low-pass filtering (5 Hz, 12 dB/octave) and analyzed by applying the jackknife-based procedure (Miller, Patterson, & Ulrich, 1998). The S-LRP was aligned to a 0.25-sec baseline before stimulus onset; the LRP-R was aligned to a 0.25-sec baseline interval starting at 1.25 sec before response onset (note that the results and conclusions were the same with an LRP-R baseline that started 0.55 sec before response onset; see Eder et al., 2012). S-LRP onset was determined at the point in time when the LRP amplitude reached 50% of the LRP peak amplitude, whereas LRP-R onset was calculated with a fraction of 30% as suggested by Miller et al. (1998). LRP onset latency measures were submitted to ANOVAs with F values corrected to $F_{\text{corr}} = F/(n - 1)^2$, where F_{corr} denotes the corrected F value and n denotes the number of participants (see Ulrich & Miller, 2001). Post hoc comparisons between conditions were calculated using jackknife-based t_{corr} statistics (see Miller et al., 1998).

Spectral EEG Analysis

The EEG data were transformed into the time–frequency domain using a complex demodulation algorithm, which is implemented in BESA Research (v6.1; see Hoehstetter et al., 2004). The algorithm consists of a multiplication of the time domain signal with a complex periodic exponential function, having a frequency equal to the frequency under analysis, and subsequent low-pass filtering. The low-pass filter is a finite impulse response filter of Gaussian shape in the time domain, which is related to the envelope of the moving window in wavelet analysis. The data were filtered in a frequency range from 1 to 30 Hz. Time resolution was set to 78.8 msec (FWHM), and frequency resolution was set to 1.42 Hz (FWHM). Time–frequency data were exported in bins of 50 msec and 1 Hz.

Both stimulus- and response-locked power changes were calculated, time-locked to stimulus or response onset, respectively. Stimulus- and response-locked changes in power were determined by calculating the temporal-spectral evolution, that is, power changes for all time–frequency points with power increases or decreases at time point t and frequency f related to mean power at frequency f over a preceding baseline interval (Pfurtscheller & Aranibar, 1977). Stimulus-locked power changes were determined in relation to a prestimulus baseline interval that was set from -0.25 to 0 sec time-locked to stimulus onset, whereas response-locked power changes were determined in relation to a baseline interval that was set from -1.25 to -1 sec time-locked to response onset. In addition to total power, both induced and evoked power changes were estimated. Evoked power changes were estimated by calculating the temporal-spectral evolution of the ERP, separately for each condition, electrode, and participant. Induced power changes were estimated by calculating the temporal-spectral evolution of the EEG signal after subtracting the ERP on each trial, separately for each condition, electrode, and participant (Kalcher & Pfurtscheller, 1995).

The following steps were taken to examine the effects of response (in)compatibility between the COM and INC conditions. First, the topography of response conflict effects in total power around response onset (-0.5 to 0.5 sec, response-locked) between compatible and incompatible trials was examined with permutation-based cluster analysis, which controls for the problem of multiple testing (Maris & Oostenveld, 2007) using BESA Statistics (v2.0, BESA Software). Specifically, paired t tests for all data points (21 [time bins] \times 30 [frequency bins] \times 65 [electrodes]) were calculated and 3-D clusters of contiguous data points that fell below a p value of $.01$ in the single t tests were derived. For each empirical cluster, the sum of t values of the single significant data points was kept as a test statistic. Next, 5000 random permutations were run in which the sum test statistic was repeatedly calculated for randomly shuffled data sets, with the data randomly reordered across COM and INC conditions and

the permutation-based cluster with the highest sum of t values was kept. By these means, a null distribution was created from the random permutation runs, and the critical p_{crit} values for the empirically derived clusters were calculated. Empirical clusters with a critical p_{crit} value below $.05$ went into further analysis. For those clusters, mean power changes were calculated for total, evoked, and induced power, averaged across data points of the cluster's maximum time range, maximum frequency range, and corresponding electrodes, separately for each experimental condition. Time courses of total power changes in a cluster were compared between the three experimental conditions (COM, INC, NEU); time courses of evoked and induced power change in a cluster were compared between the COM and INC conditions. Power changes were time-locked to stimulus and response onsets in different analyses. Repeated-measures ANOVAs that examined the interactions of Experimental conditions, Time, and Activity (evoked vs. induced) were calculated. In all ANOVAs, Greenhouse–Geisser correction was applied where appropriate, and Tukey HSD $_{.05}$ was used for post hoc testing.

Permutation-based cluster analysis was also used to examine the topography of (sensory) lateralization effects in total power changes related to stimulus onset (0 – 0.5 sec) between trials with left-hemifield distractor presentation and right-hemifield distractor presentation, independent of experimental condition (13 [time bins] \times 30 [frequency bins] \times 65 [electrodes]). In the permutation analysis, the data were randomly reordered across left-hemifield and right-hemifield distractor presentations. Only clusters with a critical p_{crit} value below $.05$ went into further analysis. As it turned out, two clusters over the left and right occipital cortex did show very similar time–frequency characteristics, indicating a sensory lateralization effect over occipital sites. Therefore, a sensory lateralization index (SLI) was calculated by subtracting mean power changes of the electrodes from the cluster ipsilateral to distractor presentation from mean power changes of the electrodes from the cluster contralateral to distractor presentation, averaged across left- and right-hemifield distractor presentations. SLIs were calculated for total, evoked, and induced power changes, separately for conditions, and the time courses of sensory lateralization effects were contrasted time-locked to the onset of stimuli or responses. In all ANOVAs, Greenhouse–Geisser correction was applied where appropriate. Tukey HSD $_{.05}$ was used for post hoc tests.

RESULTS

Behavioral Results

RTs

Mean RTs are depicted in Figure 2. A one-way repeated-measures ANOVA with the factor of Experimental condition (COM vs. INC vs. NEU) revealed a significant effect,

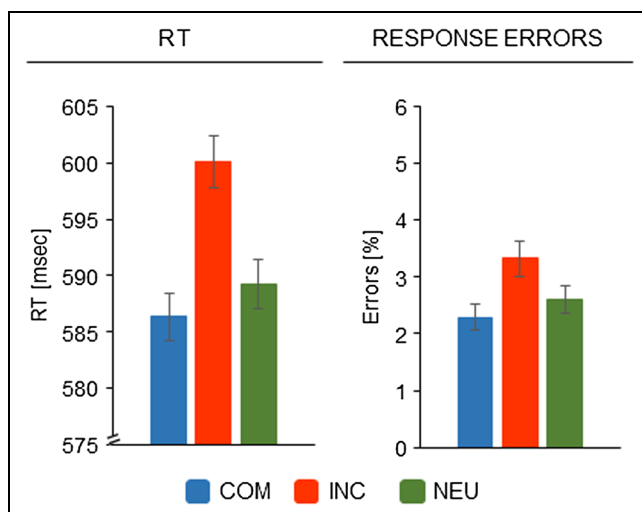


Figure 2. Behavioral results. Both mean RTs and error rates showed reliable response conflict effects, that is, slower and more error-prone responses on incompatible than compatible trials. In neutral trials, responding was reliably faster than in incompatible trials; other differences were not significant. Error bars represent within-subject standard errors (Cousineau, 2005).

$F(2, 66) = 9.38, p < .001$. Post hoc testing indicated that the differences in RT between incompatible trials (600.1 msec) and compatible trials (586.3 msec) and between incompatible and neutral trials (589.3 msec) were significant, whereas the difference between compatible and neutral trials was not significant (Tukey HSD_{.05} = 8.0 msec).

Response Errors

Error rates are also shown in Figure 2. A one-way repeated-measures ANOVA with the factor of Experimental condition (COM vs. INC vs. NEU) revealed a significant effect, $F(2, 66) = 3.44, p = .038$. Post hoc testing showed that there was a significant difference in error rates between incompatible (3.32%) and compatible trials (2.29%); the other differences were not significant (neutral trials: 2.60%; Tukey HSD_{.05} = 0.97%).

Physiological Results: LRPs

S-LRP

Figure 3 depicts the S-LRP waveforms for the three experimental conditions. A one-way repeated-measures ANOVA on S-LRP onset with the factor of Experimental condition (COM vs. INC vs. NEU) revealed a significant effect, $F_{\text{corr}}(2, 66) = 3.68, p = .031$. Indeed, S-LRP onset in the INC condition (364.5 msec; time-locked to stimulus onset, 50% peak amplitude) was significantly later than in the COM condition (330.1 msec), $t_{\text{corr}}(33) = 2.05, p = .048$, and the NEU condition (319.0 msec), $t_{\text{corr}}(33) = 2.25, p = .031$. The difference between the COM and NEU conditions was not significant, $t_{\text{corr}}(33) < 1$. Thus, the S-LRP results

suggest a longer duration of premotor processes in incompatible trials than in compatible and neutral trials.

LRP-R

Figure 3 also shows the LRP-R waveforms. A one-way repeated-measures ANOVA on LRP-R onset with the factor of Experimental condition (COM vs. INC vs. NEU) showed no significant effect, $F_{\text{corr}}(2, 66) = 0.44, p = .645$. LRP-R onset was -192.8 msec in the COM condition, -186.8 msec in the INC condition, and -197.8 msec in the NEU condition (time-locked to response onset, 30% peak amplitude). Thus, the LRP-R results suggest no difference in the duration of motor processes between experimental conditions.

Physiological Results: Power

Response Conflict

In the time–frequency analysis of response-locked conflict effects, the first step was to examine significant clusters of differences in total power between the COM and INC conditions. Permutation-based cluster analysis revealed a single significant cluster over midfrontal electrode sites (F1, Fz, F2, FC1, FCz, FC2, C1, and Cz), which showed a larger response-locked theta power increase (6–9 Hz) in the INC condition than in the COM condition from -0.2 to 0.2 sec around response onset, $p_{\text{crit}} < .001$ (Figure 4A). In the said time window, the cluster's total theta power increase in the NEU condition (31.1%) was significantly smaller than in the INC condition (45.1%), $t(33) = 3.53, p = .001$, but comparable with the COM condition (30.5%), $t(33) < 1$. Therefore, to increase statistical power in the analysis of conflict effects in the midfrontal cluster, subsequent analyses contrasted theta activities between the COM and INC conditions only. Time courses of total theta power changes in the three experimental conditions are depicted in Figure 4B.

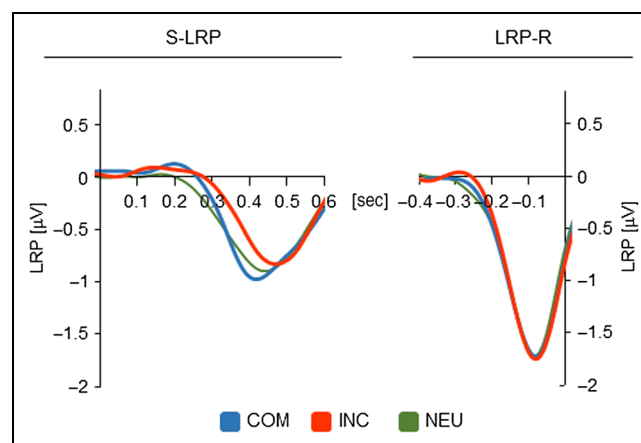
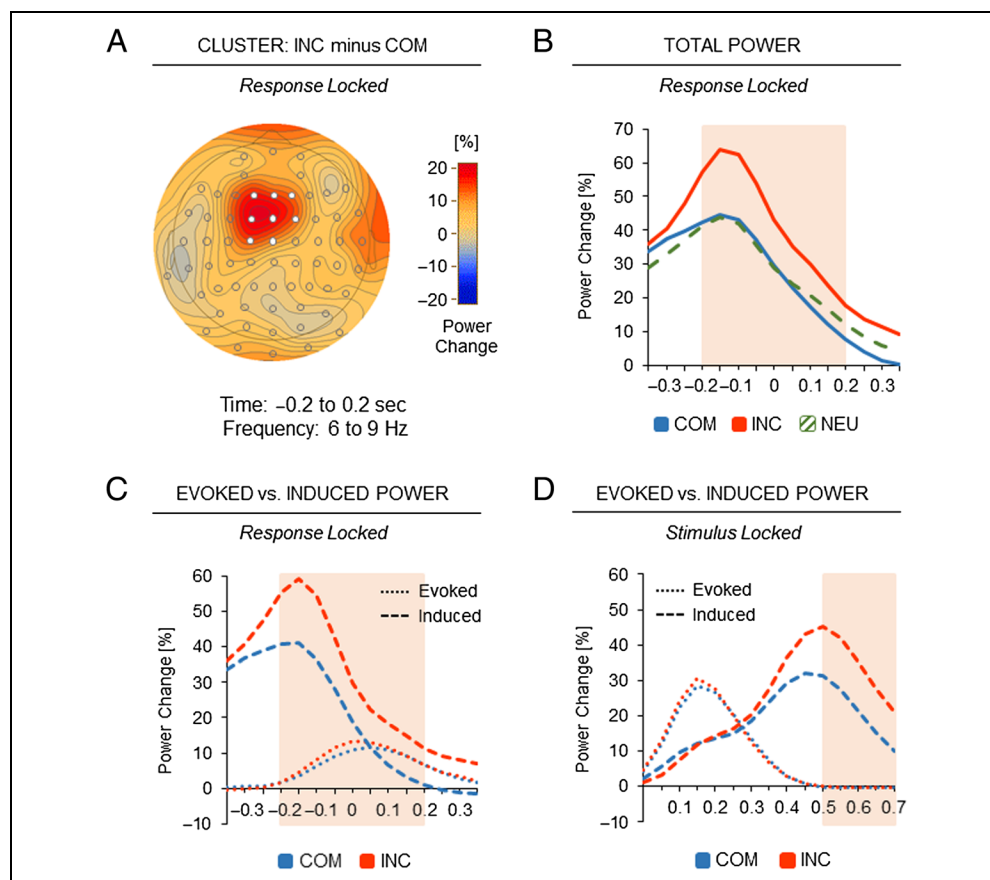


Figure 3. S-LRP and LRP-R for the three experimental conditions. S-LRP onset was generally later in the INC condition than in the other conditions; LRP-R onset did not differ between conditions (COM, INC, NEU).

Figure 4. Response conflict. (A) Topography of the response conflict effect in midfrontal theta power (difference between the INC and COM conditions). Electrodes in white depict the significant cluster in theta power (6–9 Hz; -0.2 to 0.2 sec around response onset). (B) Response-locked time course of midfrontal theta power changes in the significant cluster as a function of experimental condition (NEU). The red-shaded area indicates significant differences between incompatible and compatible trials, $p < .05$. (C, D) Response-locked and stimulus-locked time courses of midfrontal theta power changes in the significant cluster as a function of response conflict (COM vs. INC). Dotted lines refer to evoked theta power modulations; dashed lines refer to induced theta power modulations. The red-shaded areas indicate significant differences in induced theta power between compatible and incompatible trials, $p < .05$.



Contrasting the time courses of theta activities between the COM and INC conditions, a repeated-measures ANOVA with the factors of Condition (COM vs. INC) and Time (four 100-msec time intervals from -0.2 to 0.2 sec around response onset) revealed a significant main effect of Condition, $F(1, 33) = 13.94$, $p < .001$, and a significant main effect of Time, $F(3, 99) = 12.67$, $p < .001$, but no significant interaction between the two factors, $F(3, 99) = 1.21$, $p = .309$. These results suggest that the midfrontal conflict effect in total theta power was equally present before and after response execution.

The contribution of evoked and induced theta activities to the midfrontal conflict effect around response onset (-0.2 to 0.2 sec) was analyzed by calculating a repeated-measures ANOVA with the factors of Condition (COM vs. INC) and Activity (evoked vs. induced). The analysis showed a significant main effect of Condition, $F(1, 33) = 13.76$, $p < .001$, and a significant main effect of Activity, $F(1, 33) = 11.70$, $p = .002$, due to generally higher induced than evoked theta power. More important, the analysis revealed a significant interaction between the two factors, $F(1, 33) = 13.07$, $p < .001$. Indeed, a significant conflict effect emerged for induced (COM: 23.0% vs. INC: 36.5%), but not for evoked theta power (7.5% vs. 8.6%; Tukey HSD_{.05} = 6.6%). Time courses of induced and evoked theta activities are depicted in Figure 4C.

Figure 4D shows the results of the stimulus-locked analyses. Repeated-measures ANOVAs with the factors of Condition (COM vs. INC) and Time (seven 100-msec time intervals from 0 to 0.7 sec following stimulus onset) were calculated separately for induced and evoked theta power changes. Concerning induced theta power, the analysis showed a significant main effect of Condition, $F(1, 33) = 4.60$, $p = .039$, a significant main effect of Time, $F(6, 198) = 10.64$, $p < .001$, and also a significant interaction between the two factors, $F(6, 198) = 6.71$, $p = .001$. Indeed, reliable differences between the COM and INC conditions arose for the later time intervals from 500 to 700 msec only (means: 23.7% vs. 37.3%; Tukey HSD_{.05} = 9.55%). Regarding evoked theta power, there was a significant main effect of time, $F(6, 198) = 46.30$, $p < .001$, but neither a significant main effect of Condition nor a significant interaction, both F s < 1 , suggesting that evoked theta power time-locked to stimulus onset was unaffected by response conflict.¹

Sensory Lateralization

Examination of lateralization effects in stimulus-locked power changes between trials with left- and right-hemifield distractor presentations revealed two significant clusters, one in the left hemisphere over occipital electrodes P5, P7, and PO7, $p_{\text{crit}} = .015$, and one in the right hemisphere

over occipital electrodes P6, P8, and PO8, $p_{\text{crit}} = .019$ (Figure 5A). The two clusters showed concurrent theta power effects with similar time–frequency characteristics (3–6 Hz; minimum of 0.05 to maximum of 0.25 sec after stimulus onset), thus indicating a sensory lateralization effect. Therefore, for each time point, an SLI was calculated by subtracting mean power changes of the cluster ipsilateral to distractor presentation side from mean power changes of the cluster contralateral to distractor presentation side, averaged across left and right hemifield presentations. Time courses of the SLI for total power changes are depicted in Figure 5B, separately for the three experimental conditions.

Following the same steps as in the analysis of the mid-frontal conflict effect reported above, next, we compared the time courses of the SLI between the COM and INC conditions. First, a repeated-measures ANOVA with the factors of Condition (COM vs. INC) and Time (six 100-msec time intervals from 0 to 0.6 sec following stimulus onset) was calculated. The analysis showed a significant main effect of Condition, $F(1, 33) = 4.39$, $p = .044$, a significant main effect of Time, $F(5, 165) = 10.95$, $p < .001$, and also a significant interaction between the two factors, $F(5,$

165) = 3.00, $p = .013$. Indeed, reliable differences between conditions arose from 0.2 to 0.4 sec after stimulus onset with stronger sensory lateralization of total theta power in incompatible than compatible trials (means: 14.1% vs. -1.4% ; Tukey HSD_{.05} = 14.2%). Additional analysis showed that, in the said time interval, reliable differences between conditions were similarly present in the first and second half of the experiment, $F(1, 33) = 1.26$, $p = .270$.

In the analysis of the evoked and induced parts of the stimulus-locked sensory lateralization effect, theta activities were averaged from 0.2 to 0.4 sec following stimulus onset and contrasted between the COM and INC conditions. A repeated-measures ANOVA with the factors of Condition (COM vs. INC) and Activity (evoked vs. induced) revealed significant main effects of Condition, $F(1, 33) = 5.30$, $p = .028$, and activity, $F(1, 33) = 23.20$, $p < .001$, but no significant interaction between the two factors, $F(1, 33) < 1$. The results indicate that evoked theta activity showed a stronger stimulus-locked sensory lateralization effect than induced theta activity. More important, comparable conflict effects arose for evoked (8.4% vs. 15.0%) and induced theta activities (-9.7% vs. -0.9%) contributing

Figure 5. Sensory lateralization.

(A) Topography of the sensory lateralization effect in occipital theta power (difference between left distractor presentation and right distractor presentation trials). Electrodes in white depict the two significant clusters in theta power (3–6 Hz; 0.05–0.25 sec after stimulus onset). (B) Stimulus-locked time course of the SLI (theta power changes in the cluster contralateral minus theta power changes in the cluster ipsilateral to distractor presentation side) as a function of experimental condition (COM, INC, NEU). The purple-shaded area indicates significant differences between incompatible and compatible trials, $p < .05$. (C, D) Response-locked and stimulus-locked time courses of the SLI as a function of response conflict (COM vs. INC). Dotted lines refer to the SLI of evoked theta power changes; dashed lines refer to the SLI of induced theta power changes. The purple-shaded areas indicate significant differences in the SLIs of both evoked and induced theta power changes between compatible and incompatible trials, $p < .05$.

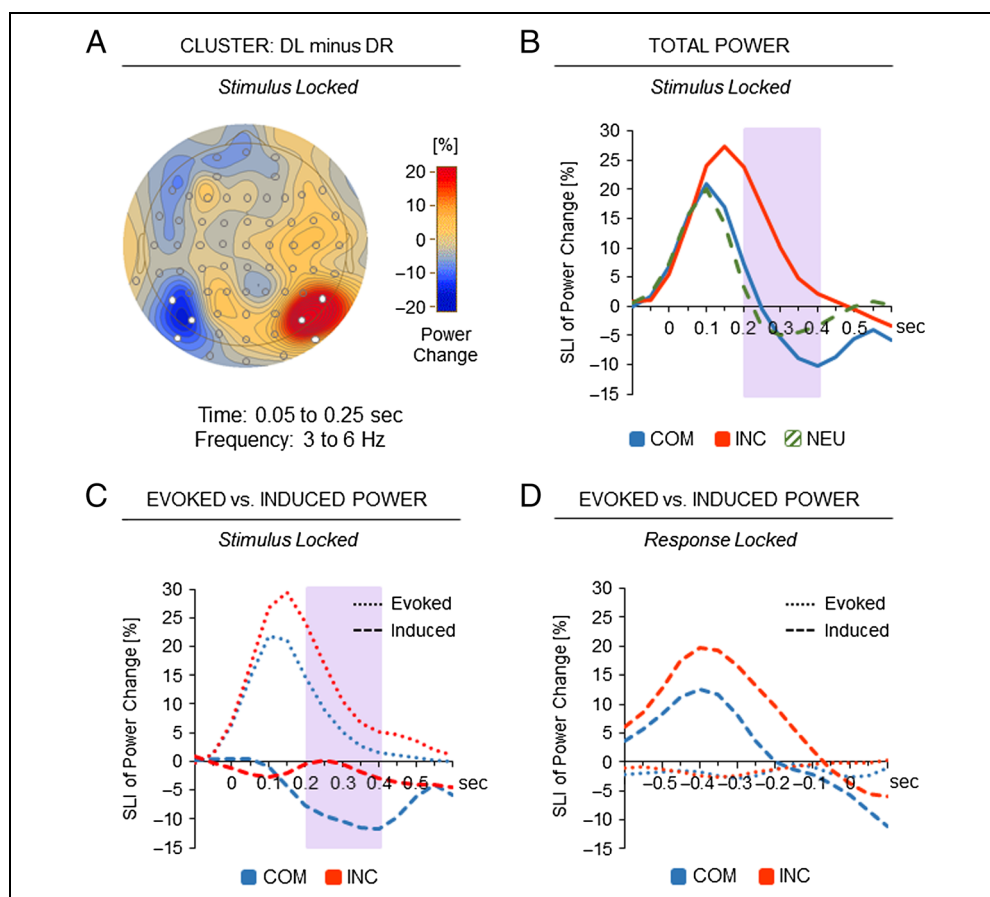
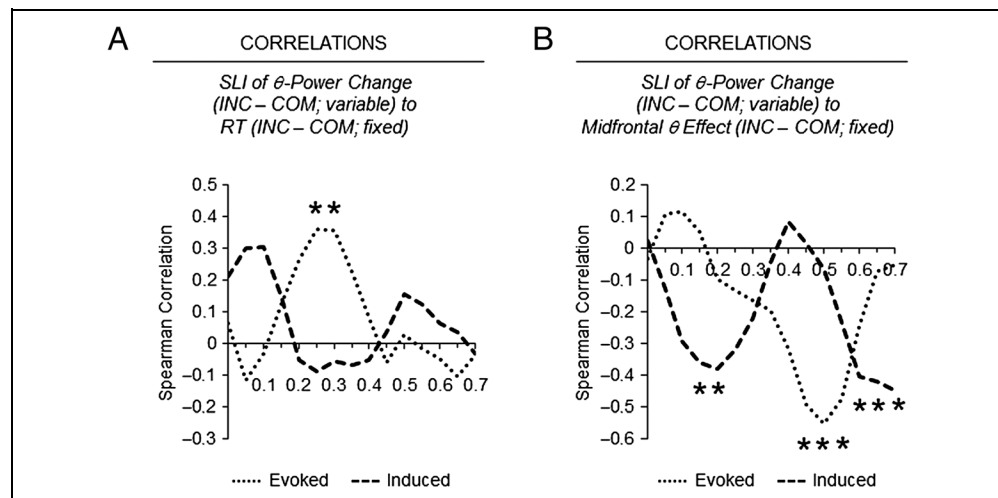


Figure 6. Spearman correlations. Relationship of the sensory lateralization effect in evoked and induced theta power (INC minus COM; variable across time) with (A) the behavioral conflict effect in RT (INC minus COM; fixed) and (B) the midfrontal conflict effect in induced theta power (INC minus COM; fixed; based on the significant cluster in the response-locked analysis shown in Figure 4A). Asterisks mark significant correlations, $p < .05$, uncorrected.



to the stimulus-locked sensory lateralization effect. The time courses are depicted in Figure 5C.

In addition, the evoked and induced parts of the response-locked sensory lateralization effect were calculated in the 500-msec interval before response onset (see Figure 5D). Repeated-measures ANOVAs with the factors of Condition (COM vs. INC) and Time (five 100-msec time intervals from -0.5 to 0 sec before response onset) were calculated separately for evoked and induced theta activities. The analyses showed a main effect of Time for induced theta, $F(4, 132) = 5.93$, $p = .008$, but not for evoked theta, $F(4, 132) < 1$. No significant main effect of Condition was found, neither for induced theta, $F(1, 33) = 2.42$, $p = .130$, nor for evoked theta, $F(1, 33) < 1$, and also no significant interaction arose, both F s < 1 . Together with the stimulus-locked analyses above, these results suggest that the modulation of sensory distractor processing induced by response conflict was primarily driven by stimulus-related theta activities and less, if at all, by response-related activities.²

Finally, correlational brain–behavior and brain–brain analyses were calculated. Figure 6 shows the results. Regarding brain–behavior correlations, the results showed that the behavioral conflict effect in RT (individual differences between the INC and COM conditions) was positively related to the conflict effect in the SLI of evoked theta power change (individual differences between the INC and COM conditions) from 0.25 to 0.3 sec following stimulus onset (see Figure 6A). Regarding brain–brain correlations, the midfrontal conflict effect in induced theta power (response-locked; averaged from -0.2 to 0.2 sec around response onset) was negatively related to the conflict effect in the SLIs of both evoked and induced theta power change in different time intervals following the onset of stimuli (see Figure 6B). No significant correlation between the midfrontal conflict effect in induced theta power and the behavioral conflict effect in RT arose, $r = .09$, $p = .599$.

DISCUSSION

This study examined the behavioral and electrophysiological effects of response conflict in a lateralized version of the Eriksen flanker task. Behaviorally, the results showed effects of response (in)compatibility in both RT and accuracy, characterized by slower and more error-prone responses on incompatible than compatible trials, which is consistent with the findings from previous behavioral work (e.g., Frings & Spence, 2010; Evans & Craig, 1992; Eriksen & Eriksen, 1974). At the electrophysiological level, the results showed a conflict effect on S-LRP onset, but no conflict effect on LRP-R onset, indicating that conflict affected the duration of premotor processes but did not influence the duration of motor processes (see Kopp et al., 1996; Gratton et al., 1988, for similar findings). With regard to EEG oscillatory activities, we found a prominent effect of response conflict in (induced) midfrontal theta power (6 – 9 Hz), which is consistent with the findings from previous EEG work (e.g., Nigbur et al., 2011, 2012). Going beyond the previous work, the results showed that sensory lateralization of (both evoked and induced) theta activities (3 – 6 Hz) over occipital electrode sites was stronger on incompatible than compatible trials, thus indicating a modulation of early sensory distractor processing induced by late response conflict.

Earlier research has shown that occipital brain activity in general and sensory lateralization in particular can be modulated by the processing of conflicting information in the Eriksen flanker task (e.g., Marini et al., 2016; Appelbaum et al., 2011). In this earlier research, occipital brain activity was contrasted between trials with conflicting and (partially) nonconflicting distractor information. In partial-conflict trials, the distractors were conflicting (stimulus incongruent and response incompatible) in one hemifield but nonconflicting (stimulus congruent and response compatible) in the other hemifield. Examining ERPs,

Appelbaum et al. (2011) demonstrated a sensory lateralization effect in partial-conflict trials, with more positive ERPs over occipital sites contralateral than ipsilateral to the conflicting distractor presentation side. The effect arose from 0.2 to 0.55 sec after stimulus onset, simultaneously in time with the midfrontal N200 conflict effect. The researchers proposed that the sensory lateralization effect reflects attentional distraction toward the conflicting information. However, because of the nonorthogonal manipulation of stimulus and response conflict, it is not clear whether the distraction is caused by stimulus conflict, response conflict, or both. In this study, we examined whether occipital brain activity is modulated by response conflict arising at the response selection level. The results showed a clear modulation of early sensory distractor processing induced by response conflict. Indeed, both evoked and induced theta power over occipital electrode sites showed a stronger lateralization effect in incompatible than compatible trials from 0.2 to 0.4 sec following stimulus onset. On the individual subject level, the sensory lateralization effect in evoked theta power was correlated with the behavioral conflict effect in RT. Because theta oscillations in the visual system have been linked to lateralized control of visuospatial attention (e.g., Van der Lubbe et al., 2014; Green & McDonald, 2008), the sensory lateralization effect in theta power is suggested to reflect attentional distraction to conflicting distractor information. This view is consistent with the view by Appelbaum et al. (2011), with the additional proposal that it is response conflict at the response selection level that influences the processing of sensory distractor information. Future EEG work is needed that manipulates stimulus and response conflict orthogonally to evaluate the separate contribution of stimulus and response conflict to the sensory lateralization effect in a single experiment.

TEC provides a theoretical framework for explaining the present results. TEC suggests a close link between the processes of stimulus perception and response activation and the processing of stimulus and response conflict, respectively. TEC assumes that the perception of a stimulus and the action associated with this stimulus share a common code and therefore are representationally and functionally related (Hommel, 2004, 2009). The idea is that, even after a single pairing of a stimulus and a response, an S-R episode is bound into a common memory, and upon repetition of any part of the episode, this memory is instantly retrieved. Imaging studies have suggested that posterior prefrontal, ventral temporal, and higher-order visual brain areas contribute to the processing of S-R bindings (Horner & Henson, 2008; Dobbins et al., 2004). These brain areas show an increase in activation when the response associated to a stimulus changes between stimulus presentations. With respect to the present flanker task, TEC predicts that—after an initial S-R pairing—reencountering a flanker stimulus should instantly activate the S-R episode and directly retrieve the associated response. This should lead to fast processing of response

conflict in incompatible trials. In addition, TEC predicts that—due to S-R bindings—interference due to response conflict in incompatible trials could influence the processing at early levels of (sensory) information processing. This is exactly what the present results suggest, showing an early modulation of lateralized theta power over occipital electrodes induced by response conflict. Moreover, the modulation was found to be robust, that is, equally present in the first and second half of the experiment, which further corroborates the S-R binding view on the effect. Indeed, S-R bindings do not need to be gradually learned but are promptly constructed and stably retained (see Henson et al., 2014).

In addition to the sensory lateralization effect, a prominent nonlateralized conflict effect in induced theta power (6–9 Hz) over midfrontal electrode sites was observed. This finding is in line with previous EEG studies that have demonstrated reliable conflict effects for induced theta power around response onset in various conflict tasks (e.g., Cohen & Donner, 2013; Cavanagh et al., 2012). The finding is also in line with previous studies that have reported conflict effects in induced theta power regardless of whether the evoked part of the signal was removed in the analysis or not (e.g., Cohen & Donner, 2013; Pastötter, Dreisbach, & Bäuml, 2013; Pastötter et al., 2012). The midfrontal conflict effect in theta power has been source localized to ACC (e.g., Töllner et al., 2017; Nighur et al., 2011; Pastötter et al., 2010; Hanslmayr et al., 2008), which is believed to monitor and detect conflict between concurrent stimuli and responses (Botvinick et al., 2004; Van Veen & Carter, 2002a). According to the conflict-monitoring view, ACC is the key structure to initiate the temporal cascade of processes by which the brain responds to conflict and regulates attentional control. In this study, the midfrontal conflict effect in induced theta power began 0.5 sec after stimulus onset and thus followed in time the occipital conflict effect in lateralized theta power. This finding suggests that the occipital cortex, but not ACC, was the first structure to “detect” the conflict in the present task. Arguably, ACC thus may not have “detected” but may have “registered” conflicting information and “communicated” the information to other brain areas in the present task. In fact, the present correlational analyses suggest that the conflict effect in lateralized theta power over occipital sites was negatively related to the midfrontal conflict effect in theta power, which indicates that conflict processing in the occipital cortex may have even reduced the processing of conflict in ACC. The finding of a negative correlation is consistent with recent work showing that early stimulus-related interregional phase coupling between parietal and frontal electrode sites in the theta-to-alpha frequency range is negatively related to midfrontal theta power increase induced by response conflict that was elicited by task-irrelevant motion direction of stimuli in a feature-based Simon task (Vissers, Ridderinkhof, Cohen, & Slagter, 2018).

The proposal that ACC registers and communicates the conflict is in line with the cognitive control literature,

which assumes that ACC detects (or registers) conflict on a current trial n and engages control functions in the DLPFC that bias future processing and reduce (potential) conflict on the following trial $n + 1$ (see Carter & van Veen, 2007, for a review). Consistent with this view, both behavioral and physiological conflict effects on trial $n + 1$ have been found to be modulated by conflict in trial n , indicating conflict adaptation effects (e.g., Gratton, Coles, & Donchin, 1992). Indeed, imaging studies have shown that ACC activity is typically reduced on conflict trials following conflict trials as compared with conflict trials following nonconflict trials (e.g., Kerns, 2006; Kerns et al., 2004; Botvinick et al., 1999). Corresponding evidence also arose from EEG studies that examined the oscillatory signature of the conflict adaptation effect and showed a sequential modulation in midfrontal theta power (Töllner et al., 2017; van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015; Pastötter et al., 2013; Cohen & Cavanagh, 2011). Addressing the interplay between ACC and DLPFC, an intracranial EEG study by Oehm et al. (2014) further showed that, in the Stroop task, the detection (or registration) of conflict in trial n is related to theta power increase in ACC, whereas the communication of conflict to the DLPFC in trial $n + 1$ is mediated by theta phase synchronization between ACC and DLPFC and an increase in DLPFC gamma power (30–100 Hz). Addressing the contribution of visual brain regions to the sequential conflict adaptation effect in a Stroop task, an fMRI study by Egner and Hirsch (2005) showed that the processing of relevant targets (i.e., prominent faces) in high-level visual brain regions (i.e., the fusiform face area) can be enhanced in trials that followed the processing of conflicting distractors (i.e., incongruent names), whereas activity in the early visual cortex showed no conflict adaptation effect. In this study, we found a modulation of visual processes induced by conflict that was induced in the same trial n . Future EEG work is needed that examines possible sequential modulations of early visual processing in the present flanker and other conflict tasks (e.g., the accessory Simon task; see Footnote 2) with higher temporal resolution than fMRI.

To conclude, previous fMRI and EEG work employing lateralized versions of the Eriksen flanker task have revealed modulations of early sensory distractor processing induced by conflict but did not further evaluate the separate contribution of stimulus and response conflict to sensory distraction. In the present EEG study, we took a first step in this direction and examined the contribution of response conflict to the lateralized sensory distraction effect. The results showed a clear conflict modulation in lateralized theta power over occipital sites, indicating that early sensory distractor processing is modulated by late response conflict. The finding is consistent with theories of action control emphasizing S-R bindings (Henson et al., 2014; Hommel, 2004, 2009), which suggest a close link between stimulus and response representations, and the processing of stimulus and response conflict, respectively.

Acknowledgments

The authors thank B. Hommel and one anonymous reviewer for their comments on a previous version of the manuscript and T. Brinkmann, J. Paulus, J. Becker, and J. Lohner for their help with experimental setup and data collection.

Reprint requests should be sent to Bernhard Pastötter, Department of Psychology, University of Trier, Universitätsring 15, 54286 Trier, Germany, or via e-mail: pastoetter@uni-trier.de.

Notes

1. Regarding evoked theta power time-locked to stimulus onset, Figure 4D shows that there was a small but not significant difference between compatible and incompatible trials at peak power latency of 150 msec (28.4% vs. 30.6%), $t(33) = 1.12$, $p = .273$. Bayes hypothesis testing showed that the Bayes factor was 3.074, in favor of the null hypothesis over the two-sided alternative hypothesis (calculated with default settings in the JASP software package; Wagenmakers et al., 2018). This indicates that the observed data were 3.074 times more likely under the null hypothesis than under the alternative hypothesis, thus providing moderate evidence for the null hypothesis (see Lee & Wagenmakers, 2013), which assumes that evoked theta power (150 msec after stimulus onset) was unaffected by response conflict.

2. The present flanker task additionally featured a Simon-like conflict effect, which has been called accessory Simon effect in the literature (e.g., Nishimura & Yokosawa, 2010). The effect refers to the finding that responses to centrally located targets are faster and less error-prone when the presentation side of the lateralized distractors is spatially congruent with the responses to the targets. Therefore, we examined whether Simon congruency interacted with the major outcomes of the present task. ANOVAs on (median) RT, error rate, SLI of total theta power change, and induced midfrontal theta power change were calculated with the additional factor of Simon congruency. All analyses showed a main effect of Simon congruency, due to slower RT, more response errors, stronger theta SLI, and higher midfrontal theta power in Simon-incongruent than Simon-congruent trials, all $ps < .030$. Importantly, none of the analyses showed a significant interaction between Simon congruency and Experimental condition, all $ps > .156$, thus suggesting that the major outcomes in the present task were unaffected by Simon congruency. The nonfinding of an interaction between Simon congruency and experimental condition is consistent with the findings from an earlier behavioral study by Diedrichsen, Ivry, Cohen, and Danziger (2000), which also showed no modulation of response conflict effects induced by Simon congruency (but did find such modulation of stimulus-conflict effects). Notably, the present EEG finding of a main effect of Simon congruency on theta SLI indicates that the modulation of early sensory distractor processing induced by (response) conflict may not be restricted to the present flanker task but may generalize to other (response) conflict tasks.

REFERENCES

- 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. *Journal of Cognitive Neuroscience*, 23, 2620–2628.
- Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, 402, 179–181.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8, 539–546.

- Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: An update of theory and data. *Cognitive, Affective, & Behavioral Neuroscience*, *7*, 367–379.
- Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, *18*, 414–421.
- Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology*, *49*, 220–238.
- Chan, J. S., Merrifield, K., & Spence, C. (2005). Auditory spatial attention assessed in a flanker interference task. *Acta Acustica United With Acustica*, *91*, 554–563.
- Cohen, M. X., & Cavanagh, J. F. (2011). Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. *Frontiers in Psychology*, *2*, 30.
- Cohen, M. X., & Donner, T. H. (2013). Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *Journal of Neurophysiology*, *110*, 2752–2763.
- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorial in Quantitative Methods for Psychology*, *1*, 42–45.
- 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. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 113–126.
- Dobbins, I. G., Schnyer, D. M., Verfaellie, M., & Schacter, D. L. (2004). Cortical activity reductions during repetition priming can result from rapid response learning. *Nature*, *428*, 316–319.
- Donohue, S. E., Todisco, A. E., & Woldorff, M. G. (2013). The rapid distraction of attentional resources toward the source of incongruent stimulus input during multisensory conflict. *Journal of Cognitive Neuroscience*, *25*, 623–635.
- Eder, A. B., Leuthold, H., Rothermund, K., & Schweinberger, S. R. (2012). Automatic response activation in sequential affective priming: An ERP study. *Social Cognitive and Affective Neuroscience*, *7*, 436–445.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, *8*, 1784–1790.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters on the identification of target letters in a non-search task. *Perception & Psychophysics*, *16*, 143–149.
- Eriksen, C. W. (1995). The flankers task and response competition: A useful tool for investigating a variety of cognitive problems. *Visual Cognition*, *2*, 101–118.
- Evans, P. M., & Craig, J. C. (1992). Response competition: A major source of interference in a tactile identification task. *Attention, Perception, & Psychophysics*, *51*, 199–206.
- Frings, C., & Rothermund, K. (2011). To be or not to be... included in an event file: Integration and retrieval of distractors in stimulus-response episodes is influenced by perceptual grouping. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *37*, 1209–1227.
- Frings, C., Rothermund, K., & Wentura, D. (2007). Distractor repetitions retrieve previous responses to targets. *Quarterly Journal of Experimental Psychology*, *60*, 1367–1377.
- Frings, C., & Spence, C. (2010). Crossmodal congruency effects based on stimulus identity. *Brain Research*, *1354*, 113–122.
- Frings, C., Wentura, D., & Wühr, P. (2012). On the fate of distractor representations. *Journal of Experimental Psychology: Human Perception & Performance*, *38*, 570–575.
- Gratton, G., Coles, M. G., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, *121*, 480–506.
- Gratton, G., Coles, M. G., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and poststimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 331–344.
- Green, J. J., & McDonald, J. J. (2008). Electrical neuroimaging reveals timing of attentional control activity in human brain. *PLoS Biology*, *6*, e81.
- Hanslmayr, S., Pastötter, B., Bäuml, K.-H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*, *20*, 215–225.
- Heil, M., Osman, A., Wiegelmann, J., Rolke, B., & Hennighausen, E. (2000). N200 in the Eriksen task: Inhibitory executive processes? *Journal of Psychophysiology*, *14*, 218–225.
- Henson, R. N. (2009). Priming. In L. Squire, T. Albright, F. Bloom, F. Gage, & N. Spitzer (Eds.), *Encyclopedia of neuroscience* (pp. 1055–1063). Amsterdam: Elsevier.
- Henson, R. N., Eckstein, D., Waszak, F., Frings, C., & Horner, A. (2014). Stimulus-response bindings in priming. *Trends in Cognitive Sciences*, *18*, 376–384.
- Hoehstetter, K., Bornfleth, H., Weckesser, D., Ille, N., Berg, P., & Scherg, M. (2004). BESA source coherence: A new method to study cortical oscillatory coupling. *Brain Topography*, *16*, 233–238.
- Hommel, B. (2004). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences*, *8*, 494–500.
- Hommel, B. (2009). Action control according to TEC (theory of event coding). *Psychological Research*, *73*, 512–526.
- Hommel, B., Müssele, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 849–878.
- Horner, A. J., & Henson, R. N. (2008). Priming, response learning and repetition suppression. *Neuropsychologia*, *46*, 1979–1991.
- Horner, A. J., & Henson, R. N. (2012). Incongruent abstract stimulus-response bindings result in response interference: fMRI and EEG evidence from visual object classification priming. *Journal of Cognitive Neuroscience*, *24*, 760–773.
- Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology*, *19*, 113–124.
- Kalcher, J., & Pfurtscheller, G. (1995). Discrimination between phase-locked and non-phase-locked event-related EEG activity. *Electroencephalography and Clinical Neurophysiology*, *94*, 381–384.
- Kelley, T. A., & Lavie, N. (2011). Working memory load modulates distractor competition in primary visual cortex. *Cerebral Cortex*, *21*, 659–665.
- Kerns, J. G. (2006). Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the Simon task. *Neuroimage*, *33*, 399–405.
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., III, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*, 1023–1026.
- Kopp, B., Rist, F., & Mattler, U. (1996). N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology*, *33*, 282–294.
- Lamers, M. J. M., & Roelofs, A. (2011). Attentional control adjustments in Eriksen and Stroop task performance can be independent of response conflict. *The Quarterly Journal of Experimental Psychology*, *64*, 1056–1081.
- Lee, M. D., & Wagenmakers, E.-J. (2013). *Bayesian cognitive modeling: A practical course*. Cambridge: Cambridge University Press.

- 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.
- MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, *288*, 1835–1838.
- Marini, F., Demeter, E., Roberts, K. C., Chelazzi, L., & Woldorff, M. G. (2016). Orchestrating proactive and reactive mechanisms for filtering distracting information: Brain–behavior relationships revealed by a mixed-design fMRI study. *Journal of Neuroscience*, *36*, 988–1000.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190.
- Mayr, S., & Buchner, A. (2006). Evidence for episodic retrieval of inadequate prime responses in auditory negative priming. *Journal of Experimental Psychology: Human Perception & Performance*, *32*, 932–943.
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, *35*, 99–115.
- Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*, 1–17.
- Nigbur, R., Cohen, M. X., Ridderinkhof, K. R., & Stürmer, B. (2012). Theta dynamics reveal domain-specific control over stimulus and response conflict. *Journal of Cognitive Neuroscience*, *24*, 1264–1274.
- Nigbur, R., Ivanova, G., & Stürmer, B. (2011). Theta power as a marker for cognitive interference. *Clinical Neurophysiology*, *122*, 2185–2194.
- Nishimura, A., & Yokosawa, K. (2010). Visual and auditory accessory stimulus offset and the Simon effect. *Attention, Perception, & Psychophysics*, *72*, 1965–1974.
- Oehm, C. R., Hanslmayr, S., Fell, J., Deuker, L., Kremers, N. A., Do Lam, A. T., et al. (2014). Neural communication patterns underlying conflict detection, resolution, and adaptation. *Journal of Neuroscience*, *34*, 10438–10452.
- Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin*, *116*, 220–244.
- Pastötter, B., Berchtold, F., & Bäuml, K.-H. T. (2012). Oscillatory correlates of controlled speed-accuracy tradeoff in a response-conflict task. *Human Brain Mapping*, *33*, 1834–1849.
- Pastötter, B., Dreisbach, G., & Bäuml, K.-H. T. (2013). Dynamic adjustments of cognitive control: Oscillatory correlates of the conflict adaptation effect. *Journal of Cognitive Neuroscience*, *25*, 2167–2178.
- Pastötter, B., Hanslmayr, S., & Bäuml, K.-H. T. (2010). Conflict processing in the anterior cingulate cortex constrains response priming. *NeuroImage*, *50*, 1599–1605.
- Peterson, B. S., Kane, M. J., Alexander, G. M., Lacadie, C., Skudlarski, P., Leung, H.-C., et al. (2002). An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Cognitive Brain Research*, *13*, 427–440.
- Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalography and Clinical Neurophysiology*, *42*, 817–826.
- Shin, Y. K., Proctor, R. W., & Capaldi, E. J. (2010). A review of contemporary ideomotor theory. *Psychological Bulletin*, *136*, 943–974.
- Stock, A., & Stock, C. (2004). A short history of ideomotor action. *Psychological Research*, *68*, 176–188.
- Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*, 151–162.
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuo-spatial attention bias and predicts visual target detection. *Journal of Neuroscience*, *26*, 9494–9502.
- Töllner, T., Wang, Y., Makeig, S., Müller, H. J., Jung, T. P., & Gramann, K. (2017). Two independent frontal midline theta oscillations during conflict detection and adaptation in a Simon-type manual reaching task. *Journal of Neuroscience*, *37*, 2504–2515.
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, *38*, 816–827.
- Van der Lubbe, R. H., Bundt, C., & Abrahamse, E. L. (2014). Internal and external spatial attention examined with lateralized EEG power spectra. *Brain Research*, *1583*, 179–192.
- van Driel, J., Swart, J. C., Eegner, T., Ridderinkhof, K. R., & Cohen, M. X. (2015). (No) time for control: Frontal theta dynamics reveal the cost of temporally guided conflict anticipation. *Cognitive, Affective, & Behavioral Neuroscience*, *15*, 787–807.
- Van Veen, V., & Carter, C. S. (2002a). The anterior cingulate as a conflict monitor: fMRI and ERP studies. *Physiology & Behavior*, *77*, 477–482.
- Van Veen, V., & Carter, C. S. (2002b). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, *14*, 593–602.
- Van Veen, V., Cohen, J. D., Botvinick, M. M., Stenger, V. A., & Carter, C. S. (2001). Anterior cingulate cortex, conflict monitoring, and levels of processing. *NeuroImage*, *14*, 1302–1308.
- Vissers, M. E., Ridderinkhof, K. R., Cohen, M. X., & Slagter, H. A. (2018). Oscillatory mechanisms of response conflict elicited by color and motion direction: An individual differences approach. *Journal of Cognitive Neuroscience*, *30*, 468–481.
- Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, A. J., et al. (2018). Bayesian inference for psychology. Part II: Example applications with JASP. *Psychonomic Bulletin & Review*, *25*, 58–76.
- White, C. N., Ratcliff, R., & Starns, J. J. (2011). Diffusion models of the flanker task: Discrete versus gradual attentional selection. *Cognitive Psychology*, *4*, 210–238.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, *20*, RC63.
- Wühr, P., & Frings, C. (2008). A case for inhibition: Visual attention suppresses the processing of irrelevant objects. *Journal of Experimental Psychology: General*, *137*, 116–130.