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Theta Dynamics Reveal Domain-specific Control over Stimulus and Response Conflict

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Abstract

■ Cognitive control allows us to adjust to environmental changes. The medial frontal cortex (MFC) is thought to detect conflicts and recruit additional resources from other brain areas including the lateral prefrontal cortices. Here we investigated how the MFC acts in concert with visual, motor, and lateral prefrontal cortices to support adaptations of goal-directed behavior. Physiologically, these interactions may occur through local and long-range synchronized oscillation dynamics, particularly in the theta range (4–8 Hz). A speeded flanker task allowed us to investigate conflict-type-specific control networks for perceptual and response conflicts. Theta power over MFC was sensitive to both perceptual and response conflict. Interareal theta phase synchrony, however, indicated a selective enhancement specific for response conflicts between MFC and left frontal cortex as well as between MFC and the presumed motor cortex contralateral to the response hand. These findings suggest that MFC theta-band activity is both generally involved in conflict processing and specifically involved in linking a neural network controlling response conflict. ■

INTRODUCTION

Executive cognitive control functions are key to goal-directed behaviors. However, we only yet begin to understand how the brain deals with conflicts in various processing domains like perception and action selection to achieve goal-directed behavior. Recently, it has been shown that cognitive control demands in conflict situations lead to an increase in theta power (Cohen & Cavanagh, 2011; Nigbur, Ivanova, & Stürmer, 2011; Hanslmayr et al., 2008). With the present study, we address conflict-domain-specific enhancement of interareal long-range synchrony in the theta range between brain areas specific for different types of cognitive conflicts.

We deployed an Eriksen flanker task as useful tool for investigating conflicts in both perception and response selection. In the classical version of this task (Eriksen & Eriksen, 1974), four letters are mapped onto two responses, resulting in three congruency conditions: In the (1) congruent (C) condition the target letter is flanked by identical letters; (2) in the stimulus incongruent condition (I_S) flanker letters differ from the target whereas both require the same response, hence inducing conflict during perceptual processing without response conflict; (3) in the response incongruent condition (I_R) target and flankers indicate different responses, thereby inducing both stimulus and response conflict. Congruent trials act as a baseline condition and the "flanker effect" manifests in I_S

an I_R trials; both resulting in longer RTs and reduced accuracy for I_R trials when compared with C trials.

Recent theories focus on a predominant role of medial frontal cortex (MFC) and lateral prefrontal cortices (LPFC) as the neural underpinnings of mechanisms implementing cognitive control such as conflict detection, performance monitoring, inhibition, error processing, or reinforcement learning (Botvinick, Cohen, & Carter, 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Rushworth, Walton, Kennerley, & Bannerman, 2004; Holroyd & Coles, 2002). The conflict monitoring approach proposes that the ACC signals conflict and triggers compensatory adjustments via LPFC (Botvinick et al., 2004). Others, however, suggest that the MFC is directly involved in resolving conflict (Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011; Posner & DiGirolamo, 1998).

From an electrophysiological perspective, brain ERP markers such as the N2 or the error-related negativity (ERN) are seen as indices of performance monitoring in situations where conflicts are possible and call for executive control (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Heil, Osman, Wiegelmann, Rolke, & Hennighausen, 2000; Kopp, Rist, & Mattler, 1996; Gehring, Goss, Coles, Meyer, & Donchin, 1993).

However, it is not yet clear whether the engagement of a prefrontal network, including MFC and LPFC, is generic for all kinds of conflicts or specialized for different types of conflicts. Studies comparing neural signatures of stimulus and response conflict revealed inconsistent findings: fMRI recordings (van Veen, Cohen, Botvinick, Stenger, &

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Carter, 2001) and ERPs (van Veen & Carter, 2002) showed activations of the ACC exclusively during response conflict and not during stimulus conflict. In contrast, Wendt, Heldmann, Munte, and Kluwe (2007) reported an N2 effect in the ERP for both stimulus and response conflict that did not distinguish between conflict types.

Here, the use of time–frequency transformed EEG data can broaden the understanding of cognitive processes and their neuronal counterparts by two measures: First, certain frequency bands have been implicated in the generation of ERPs and might therefore provide another window on how neural assemblies are involved in cognitive processes. Frontal theta-band activity (4–8 Hz), for example, has been linked to response control (Basar, Schurmann, & Sakowitz, 2001) and several other top–down control functions such as control mechanisms in working memory, learning, memory encoding, or navigation (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Fries, 2005; Ward, 2003; Kahana, Seelig, & Madsen, 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Luu and Tucker (2001) filtered response-locked error data with a 4–7 Hz band pass and observed that ongoing midline oscillations were enhanced in case an ERN was elicited. Trujillo and Allen (2007) compared empirical with simulated ERN data and concluded that the ERN is most likely generated by a partial phase-resetting plus an amplitude enhancement of ongoing theta activity in ACC, which may be part of a broader limbic network generating theta activity relevant to learning and reward (Caplan et al., 2003). Taken together, theta oscillations seem to play a pivotal role in performance monitoring and conflict resolution processes.

As a second measure, long-range phase synchrony reflects neural communication across different brain sites (Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007; Ward, 2003; Engel, Fries, & Singer, 2001; Varela et al., 2001). One mechanism regarding interareal theta communication during increased cognitive control demands has been described by Cavanagh, Cohen, and Allen (2009). In this study, transient synchronous oscillations in the theta range occurred during error commission between medial frontal sites and lateral prefrontal sites. Furthermore, the extent of synchronized activity between these regions predicted post-error slowing in the upcoming trial. Interareal oscillatory synchrony in the theta range was, hence, interpreted as one mechanism by which the detection of errors is linked to the subsequent recruitment of cognitive control as exerted by lateral frontal brain areas. Similarly, increased coupling between sources in the MFC and the left LPFC was observed for conflict trials in a Stroop task that resulted in correct responses (Hanslmayr et al., 2008).

Motivated by several studies that used theta power as a measure for enhanced top–down control during error commission and conflict resolution (Cavanagh et al., 2009; Cohen, van Gaal, Ridderinkhof, & Lamme, 2009; Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008; Trujillo & Allen, 2007; Luu, Tucker, & Makeig, 2004), we aimed at testing whether processing of cognitive conflicts can be characterized according to their time–frequency dynamics. On the basis of previous evidence theta power over MFC should reflect the amount of conflict. Moreover, changes in interchannel phase synchrony (ICPS) between brain areas such as LPFC, motor cortices, and sensory areas should be observed according to the type of conflict. For perceptual conflict, we assumed an increase in synchrony mainly between MFC and visual areas (Cohen et al., 2009). For response conflicts, we expected enhanced synchrony between MFC and the motor cortex as well as LPFCs.

METHODS

Participants

Eighteen right-handed and two left-handed participants (mean = 73.6, according to the Handedness Inventory; Oldfield, 1971) were tested, in exchange for course credits or money (7.5 €/hr). The mean age of the group (10 women) was 23.2 years ($SD = 3.3$ years) ranging from 19 to 29 years. They were all healthy with no history of neurological illnesses (according to self report) and had normal or corrected-to-normal vision. Participants gave their informed written consent in accordance with the declaration of Helsinki (1964).

Procedure

Participants were seated in a sound-attenuated, electrically shielded, and dimly lit chamber. Responses were recorded with two keys placed horizontally on a table at a distance of 25 cm. All stimuli were displayed in white on dark gray on a computer monitor. Participants were tested with a flanker task mapping four stimulus letters (N, P, K, L) on two responses. Two flanker letters on each side preceded the target by 150 msec, after target onset all letters were visible together with the target for further 200 msec ($2.1° \times 0.4°$). Two of the letters required a right-hand response, whereas the other two called for a left-hand response. The letter-hand mapping was counterbalanced over participants. After a practice block, 576 trials were presented in eight blocks of 72 trials, yielding 192 trials per condition. A fixation point ($0.07° \times 0.07°$) was visible whenever no stimulus was presented and during the 1700 msec response-to-stimulus interval. A 50-msec feedback tone (40 Hz) provided 550-msec poststimulus stressed participants to speed response. Participants were still able to press the target button until 1000 msec posttarget. The experimental design yielded three conditions, namely (1) a congruent condition (C) with identical target and flanker stimuli, (2) a stimulus incongruent condition (I_S) where target and flankers differed but indicate the same response hand, and (3) a response incongruent condition (I_R) with flankers and target mapped on different response hands.

Behavioral Analyses

Only correct trials following correct responses entered repeated measurements ANOVAs and subsequent pairwise comparisons were Bonferroni corrected if necessary.

EEG Recording

The EEG was recorded at 500 Hz sampling rate using 58 scalp and 4 periocular electrodes of a Brain Amp recording system. Impedances were kept below 5 kΩ. All analyses were conducted in Matlab using in-house written code supplemented by EEGLAB (independent component analysis and topographical plotting; Delorme & Makeig, 2004). Data were rereferenced off-line to the average of the activity recorded at the two mastoid electrodes. After visual inspection trials containing artifacts were identified and removed. Blink artifacts were removed from the data using independent component analyses in EEGLAB. EEG data were first current source–density transformed (Kayser & Tenke, 2006) to increase spatial selectivity and minimize volume conduction by the contribution of deep sources that project to many electrodes and increase spatial resolution (Srinivasan, Winter, Ding, & Nunez, 2007). Continuous EEG data were epoched into segments of 4000 msec around target presentation starting 1000 msec pretarget.

Time–Frequency Calculation

Time–frequency calculations were computed using custom-written Matlab (MathWorks, Natick, MA) routines (Cohen et al., 2008). Power and intertrial phase coherence (ITPC) were calculated over the raw CSD-EEG epochs at all electrodes. The CSD-EEG time series in each epoch was convolved with a set of complex Morlet wavelets, defined as a Gaussian-windowed complex sine wave:

$$e^{i2\pi tf}e^{-t^2/(2\sigma^2)},$$

where t is time, f is frequency (which increased from 2 to 50 Hz in 30 logarithmically spaced steps), and σ defines the width (or "cycles") of each frequency band, set according to $4.5/(2\pi f)$. A width of 4.5 provides an adequate trade-off between temporal and frequency resolution (Trujillo & Allen, 2007). From the resulting analytic signal, we obtained the following: (1) estimates of instantaneous power (the magnitude of the analytic signal), defined as $Z(t)$ (power time series: $p(t) = \text{real}[z(t)]^2 + \text{imag}[z(t)]^2$) and (2) phase angle defined as $\phi_t = \arctan(\text{imag}[z(t)]/\text{real}[z(t)])$. Each epoch was then truncated in length (−2000 to 2000 msec posttarget presentation) and baseline corrected to the average frequency power from −500 to −300 msec before the onset of the cue (Cohen et al., 2008). Power was normalized by conversion to a decibel (dB) scale (10 × log10 [power (t)/power (baseline)]), allowing a direct comparison of effects across frequency bands.

Two different types of oscillation phase coherence were examined: ITPC and ICPS. ITPC measures the consistency of phase values for a given frequency band at each point in time over trials, in one particular electrode. Phase coherence values vary from 0 to 1, where 0 indicates random phases at that time–frequency point across trials and 1 indicates identical phase values at that time–frequency point across trials. The phase coherence value is defined as follows:

$$\text{ITPC} = \Big| \frac{1}{n} \times \sum_{x=1}^{n} e^{i\phi_{xt}} \Big|,$$

where n is the number of trials for each time and each frequency band. ITPC thus reflects the extent to which oscillation phase values are consistent over trials at that point in time–frequency space (power, in contrast, represents the intensity of that signal). Note that this measure of phase coherence does not differentiate between possible biophysical mechanisms underlying phase consistency, such as phase reset or phase "smearing". Rather, this measure simply indicates the statistical probability of increased phase consistency between trial and baseline epochs. ICPS measures the extent to which oscillation phases are similar across different electrodes over time–frequency and is calculated as follows:

$$\text{ICPS} = \Big| \frac{1}{n} \times \sum_{t=1}^{n} e^{i[\phi_{jt} - \phi_{kt}]} \Big|,$$

where n is the number of trials, ϕ_j and ϕ_k are the phase angles of electrode j and k. Thus, phase angles are extracted from two electrodes and then subtracted: If the phase angles from the two electrodes fluctuate in synchrony over a period, their difference will be constant (i.e., nonuniformly distributed), leading to ICPS values close to 1.

To measure phase synchrony between MFC and LPFC F5–FCz and F6–FCz sites were used. We selected both F5 and F6 phase synchrony because the literature does not provide an unequivocal indication about whether pFC-based cognitive control is left- or right-lateralized (Kerns, 2006; Kerns et al., 2004; Garavan, Ross, Murphy, Roche, & Stein, 2002).

Rationale for Timing and Condition Selection

We focused our analyses on a fixed time window from 200 to 400 msec posttarget to cover theta differences for all congruency conditions. We assumed that if any communication between MFC and LPFC (measured as synchrony between FCz and F5/F6) should be observable, then these should also take part within the usual N2 time windows which are used for analysis of conflict processing in ERPs. We focused on trials following correct congruent trials because here behavioral effects of stimulus and response

incongruent trials are at their maximum (Gratton, Coles, & Donchin, 1992). These trials therefore provide optimal conflict conditions to study on-line within-trial conflict processing and at the same time avoided potential confounds such as post-error slowing or conflict adaptation effects (Egner, Delano, & Hirsch, 2007; Sturmer & Leuthold, 2003). After visual inspection of the theta power data, we decided to post hoc analyze the time window 400–600 msec because differences between stimulus and response incongruent trials were most pronounced in that later time window.

RESULTS

Behavioral Data

Congruent trials (mean RT = 404 msec; SEM = 8.1 msec) were faster than I_S trials (mean RT = 433 msec; SEM = 9.3 msec) and I_R trials (mean RT = 475 msec; SEM = 8.6 msec) resulting in a main effect of Flanker Congruency, $F(2, 38) = 135.341$, $p < .01$. Pairwise comparisons of incongruent flankers to congruent trials yielded significant effects for both the stimulus-incongruent condition, $t(19) = 7.95$, $p < .001$, and the response-incongruent condition, $t(19) = 14.6$, $p < .001$. The difference between the stimulus-incongruent and response-incongruent conditions was also significant: $t(1, 19) = 9.5$, $p < .001$. The average error rate was 14.4%; significantly more errors were made in the response incongruent condition ($M = 23.4\%$) compared with congruent flankers ($M = 10.5\%$), $t(19) = 6.021$, $p < .01$, and compared with the stimulus incongruent condition ($M = 9.3\%$), $t(19) = 7.851$, $p < .01$. Differences between congruent and stimulus incongruent trials were not significant (Figure 1), $t(19) < 1.183$, $p = .25$.
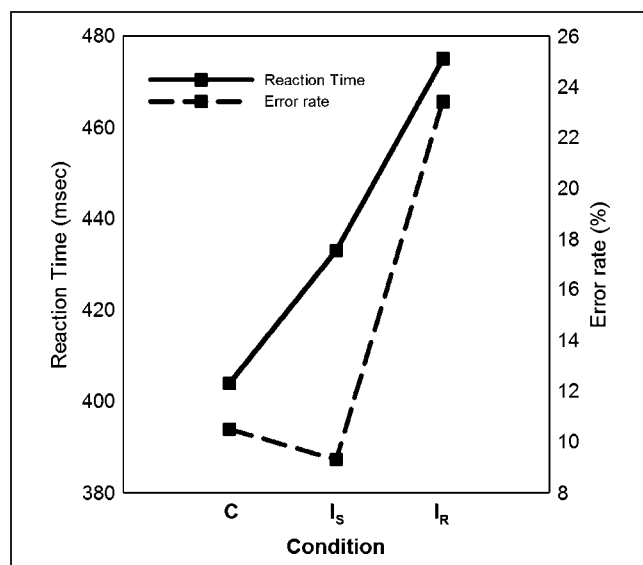
Figure 1. RT data and error rates depicted for the three experimental conditions, congruent (C), stimulus incongruent (I_S), and response incongruent (I_R).

Theta Power Modulations over MFC

Theta power between 200 and 400 msec post-target was enhanced during both stimulus and response conflict (Figure 2), as reflected in a main effect of Congruency Condition, $F(2, 38) = 19.82$, $p < .001$. Pairwise comparisons revealed significant differences between congruent and stimulus incongruent trials, $t(19) = 4.35$, $p < .001$, as well as between congruent and response incongruent trials, $t(19) = 5.61$, $p < .001$. In contrast, no main effect was obtained for Current Congruency Type in ITPC measures. Further power analyses of the later time window from 400 to 600 msec yielded a significant main effect of Congruency Condition with higher amplitudes for stimulus and response incongruent trials compared with congruent trials, $F(2, 38) = 51.71$, $p < .001$. Pairwise comparisons confirmed significant differences between congruent trials and stimulus incongruent trials, $t(19) = 6.88$, $p < .001$, as well as response incongruent trials, $t(19) = 8.89$, $p < .001$. Furthermore, in this time window stimulus and response incongruent trials differed significantly, $t(19) = 3.75$, $p < .03$.

MFC Theta Phase Synchrony

To test whether different types of conflict elicit the same or different top–down control mechanisms, we examined synchrony between MFC and LPFC electrode sites. As mentioned above, we restricted the data set to trials with a congruent predecessor because, here, strongest conflict effects were expected and observed in behavior. ANOVAs were conducted separately for left and right pFC. We found a main effect of Congruency Type for left, $F(2, 38) = 6.22$, $p < .01$, and right, $F(2, 38) = 5.19$, $p = .01$, LPFC synchrony with FCz. Furthermore, pairwise analyses for both hemispheres showed that increased top–down control in terms of enhanced coupling between MFC and LPFC was only apparent during response incongruent trials but not during stimulus incongruent trials (Figure 3) at the left hemisphere, $t(19) = 2.96$, $p < .01$, as well as the right hemisphere, $t(19) = 3.06$, $p < .01$.

Response-related control should be mirrored in enhanced coupling between MFC and motor areas contralateral to the response hand. We, therefore, calculated synchrony between FCz located above the MFC and C3 or C4 above the motor cortex depending on response hand. An ANOVA with the factor Congruency (C, I_S, I_R) yielded a significant main effect, $F(2, 38) = 3.82$, $p < .05$. Pairwise comparisons revealed that only response incongruent trials enhanced synchrony compared with congruent trials [$t(19) = 2.76$, $p < .05$], but not stimulus incongruent trials ($t < 1$).[1]

Comparisons of synchrony between FCz and Oz, depending on the congruency condition, yielded no significant effects. However, inspection of the FCz synchrony map (Figure 4) led to post hoc analyses of FCz–P4 coupling in the theta range and yielded significant differences in a late time window (400–600 msec) for both stimulus incongruent trials, $t(19) = 3.97$, $p < .01$, and response
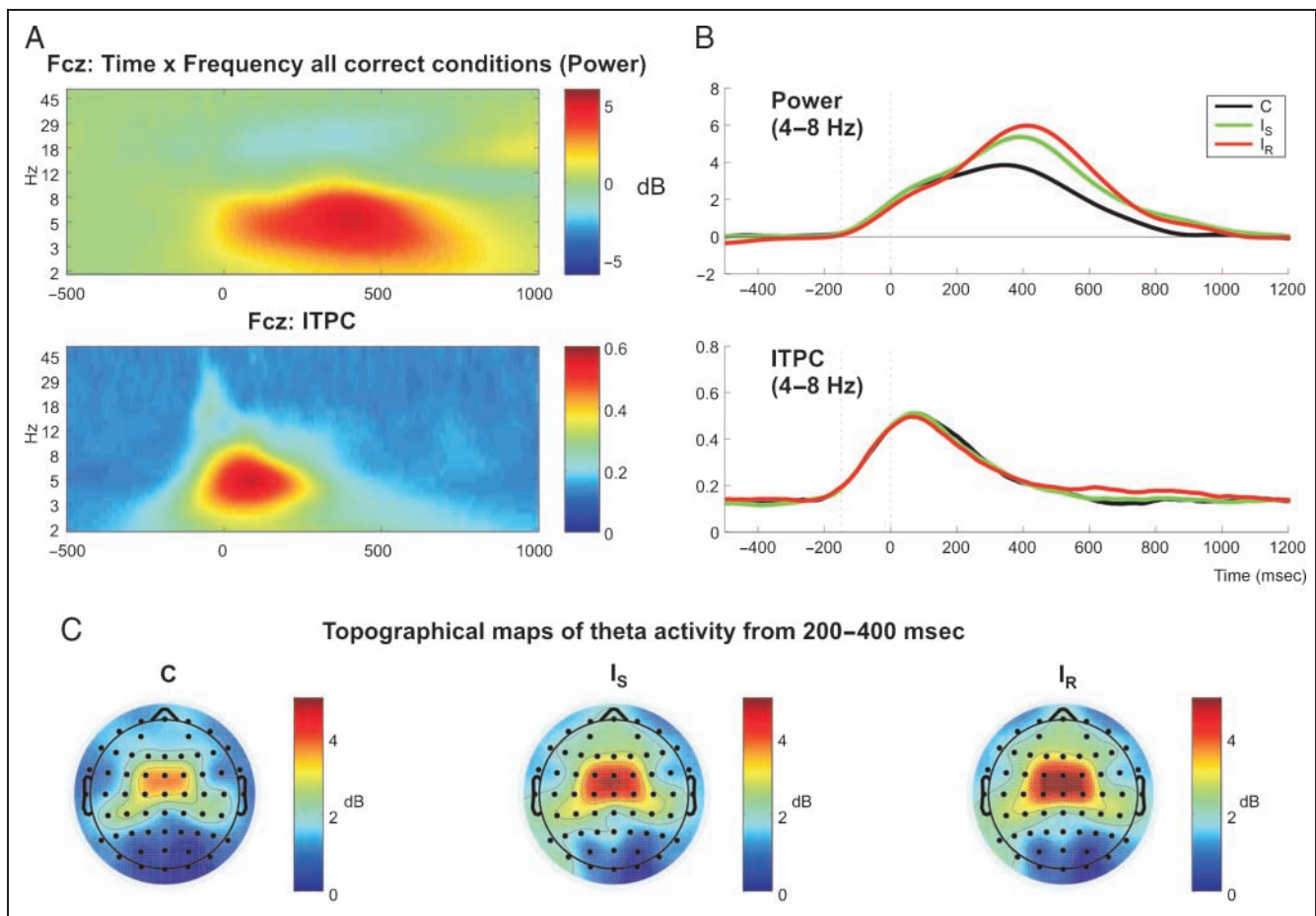
Figure 2. (A) Time–frequency representation for power and ITPC over all correct conditions over electrode FCz. (B) Power and ITPC over FCz for congruent, stimulus, and response conflict following congruent trials; as can be seen, ITPC cannot account for power differences. (C) Respective theta maps indicating maximal power differences over medial frontal areas.

incongruent trials, $t(19) = 4.88$, $p < .05$, compared with congruent trials; differences between synchrony during stimulus incongruent and response incongruent trials (see Figure 4) were marginally significant, $t(19) = 2.07$, $p = .052$ (Figure 5).

DISCUSSION

We tested whether resolving conflicts in information processing relates to electrophysiological brain responses in terms of enhanced theta power over the MFC. More specifically, we were interested in whether a network achieving conflict control is established by synchronized activity between brain regions related to conflict control and those that are involved in provoking the conflict. To this end, we applied a flanker task and observed a flanker effect in RT for both stimulus and response incongruent trials and increased error rates for the latter.

MFC Theta Power during Perceptual and Response Conflict

On the electrophysiological level, we observed a phasic increase in theta power in stimulus and response incon-

gruent trials—situations calling for conflict control at a perceptual or response level. Our results contrast to reports by van Veen et al. (van Veen & Carter, 2002; van Veen et al., 2001) who conducted a letter flanker experiment and reported enhanced activity within the MFC only during response conflict but not during perceptual conflict in an fMRI study (2001). In an ERP study (van Veen & Carter, 2002), they replicated this finding with N2 enhancements only during response conflict trials whereas Wendt et al. (2007) found N2 enhancements both for stimulus and response conflicts. In the latter study, however, the N2 effects did not dissociate between response and stimulus conflict. Our results are in line with an enhancement of MFC activation during both stimulus and response conflict indicating a general involvement of MFC during conflict processing, which has also been demonstrated using single-trial regression on theta power in a flanker task (Cohen & Cavanagh, 2011) and lately for potentially invalid cued stimuli in a response-priming task (Pastötter, Hanslmayr, & Bäuml, 2010). When comparing response and stimulus conflict at a later time window, theta power distinguished between these conflict types. Thus, our data suggests that MFC theta activity is not restricted to response conflict but is also sensitive to stimulus conflicts

and differs between conflict types in different time windows.

Distributed Networks for Cognitive Control

The idea that different parts of the brain are involved in perceptual and response conflict raised the question whether communication between these regions can be enabled by means of neuronal synchronization in the theta band. We focused on areas that have been shown to be involved in such processes, namely the LPFCs, the motor cortices, and posterior sensory areas. However, even with spatial filtering, there is no necessary one-to-one mapping between electrode location on the scalp and underlying brain source.

In agreement with previous studies analyzing theta phase coupling between medial frontal and lateral frontal electrode sites, we found enhancements only during response conflict. Cavanagh et al. (2009) showed that during error commission theta power amplitude as well as theta phase coupling between FCz and lateral prefrontal electrodes (such as F5 and F6) were enhanced. Concordant with this observation, we found a similar pattern during response conflict trials resulting in correct responses. Such interareal communication was also observed by Hanslmayr et al. (2008) during incongruent Stroop trials, although participants responded with only one hand. This finding is in line with the proposal that the MFC serves conflict detec-tion and signals control demands to the LPFC (Botvinick et al., 2004). However, at odds with the classical conflict monitoring approach is our finding that the MFC itself might serve not only conflict detection but also some response controlling function. Although we cannot rule out an involvement of LPFC (see Figure 6),[2] our data contrib-ute to a growing literature emphasizing the controlling functions of different portions of MFC during response se-lection (Danielmeier et al., 2011; Cohen et al., 2009; Aarts, Roelofs, & van Turennout, 2008; Matsumoto, Matsumoto, & Abe, 2006; Milham & Banich, 2005; Posner & DiGirolamo, 1998).

In contrast to studies emphasizing the role of left prefron-tal areas (Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000) for control functions, our data suggest that also right prefrontal areas are involved during demand-ing response conflict situations. This finding is in line with data from go/no-go or stop/signal studies assigning a crucial role to right prefrontal areas in inhibiting motor activations (Forstmann et al., 2008; Aron, Robbins, & Poldrack, 2004; Fassbender et al., 2004). One could argue that areas en-gaged in response inhibition in these studies are as well relevant in the flanker task when during an incongruent trial a response primed by the flankers has to be inhibited to guarantee correct responses (cf. Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2010, for a review).

Findings from studies measuring the lateralized readi-ness potential as well as excitability of motor-evoked

Figure 3. (A) Coupling between FCz–F6 electrode during the congruent (left) and response conflict (right) condition, theta synchrony differences appear visible strongest in the latter. (B) This effect as a function of time restricted to the theta band (4–8 Hz) for FCz coupling with F5 and F6 for congruent (black), stimulus (green) and response (red) conflict condition, as can be seen this effect was visible over both lateral prefrontal sites.
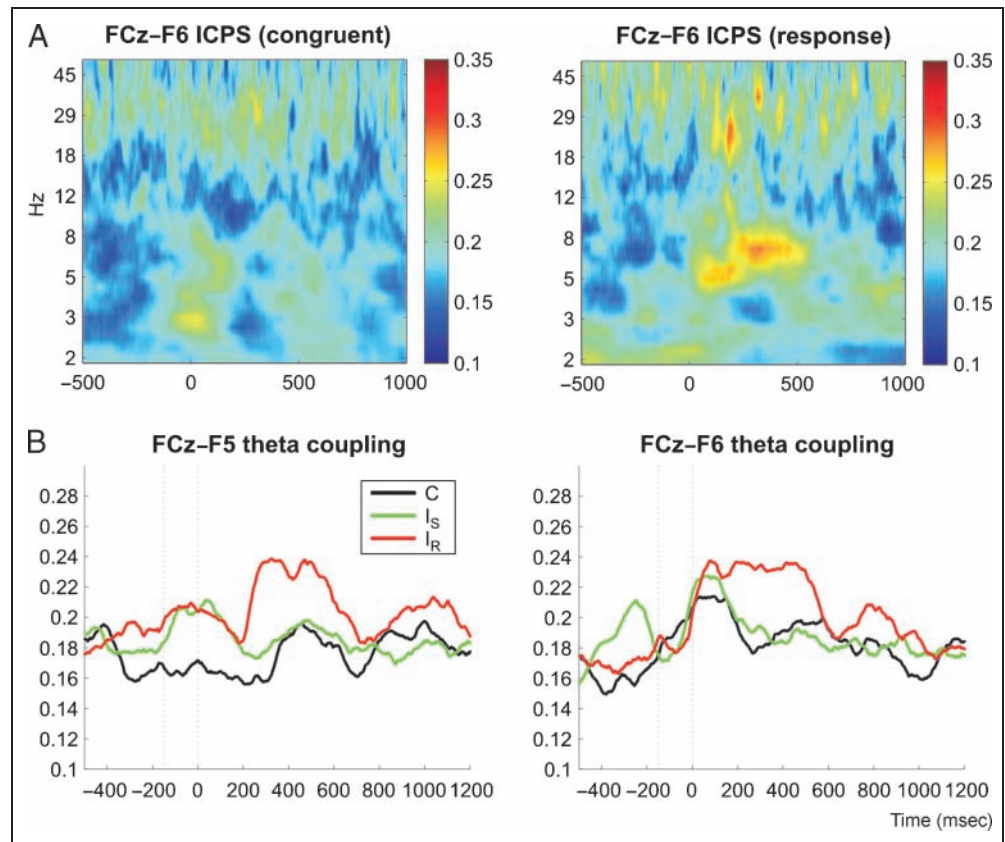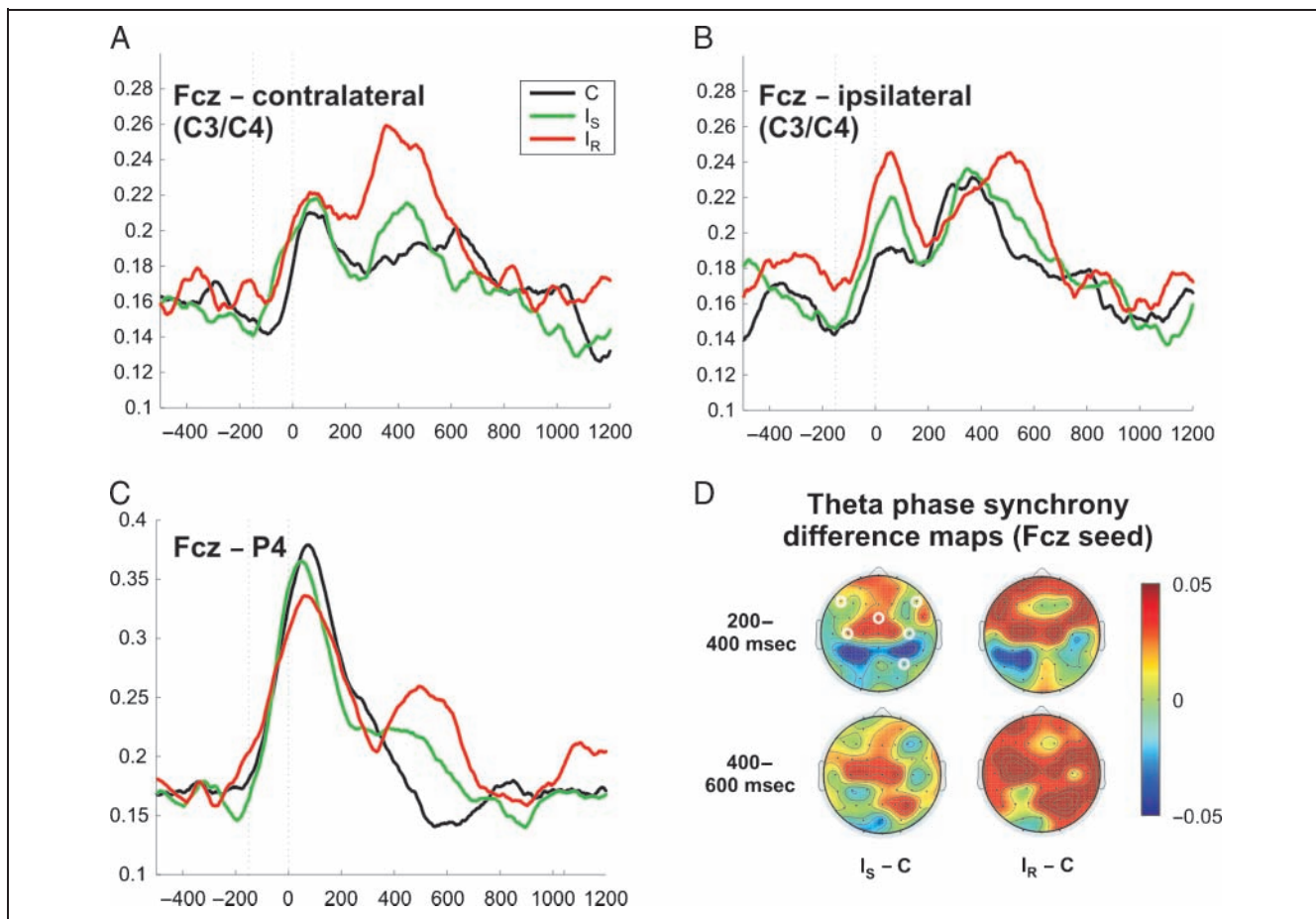
Figure 4. Time plots depicting theta synchrony for FCz and motor cortex contralateral (A) or ipsi-lateral (B) to the respective response hand. (C) Post hoc analyses revealed significant effects of FCz–P4 theta coupling for both stimulus and response incongruent conditions. (D) Illustrative theta synchrony maps and synchrony difference maps with a seed over FCz. An increase in synchrony over several prefrontal areas (including left and right lateral pFC) can be observed only in the response incongruent trials.

potentials by TMS (Verleger, Kuniecki, Moller, Fritzmannova, & Siebner, 2009; Sturmer, Siggelkow, Dengler, & Leuthold, 2000) support the theoretical assumption that a prepotent response activation of the wrong response hand develops automatically over the respective motor cortex. Our data strengthen this view because we found that theta synchrony between motor cortex contralateral to the response hand and MFC was only enhanced in the response conflict condition but not in the stimulus conflict condition. Therefore, synchrony between MFC and motor areas might mirror local control functions during conflict resolution between competing motor activations.

A further question concerns the involvement of sensory areas in perceptual conflict situations. On the basis of previous findings (Cohen et al., 2009), we expected synchronization between MFC and occipital areas following conflicts. Although these areas did not show any effect in coupling, post hoc analyses revealed a coupling between FCz and P4 electrode for stimulus and response incongruent trials, which both elicit perceptual conflict. Task differences might account for the finding that different posterior brain areas were synchronized with the MFC in both studies. First, Cohen et al. (2009) presented

dim dots in a go/no-go task as no-go signals, whereas we presented letters. Compared with the dots used in their study, letters in the present study should be identified later in the stream of visual processing. Second, the no-go stimulus used in the Cohen et al. study (2009) was visible only for 16.7 msec, which might have called for near threshold detection processes, whereas letters in our study were clearly visible. Post hoc analyses of the present flanker task revealed that theta coupling over parietal electrode sites linearly reflected the degree of conflict in stimulus incongruent and response incongruent trials. This finding is in line with previous reports that the posterior parietal cortex serves cognitive control in conflict situations (Kim, Chung, & Kim, 2010; Mansouri, Tanaka, & Buckley, 2009; Egner et al., 2007; Fan, Flombaum, McCandliss, Thomas, & Posner, 2003). The MFC–P4 synchrony effects (Figure 4) occur relatively late. Therefore, they might rather be associated with visuo-motor integration processes during response execution (Culham, Cavina-Pratesi, & Singhal, 2006) than response selection.

One important notion relates to the finding that ITPC does not differ between experimental conditions. Increases in theta power observed in stimulus and response
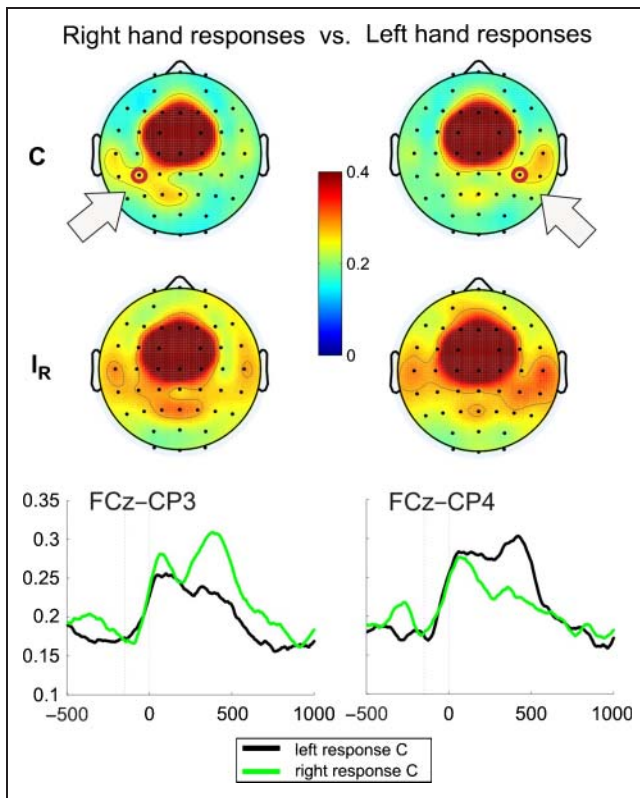
Figure 5. Theta ICPS topographies with FCz seed region for right versus left hand responses (400–600 msec). Top: Congruent condition (C); Middle: Response incongruent condition (I_R); Bottom: Theta-ICPS according to response hand over right and left motor areas (see highlighted electrodes).

conflicts can, therefore, not be attributed to an increase in ITPC across different conditions. Additionally, theta power measures for stimulus and response conflict were enhanced to a similar extent. Synchrony effects are, hence, not likely to be caused by volume conduction. A further notion regards some observed effects that occurred in a time

window which coincides with mean RT (400–500 msec). As can be seen in Figure 1, however, theta power amplitude effects are not just shifted in time, but are rather because of pure amplitude differences.

Theta Dynamics as Integration Mechanism for Cognitive Control Functions

A central challenge for future studies is to characterize the functional role of theta power and synchrony changes. Miller (1991) proposed that the theta rhythm in rats is a neural mechanism by which distant cortical structures can exchange information of local networks. Womelsdorf, Johnston, Vinck, and Everling (2010) extended this view by reporting single-cell recordings from monkeys which suggest that theta-band oscillations, most likely emerging in superficial layers of ACC, could be essential for the functional communication of different areas subserving cognitive control. Accordingly, present findings fit well with ascribing theta a role in the coordination of broader action-regulation functions in the various brain systems. The MFC therefore seems to be crucial in the allocation of control in interaction with prefrontal areas (Miller & Cohen, 2001). Apparently, the MFC controls response selection, because we observed enhanced synchrony between MFC electrodes and contralateral motor sites in response selection demanding incongruent trials.

The exact functional meaning of theta power remains elusive but on the basis of a parsimonious theoretical rationale one could speculate that theta is used to coordinate groups of neurons into a cohesive network and that it provides a temporal framework that allows integration of information from distant brain areas. Theta synchronization could be one mechanism enabling certain aspects such as conflict and error processing of cognitive control (Cohen & Cavanagh, 2011). There are other putative mechanisms of information processing and integration that might

Figure 6. Theta ICPS topographies over I_R and I_S condition for prefrontal seed regions: Left (top) and right (bottom) prefrontal seed regions (1) average activity over both conditions and (2–3) difference maps over respective time windows.
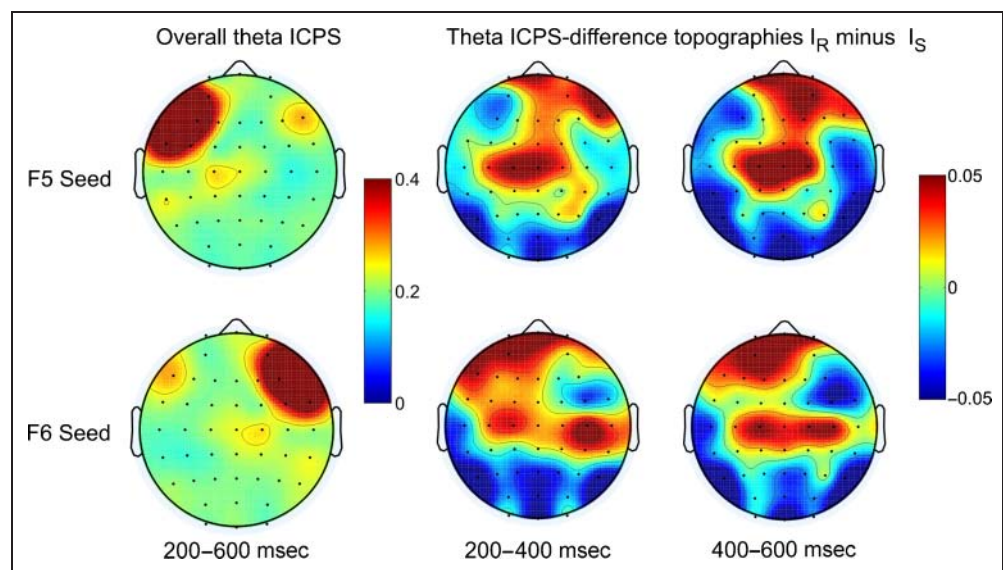
cooperate or be independent of theta synchronization, such as nested theta–gamma couplings, power-to-phase or further cross-frequency couplings (Cohen, 2011; Jensen & Colgin, 2007). It appears, within the context of response conflict and action selection, that a considerable amount of these neuronal populations seem to be situated within MFC. Future research should aim at investigating how (for example by a biasing function) and which exact aspects of control are influenced by this theta network.

Conclusions

The present results are consistent with the idea that executive conflict control functions are enabled via theta-synchronization between different cortical regions that are also involved in the conflict provoking processes. Neural assemblies within the MFC seem to increase their synchronous theta response whenever the system detects inconsistencies in perceptual processing or action selection. Furthermore, both LPFC are recruited selectively during response conflict and this communication is enabled via synchronous theta oscillations. In addition, other brain areas as the motor cortex and the posterior parietal areas were synchronized to MFC theta phase depending on the conflict domain. Theta dynamics might, therefore, be the means of integrative recursive communication allowing the implementation of cognitive control along distant cortical areas.

Notes

1. To assure that MFC synchrony effects are not just due to pure volume conduction caused by the stronger theta power amplitudes in the response conflict condition (I_R), topographies for congruent and response conflict conditions depending on response hand are also presented (Figure 5). As visible in Figure 5 coherence topographies show more activity over motor cortices contralateral to the required response hand; even when only comparing left and right hand responses in the congruent condition respective ICPS dissociated for hemisphere. An ANOVA with the factors Electrode × Response hand revealed a significant interaction of these factors by $F(1, 19) = 10.34$, $p < .01$, confirming that even at distant electrodes ICPS is increased over motor cortices contralateral to the response hand, and it is, therefore, unlikely that they are because of pure volume conduction.

2. We calculated coherence measures for seeds in lateral prefrontal cortices (electrodes F5/F6) of response conflict versus stimulus conflict to account for the involvement of lateral prefrontal regions during conflict control. As visible in Figure 6, ICPS during response conflict is enhanced over the medial portions of the MFC whereas F6 synchrony is bilaterally stronger related to the motor cortices. Response and stimulus conflict differ in both time windows statistically significantly when calculated as synchrony between the respective lateral electrode (F5/F6) and the motor area electrodes (C3/C4). Therefore, an involvement of lateral pFCs in response control cannot be ruled out.

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