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DOI

[10.1162/jocn_a_01222](https://doi.org/10.1162/jocn_a_01222)

Publication date

2018

Document Version

Final published version

Published in

Journal of Cognitive Neuroscience

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[Link to publication](#)

Citation for published version (APA):

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*(4), 468-481. https://doi.org/10.1162/jocn_a_01222

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Oscillatory Mechanisms of Response Conflict Elicited by Color and Motion Direction: An Individual Differences Approach

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and Heleen A. Slagter^{1*}

Abstract

■ Goal-directed behavior requires control over automatic behavior, for example, when goal-irrelevant information from the environment captures an inappropriate response and conflicts with the correct, goal-relevant action. Neural oscillations in the theta band (~6 Hz) measured at midfrontal electrodes are thought to form an important substrate of the detection and subsequent resolution of response conflict. Here, we examined the extent to which response conflict and associated theta-band activity depend on the visual stimulus feature dimension that triggers the conflict. We used a feature-based Simon task to manipulate conflict by motion direction and stimulus color. Analyses were focused on individual differences in behavioral response conflict elicited across different stimulus dimensions and their relationship to conflict-related midfrontal theta. We first confirmed the presence of response conflict elicited by task-irrelevant motion and stimulus color, demonstrating the usefulness of our modified version of the Simon task to assess

different sensory origins of response conflict. Despite titrating overall task performance, we observed large individual differences in the behavioral manifestations of response conflict elicited by the different visual dimensions. These behavioral conflict effects were mirrored in a dimension-specific relationship with conflict-related midfrontal theta power, such that, for each dimension, individual midfrontal theta power was generally higher when experienced response conflict was high. Finally, exploratory analyses of interregional functional connectivity suggested a role for phase synchronization between frontal and parietal scalp sites in modulating experienced conflict when color was the task-relevant visual dimension. Highlighting the importance of an individual differences approach in cognitive neuroscience, these results reveal large individual differences in experienced response conflict depending on the source of visual interference, which are predicted by conflict-related midfrontal theta power. ■

INTRODUCTION

Cognitive control is essential for goal-directed behavior in complex environments. It is particularly important when habitual, automatic behavior interferes with planned actions, for example, when irrelevant or distracting information automatically activates a response tendency that will lead to an error (Botvinick, Cohen, & Carter, 2004; Eriksen & Eriksen, 1974; Simon & Wolf, 1963). In such situations, cognitive control is essential to detect conflict between multiple competing responses and override the incorrect action impulse, by biasing neural processing toward the planned action (Miller & Cohen, 2001).

A growing body of work indicates that theta oscillations (4–8 Hz) provide an important neural mechanism through which the need for enhanced cognitive control is signaled, realized, and communicated to other areas in the brain (Cavanagh & Frank, 2014; Cohen, 2014a) and

thus critically support flexible goal-directed behavior. In particular, many studies have shown robust conflict-related increases in theta band power at midfrontal scalp sites in the time window between stimulus presentation and execution of a behavioral response (Pastötter, Dreisbach, & Bäuml, 2013; Cohen & Cavanagh, 2011; Nigbur, Ivanova, & Stürmer, 2011; Hanslmayr et al., 2008). Yet, although conflict-related theta power has been observed during perceptual as well as response conflict (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012), the degree to which conflict-related theta responses depend on the specific source and strength of sensory interference remains presently unknown.

Midfrontal conflict-related theta responses are clearly present at the group level but are typically also observable at the level of the individual participant (Cohen, 2014a; Cohen & Donner, 2013). Notably, individuals often exhibit variability in conflict-related theta that may systematically relate to variability in other conflict-related neural markers and/or behavioral performance (Cohen & Donner, 2013; Egner, 2011). Such individual differences can thus form an important source of information

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concerning the underlying constructs and/or circuits involved in the detection and resolution of response conflict (Vogel & Awh, 2008). Indeed, individual differences in conflict-related midfrontal theta power have been shown to relate to individual differences in behavioral indices of conflict adaptation (the effect of recently experienced response conflict on current performance; Pastötter et al., 2013). Furthermore, under conditions of varying conflict probability, probability-related modulations of conflict-related behavior and midfrontal theta responses have been shown to be related across individuals (van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015). Individual differences analyses relating conflict-related theta responses to individual variation in conflict-related effects on behavior can thus provide important insights into the neural mechanisms underlying conflict detection and resolution.

One precondition for studying individual differences is the presence of variation in the measure of interest across individuals (Zilles & Amunts, 2013; Vogel & Awh, 2008). In the context of response conflict, one potentially powerful way to increase individual variability in response conflict may be to minimize fast errors after the rapid and automatic activation of task-irrelevant response tendencies, for example, by assessing conflict after activation of goal-directed and automatic response tendencies with comparable time courses. According to the influential dual-route model for stimulus–response correspondence effects, such as response conflict in Simon tasks (van den Wildenberg et al., 2010; Ridderinkhof, 2002; Kornblum, Hasbroucq, & Osman, 1990), response conflict arises as a consequence of direct, automatic response activation by a task-irrelevant stimulus feature, whereas deliberate response decision processes that are associated with goal-directed actions take more time. Similarly, according to the Theory of Event Coding (Hommel, 2009; Hommel, Müsseler, Aschersleben, & Prinz, 2001), stimulus features and the corresponding response are encoded in a common space and become associated in direct stimulus–response links; the greater the association strength, the stronger and faster the activation of the response upon presentation of the stimulus feature.

In most previous research on response conflict, direct response activation typically coincides with fast response activation: Stimulus location in typical Simon tasks leads to rapid activation of the interfering response (Liu, Stevens, & Carrasco, 2007). Possibly, slower automatic response activation results in more similar time courses of direct and deliberate response activation, leading to fewer fast errors (Burle, van den Wildenberg, & Ridderinkhof, 2005), and prolonged competition between task-relevant and task-irrelevant response tendencies. Tasks in which the task-irrelevant information is accumulated in a more gradual fashion (e.g., by motion direction; Zavala et al., 2014; Donner et al., 2007), resembling the time course of activation of the goal-directed response, may thus provide a more sensitive measure for examining individual

differences in experienced response conflict than traditionally used location-based Simon tasks.

In this EEG study, we exploited individual differences in response conflict induced by distinct visual dimensions (motion-direction and stimulus color) to gain a better understanding of the mechanisms involved in inducing and resolving response conflict and the generality of these mechanisms to conflict elicited by different sensory dimensions. We further assessed whether dimension-specific response conflict is affected by top-down modulations of sensory processing before the time of response. Participants performed a Simon task with colored moving dot patterns (Galashan, Wittfoth, Fehr, & Herrmann, 2008; Wittfoth, Buck, Fahle, & Herrmann, 2006) that were always characterized by a motion direction (leftward vs. rightward) and a color (blue or green), while their brain activity was recorded with EEG. At the beginning of each block of 10 trials, participants received an instruction to selectively respond according to one of the stimulus dimensions. On a proportion of trials, the task-irrelevant stimulus dimension would activate the incorrect response hand, resulting in response conflict. This design allowed us to assess the presence and dimension specificity of response conflict and the extent to which it is associated with similar theta-band oscillatory dynamics as location-based response conflict (Cohen, 2014a; Cohen & Ridderinkhof, 2013; Nigbur et al., 2011). By leveraging individual differences, we also examined the extent to which response conflict is dependent on the stimulus dimension inducing the conflict (color, motion direction) or is instead general across stimulus dimensions. Whereas motion-based interference is generally assumed to arise from direct sensorimotor links, arisen through a natural association between motion direction and response side, color-based interference, by contrast, may arise either from similarly direct sensorimotor links (arisen via over-learned arbitrary links or via one-trial event coding; Hommel et al., 2001) or from slower and more indirect ideomotor links in which color undergoes more elaborate processing (Ridderinkhof, van den Wildenberg, & Brass, 2014). Thus, comparing neural signatures of conflict arising from different perceptual dimensions may help assess whether the task-irrelevant features of motion and color differ in their potential to induce conflict. Furthermore, we investigated whether individual differences in the effect of response conflict on behavior are similarly predicted by individual conflict-related midfrontal theta power for each stimulus dimension. Finally, we explored the role of sensory modulations in response conflict by examining whether individually experienced response conflict is affected by communication between midfrontal cortex and task-relevant sensory regions. To this end, we ran a cross-participant correlation between dimension-specific conflict-related phase synchronization between midfrontal cortex and sensory regions before the time of response on the one hand and the dimension-specific conflict-related midfrontal theta response on the other.

We had several predictions. First, we predicted to find response conflict on incongruent (IC) trials, reflected in impaired performance on IC compared with congruent (C) trials, as well as a transient increase in midfrontal theta power at the time of response, on both attend-color and attend-motion trials. Second, we predicted that individuals who would exhibit a strong conflict-related decline of performance would also show a stronger theta response at midfrontal scalp sites and predicted that this particular relationship would depend on the source of visual interference (Snyder & Foxe, 2010). Last, we hypothesized that strong conflict-related modulation of early sensory activity by medial frontal cortex, as reflected in interregional communication, would reduce response conflict signaling, as indicated by the subsequent conflict-related midfrontal theta response.

METHODS

Participants

Twenty-nine individuals ($M = 22.6$ years [$SD = 2.86$ years], 24 women) participated in this study in return for course credits or monetary compensation. A selection of participants in this experiment also performed an MRI and behavioral session, data from which have been reported elsewhere (van den Brink et al., 2014). In addition, EMG data from this EEG study have been reported previously (Cohen & van Gaal, 2014). All participants had normal or corrected-to-normal vision and were right-handed. Participants gave written informed consent before participation in the experiment. The experimental procedure was in accordance with relevant laws and institutional guidelines and was approved by the local ethics committee of the University of Amsterdam.

Experimental Task

Participants performed a visual feature-based Simon task, in which response conflict could be elicited by motion direction and stimulus color (Galashan et al., 2008; Wittfoth et al., 2006; Bosbach, Prinz, & Kerzel, 2004). The task was presented using Presentation software (Neurobehavioral Systems, Inc., Berkeley, CA; www.neurobs.com). On each trial, participants viewed a moving dot pattern that was characterized by one of two different motion directions (leftward or rightward) and one of two possible colors (green or blue). Participants were instructed to either indicate the motion direction or the color of the moving dots. The relevant dimension would always change after a block of 10 trials. Before the onset of each block of 10 trials, the relevant dimension for the upcoming 10 trials was displayed by presentation of the word “color” or “motion” in white letters on a black background (see Figure 1A). Participants were asked to attend to the stimulus dimension presented in the instruction (color or motion) and to identify the color (green or

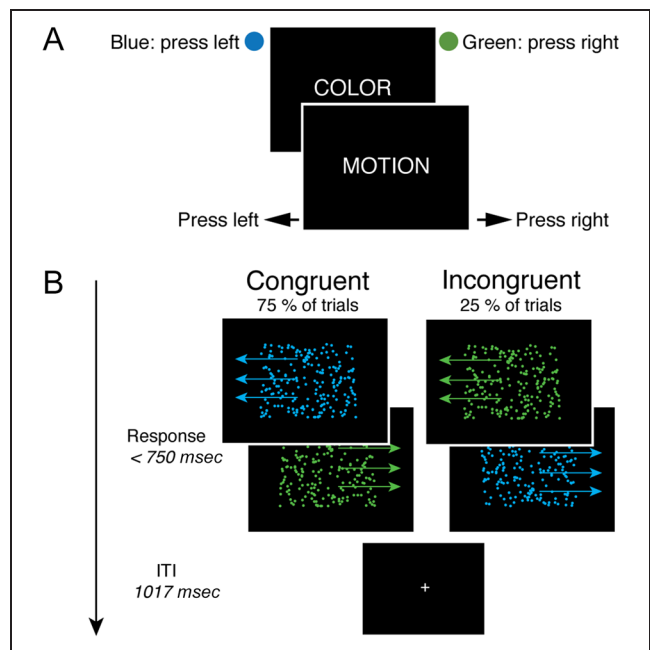


Figure 1. Feature-based Simon task with colored moving dot patterns. (A) Participants were asked to attend to the color or motion direction of the moving dot patterns. When attending to stimulus color, participants were asked to respond with a left button press if the pattern was blue and a right button press if the pattern was green. When attending to motion direction, participants were asked to respond with the response hand corresponding to the motion direction. (B) Display of the possible trial types in the task. On 75% of the trials (C trials), the task-relevant and task-irrelevant features activated the same (correct) response hand. On 25% of the trials (IC trials), the task-irrelevant dimension was associated with a different (incorrect) response hand than the task-relevant dimension, leading to response conflict. The colors and number of dots displayed here do not necessarily resemble the actual stimulus characteristics: Stimuli consisted of 200 moving dots, of which a proportion moved coherently to the left or right. All other dots moved in a random direction. The actual color of the dot patterns was titrated such that participants performed correctly on 85% of all trials by adjusting the similarity between blue and green hues. Stimuli were removed from the screen when the participant made a response or at the end of the response window (750 msec) and followed by an intertrial interval (ITI) of 1017 msec.

blue; color trials) or motion direction of the dot pattern (leftward or rightward; motion trials). They were asked to indicate their response as fast as possible by using their thumbs to press one of the response buttons attached to the left and right armrests of the chair. On motion trials, participants were asked to respond with the hand corresponding to the motion direction of the dots. On color trials, participants were asked to respond with their left hand for blue patterns and with their right hand for green patterns (the assignment of color to response hand was fixed across participants; see Figure 1A). On each trial, the task-irrelevant stimulus dimension was either congruent with the relevant feature and thus activated the same response (leftward-moving blue patterns, rightward-moving green patterns) or incongruent with the task-relevant feature and activated the incorrect response

hand (leftward-moving green patterns, rightward-moving blue patterns; see Figure 1A). In total, the task contained 1,200 trials. The proportion of IC trials was 25%, resulting in 300 IC and 900 C trials per participant. Within each block of 10 trials, C and IC trials were presented in a random order. For one participant, the experiment contained 106 additional trials compared with the typical 1200 trials included in the experiment, because of a programming error. These additional trials were proportionally sampled from the four conditions and were therefore included in subsequent analyses.

Stimuli consisted of 200 moving dots (0.06 degrees of visual angle [dva] diameter) presented within a square frame subtending 7.3×6.4 dva (note that dva measures are approximate because participants were not physically constrained during the experiment). A proportion of the dots moved coherently to the right or to the left, whereas all other dots moved in random directions. Throughout the experiment, we attempted to minimize the influence of general task difficulty on conflict experienced by the stimuli across visual features and individuals. To this end, performance was titrated to $\pm 85\%$ correct throughout the task for each participant (range = 84–86%), by adjusting the proportion of coherently moving dots during attend-motion blocks and by manipulating the similarity between the blue and green hues on attend-color blocks. Titration of stimulus characteristics was performed continuously throughout the entire task (i.e., on all trials after the first) but was always selectively performed on the attended stimulus feature. As the attended feature varied block-wise, this resulted in block-wise selective updating of color or motion coherence of the dot pattern, such that, for 10 consecutive trials within a block, the attended dimension would be updated whereas the unattended dimension remained unchanged. After a participant responded incorrectly (correctly) on an attend-motion trial, the number of coherently moving dots was increased (decreased) by multiplying the number of coherently moving dots by 0.9 (1/0.09) or 0.975 (1/0.975). Similarly, after a participant responded incorrectly (correctly) on an attend-color trial, the difference in RGB points between the greenish and bluish patterns was increased (decreased) by multiplying the number of coherently moving dots by 0.9 (1/0.09) or 0.975 (1/0.975). The number of coherently moving dots within the dot pattern was restricted to vary between 0 (no coherent motion) and 200 (maximally coherent motion). The difference in color values of the dot patterns varied on a 0–128 RGB point scale, where 0 resulted in no difference between the greenish and bluish patterns and 128 resulted in maximally different greenish and bluish dot patterns. At the group level, the mean difference in RGB points between the greenish and bluish patterns was 20 points ($SD = 17$ points, range = 5–80 points); the mean number of coherently moving dots was 149 ($SD = 149$, range = 58–196). As noted in the Results section, the titration procedure did not work as well as expected in particular for motion direction.

Moving dot patterns were removed upon response or at the end of the response window (750 msec). When a participant failed to respond within the response window, an instruction to respond faster was presented for 1000 msec (white letters on a black background). Otherwise, participants received no trial-wise feedback on their performance. Responses or the instruction to respond faster were followed by an intertrial interval (1017 msec) during which a white fixation cross (0.2 dva) was presented on a black background (see Figure 1B). Participants were given a short break every 100 trials, in which they received feedback about their average RTs, to motivate them to balance speed with accuracy.

At the start of the experiment, participants were seated in a comfortable chair in a dimly lit room at 90 cm distance from the computer screen. Before the start of the EEG recording, participants performed 40 practice trials in which they received immediate feedback about their response. Depending on the participants' timing of the breaks in the practice and experimental session, the total duration of the EEG session was approximately 50 min.

EEG: Recording, Preprocessing, and Time-Frequency Decomposition

EEG data were recorded at 512 Hz using a BioSemi (Amsterdam, The Netherlands) setup with 64 channels placed according to the International 10–20 system. Preprocessing and analysis of the EEG data were performed in MATLAB (The MathWorks, Inc., Natick, MA), using EEGlab software (Delorme & Makeig, 2004) and in-house written code (Cohen, 2014b). In addition, we used external electrodes to record data at periocular electrodes to detect blinks, the left and right thumb muscles to record EMG, and both earlobes for offline referencing. Offline EEG data were rereferenced and high-pass filtered at 0.5 Hz. Data were epoched from -1.5 to $+2.5$ sec surrounding stimulus onset, and the baseline period (200 msec prestimulus) of each epoch was subtracted from the entire epoch. All trials were visually inspected, and trials containing excessive EMG or other artifacts not related to blinks were manually removed. Independent components analysis was computed using EEGLAB software (Delorme & Makeig, 2004), and components containing blinks or other artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. Trials in which participants made an error, and trials with fast responses ($RT < 200$ msec), were excluded from further analyses. Finally, a current source density transformation was applied on the data, which is a spatial filter that increases topographical specificity by effectively subtracting out spatially broad and therefore likely volume-conducted effects (Kayser & Tenke, 2006). This approach has been validated for investigating interelectrode synchronization (Srinivasan, Winter, Ding, & Nunez, 2007; Winter, Nunez, Ding, & Srinivasan, 2007).

After preprocessing, a stimulus-locked data set and a response-locked data set were created in which time zero

reflected stimulus presentation and the time of response, respectively. Subsequently, epochs in each data set were organized according to the four experimental conditions (C vs. IC, attend color vs. motion). As the experiment contained three times as many C compared with IC trials, we performed an additional trial selection procedure on the EEG data to match trial numbers between the two C and two IC conditions before further analyses. This was done by RT matching subsets of n trials (where n reflects the number of trials in the smallest condition) from the three largest conditions to the smallest condition of each individual's EEG data set (Cohen, 2014b). This procedure furthermore helps to prevent an overestimation of the actual relationship between the effect of conflict on mid-frontal theta and behavior due to potential differences in RT between conditions (Cohen & Nigbur, 2013; Carp, Kim, Taylor, Fitzgerald, & Weissman, 2010) and would, if anything, bias our results in the opposite direction (by selecting C trials where the participant may have experienced some conflict or was less attentive). This procedure resulted in EEG data sets with four conditions with equal trial counts and optimally similar RT distributions (see Table 1 for the final RT distributions), ensuring that potential effects of our experimental manipulation in later analyses, particularly in the analysis of connectivity, are unlikely to be attributable to differences in trial count or large differences in RTs between conditions (Töllner et al., 2017; van de Vijver, Cohen, & Ridderinkhof, 2014; Niogi, Mukherjee, Ghajar, & McCandliss, 2010). To extract frequency band-specific power reflecting local activity at the time of responding, we analyzed the response-locked EEG data using time–frequency decomposition for each

channel and condition (see, e.g., Cavanagh, Cohen, & Allen, 2009). A time–frequency representation of the data was obtained by multiplying the power spectrum of the EEG (obtained through the fast Fourier transform) by the power spectrum of complex Morlet wavelets ($e^{i2\pi ft} e^{-t^2/2s^2}$, where i is the complex operator, t reflects time, f reflects frequency (1–30 Hz in 20 logarithmically spaced steps), and s defines the width of each frequency band, set according to $n/(2\pi f)$, where n is the number of wavelet cycles that increased from 3 to 10 in logarithmic steps, of which the inverse fast Fourier transform was taken. An estimate of frequency-band-specific power at each time point was defined from the resulting complex signal as the squared magnitude of the result of the convolution ($\text{real}[z(t)]^2 + \text{imag}[z(t)]^2$). After time–frequency decomposition, power was converted to a decibel scale (dB) transform ($\text{dB power} = 10 \times \log_{10}[\text{power}/\text{baseline}]$), which enables comparison of amplitude across frequency bands. For dB normalization, we used the frequency-specific, condition-average activity in the time window between 300 and 100 msec before stimulus presentation as a baseline. For computational purposes, data were down-sampled to 40 Hz after time–frequency decomposition (Cohen, 2014b).

To quantify the effect of conflicting information in a stimulus on interregional communication after stimulus presentation, frequency-band-specific intersite phase clustering (ISPC) reflecting interregional connectivity was computed using the stimulus-locked data set. ISPC was computed according to $\frac{1}{n} \times \sum_{t=1}^n e^{i(\phi_{jt} - \phi_{kt})}$, where n is the number of trials and ϕ_j and ϕ_k are the phase angles of electrodes j and k , respectively. This yields an index of the consistency of phase angle differences

Table 1. Significant Behavioral Effects

<i>Effect</i>	<i>Direction</i>	<i>df</i>	<i>F/t</i>	<i>p</i>
<i>Accuracy</i>				
Congruency	C (84 %) > IC (75%)	1,28	28.64	<.001
Dimension	C (85%) > M (75%)	1,28	12.18	.002
Congruency × Dimension	CE C (10%) > CE M (7%)	1,28	4.43	.044
<i>RTs</i>				
Congruency	C (460 msec) < IC (473 msec)	1,28	50.55	<.001
Dimension	C (451 msec) < M (482)	1,28	42.13	<.001
Congruency × Dimension	CE C (18 msec) > CE M (7 msec)	1,28	12.25	.002
<i>RT EEG data (after Trial Selection)</i>				
Congruency	C (478 msec) IC (468 msec)	1,28	12.63	<.001
Dimension	C (471 msec) M (475 msec)	1,28	2.05	.164
Congruency × Dimension	CE C (17 msec) CE M (2 msec)	1,28	10.64	.003

between two electrodes at each time–frequency point over trials, which was computed for each possible pair of electrodes and all frequencies (1–30 Hz in 20 logarithmically spaced steps). Estimates of ISPC may range from 0 (no phase synchrony between channels) to 1 (identical phase angles between channels). Similar to the power data, data were down-sampled to 40 Hz for computational purposes. Finally, baseline subtraction of ISPC values was performed using the identical time window as used for the power analyses (–300 to –100 msec).

Statistical Analyses

All behavioral analyses were performed after removal of trials with response omissions (8–108 trials [$M = 38.7$] per data set) or fast responses ($RT < 200$ msec; 0–8 trials [$M = 0.79$] per data set). The effect of congruency (C vs. IC) and stimulus dimension (color vs. motion) on accuracy and speed of responding were assessed using repeated-measures ANOVAs. In case of significant main effects or interactions, the statistical significance of differences between factor levels was assessed using follow-up t tests. The relationship between the conflict effect on accuracy of performance (% correct; C vs. IC) for the two stimulus dimensions (color vs. motion) across individuals was assessed using correlation analyses. An alpha level of .05 was used as the significance criterion.

Statistical analysis of conflict-related oscillatory dynamics was performed using the cleaned and correct trials after removal of fast responses ($RT < 200$ msec) and trials following a new instruction (the first trial of every block). Average theta power (4–8 Hz) was computed for C and IC trials collapsed across features (color vs. motion) using the response-locked data (Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013). Because the precise time window of response conflict in the present motion-based Simon task may be slightly different than in typical location-based Simon tasks, samples showing a significant conflict effect on midfrontal theta power (at channel FCz) were identified using a running t test across the time window around response (–800 to 800 msec peri response). Significant samples in the observed data were compared against significant samples observed under H_0 through permutation testing. Specifically, samples that showed a significant conflict effect on theta power in the observed data were rejected if they were not part of a cluster (i.e., series of temporally adjacent samples showing a significant conflict effect) that exceeded the cluster size observed under H_0 . The cluster size distribution under H_0 was obtained through 1,000 permutations on which the data were swapped between conditions (C vs. CI) for a random subset of participants before computation of the test statistic. On each permutation, the largest observed cluster size (i.e., series of consecutive samples showing a statistically significant conflict effect in the permuted data) was selected and saved, rendering a distribution of maximal cluster sizes observed under H_0

(computed separately for clusters showing a negative and positive effect of response conflict on theta power). The cluster size at the 95th percentile of the permuted distribution was used to determine statistical significance of consecutive samples showing a significant condition difference in the observed data.

The relationship between (feature-specific) behavioral and neural indices of response conflict was addressed by means of cross-participant correlation analyses of (feature-specific) conflict-related decline of performance (% correct; C vs. IC) and dimension-specific conflict-related midfrontal theta power (4–8 Hz; IC vs. C) in the time window showing significant conflict-related theta power across visual dimensions (defined as outlined above).

Finally, we assessed the relationship between individual differences in stimulus-locked interregional communication between sensory and midfrontal areas and the conflict-related midfrontal theta response. On the basis of previous research showing effects of attending color versus motion on parietal (Schoenfeld et al., 2007) as well as occipital (Snyder & Foxe, 2010; Zanto, Rubens, Bollinger, & Gazzaley, 2010) scalp sites, we computed attention-related ISPC between FCz and a cluster of bilateral parietal (P3/4, P5/6; see Figure 4A) and occipital channels (POz, Oz, O1/2) collapsed across visual dimensions, in the time window between 200 and 500 msec after stimulus onset. Analyses were focused on connectivity in the theta and alpha bands (Cohen & van Gaal, 2013; Zanto et al., 2010). Conflict-related ISPC (IC vs. C) between frontal and posterior clusters was then related to conflict-related theta power in the time window showing a significant conflict effect or behavior across individuals, separately for each dimension (attending to color vs. motion), using Spearman's correlation coefficient.

RESULTS

Behavior

After preprocessing, the resulting behavioral data sets contained 1160 trials on average ($SD = 57.7$). We assessed whether congruency and attended dimension affected accuracy of performance with a repeated-measures ANOVA with the factors Congruency (C vs. IC) and Visual dimension (color vs. motion). This revealed a main effect of Congruency (C vs. IC) on accuracy (Figure 2 and Table 1), indicating that perceived motion direction and stimulus color automatically induced response conflict on IC trials. The effect of visual dimension (color vs. motion) was also significant, indicating that our attempt to eliminate general differences in task difficulty across visual features did not work out as expected: In particular, participants' average performance on motion trials did not reach the level of 85% targeted during the staircase procedure. In general, responding to motion direction was thus more difficult than responding to stimulus color. Furthermore, the interaction between

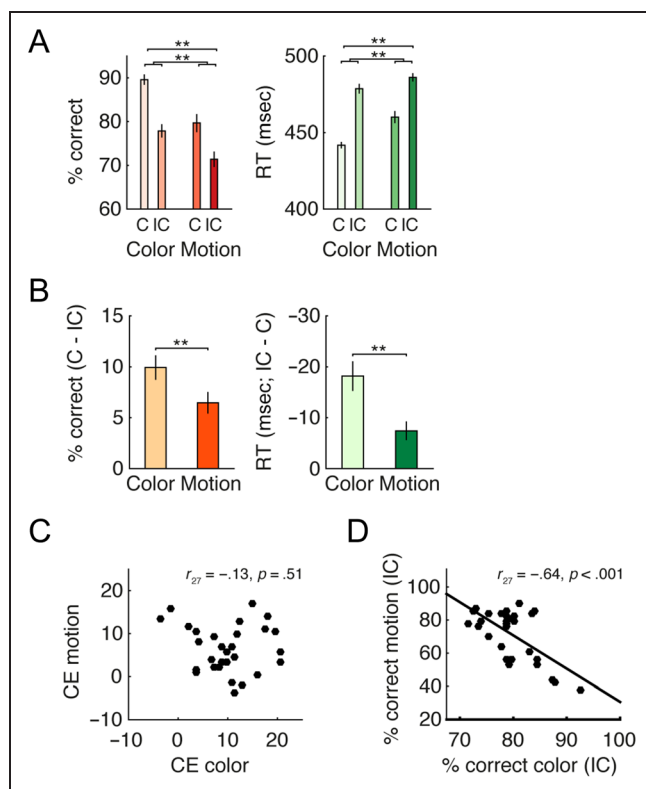


Figure 2. Behavioral performance. (A) Group-averaged accuracy of performance (left) and RTs (right) displayed for the different conditions (C vs. IC, color vs. motion). Accuracy levels were affected by congruency as well as visual dimension, and the effect of congruency and dimension interacted (see C). Similarly, RTs were affected by congruency and visual dimension and exhibited an interaction between these factors (see C). (B) Graphical display of the interaction between the effect of congruency and visual dimension. The effect of congruency was larger on color than motion trials, both for accuracy and RT. (C) The conflict effect (% correct C vs. IC) on color and motion trials was not related across individuals. (D) Accuracy of performance (% correct) on IC color and motion trials was negatively related across individuals.

the effect of congruency and visual dimension was significant and showed that perceived motion direction has a stronger effect on automatic response activation than the learned association between stimulus color and response hand. Yet, importantly, the main effect of Congruency on accuracy of performance suggests that, although the size of the conflict effect differed across visual dimensions, the present feature-based Simon task showed response conflict elicited by task-irrelevant motion direction as well as stimulus color.

Analysis of the effect of Congruency and Visual dimension on RTs revealed a comparable pattern (Figure 2 and Table 1), further indicating that response conflict was reliably elicited in our feature-based Simon task.

We next explored whether response conflict (accuracy of performance on C vs. IC trials) was correlated across the two visual dimensions (attend-color vs. attend-motion), but this was not the case ($r_{27} = -.13, p = .511$; see Figure 2C). However, when considering IC trials

only, performance across the two dimensions (attend-color vs. attend-motion) was significantly negatively correlated ($r_{27} = -.64, p < .001$; see Figure 2D). That is, although both color and motion induced response conflict, the size of the conflict effect (C vs. IC) depended on the strength of interference, which varied across visual dimensions differentially for different individuals.

EEG Power: Conflict-related Activity and Correlation with Behavior

We first assessed whether response conflict in the feature-based Simon task evoked conflict-related theta power as in typical location-based Simon tasks. Figure 3A and B shows the group-averaged topographical and time-frequency representation of baseline-corrected midfrontal theta power (4–8 Hz; channel FCz) on C and IC trials. As can be seen in this figure, a typical increase in midfrontal theta was observed around the time of response (Cohen & Donner, 2013; Nigbur et al., 2012). This increase in theta activity was centered at FCz, in line with the large body of previous research on conflict-related midfrontal theta power using location-based conflict tasks (Cohen & Donner, 2013; Figure 3A). The difference in theta power on C and IC trials was significant between –175 and 200 msec surrounding response (see Figure 3C). This time window was used to isolate conflict-related theta power for subsequent analyses. Please note that post hoc analyses of midfrontal theta power in the stimulus-locked data set revealed similar results, with a significant effect of response conflict on midfrontal theta power in the time window between 300 and 750 msec after stimulus presentation.

To assess the link between behavioral and neural correlates of response conflict, we correlated average conflict-related theta power (IC vs. C) in the time-frequency window displayed in Figure 3C to the behavioral conflict effect collapsed across visual dimensions. This revealed no evidence for a relationship between dimension-average behavioral conflict effects and dimension-average conflict-related midfrontal theta power across individuals ($r_{27} = .09, p = .611$; Figure 3D).

On the basis of the large individual variation in behavioral performance on IC color versus motion trials, we explored whether behavioral and neural measures of response conflict would be related when analyzing this relationship for each visual dimension separately (color vs. motion). To this end, we separately computed midfrontal conflict-related theta power for color and motion trials using the time-frequency window depicted in Figure 3E and F. Conflict-related (IC vs. C) midfrontal theta power in this time-frequency window was significant on color ($t_{28} = 2.13, p = .042$; see Figure 3E) as well as motion ($t_{28} = 2.21, p = .036$; see Figure 3F) trials. To test whether dimension-specific behavioral and neural correlates of response conflict were related across individuals, we subsequently correlated the size of the

Figure 3. Effects of color- and motion-based response conflict on midfrontal theta power.

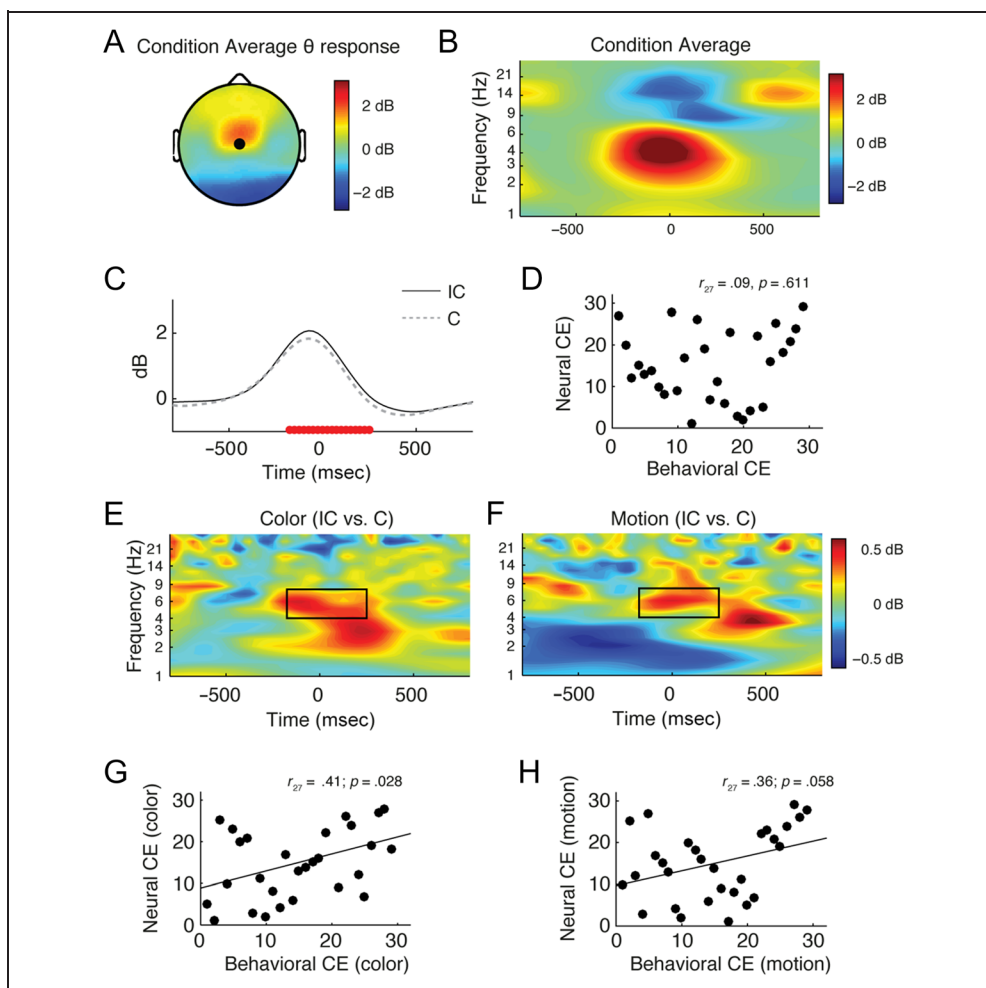
(A) Condition-average midfrontal theta power around the time of response (–100 to 100 msec, where Time 0 reflects the time of response). The black circle depicts electrode FCz. (B) Time–frequency representation of condition-average activity at FCz.

(C) Time course of conflict-related midfrontal theta power (4–8 Hz; FCz; IC – C) in the time window around response (Time 0 reflects the time of response). (D) Dimension-average conflict-related theta power

(IC – C) is not related to dimension-average conflict effect on performance across individuals. (E, F) The conflict effect on midfrontal theta power for color (E) and motion (F) trials. The black outline represents the time window that showed a significant conflict effect in the feature-average data. As can be seen, the conflict effect is present for color trials (E) and motion trials (F).

(G) Conflict-related midfrontal theta power on color trials (IC – C) is correlated with the behavioral conflict effect (% correct on C – IC trials) on color trials: Individuals with a larger behavioral conflict effect on color trials also exhibited a stronger conflict-related theta response on color trials.

(H) Conflict-related midfrontal theta power on motion trials is correlated at trend level ($p = .056$) with the behavioral conflict effect (% correct on C – IC trials) on motion trials: Individuals with a larger behavioral conflict effect on motion trials tended to exhibit stronger conflict-related theta response on motion trials.



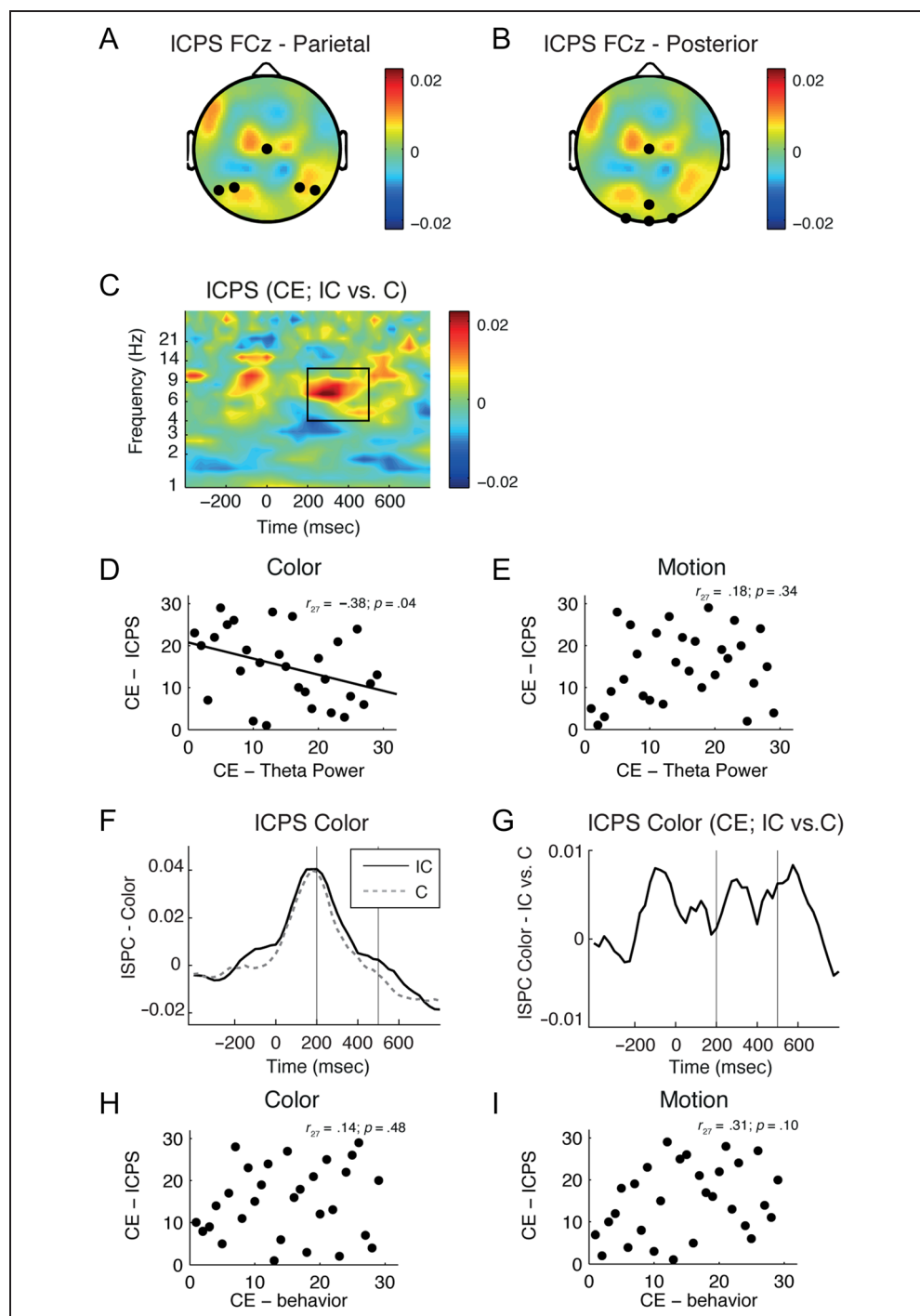
conflict-related theta response (IC vs. C) and decline in accuracy of performance (C vs. IC) across individuals separately for color and motion trials. This revealed a significant positive correlation between conflict-related theta and conflict-related performance decline on color trials ($r_{27} = .41, p = .028$; see Figure 3G) and a marginally significant correlation on motion trials ($r_{27} = .36, p = .058$; see Figure 3H). Notably, the observed conflict effects could not be explained by task difficulty or individual differences in sensitivity to sensory features per se: The average level of dot congruency of the dot patterns did not correlate with conflict-related theta power ($r_{28} = .25, p = .19$), nor did the difference between color values of the greenish and bluish dot patterns ($r_{27} = .14, p = .47$; please note that the correlation analysis for color was performed in 28 participants as the RGB values used in the task were incorrectly printed in the output file of the first participant [but were typically adapted during the task]). Thus, participants who showed a larger conflict effect on behavior also showed a larger effect of conflict on midfrontal theta at the time of response, but this relation-

ship was only present when taking individual differences in dimension-specific performance into account.

EEG Connectivity

We next examined if interregional communication associated with selective modulations of color or motion processing after stimulus presentation would predict response conflict. To this end, we examined whether baseline-corrected, stimulus-locked interregional connectivity (ISPC; Cohen, 2014b) between FCz and parietal and posterior sites (see Figure 4A and B) predicted subsequent conflict effects on midfrontal theta power. At the group level, feature-average conflict-related ISPC (IC vs. C) between frontal and posterior clusters was selective to the parietal cluster in the time window between 200 and 500 msec poststimulus ($t_{28} = 1.84, p = .05$; see Figure 4C): There was no significant conflict-related synchrony between FCz and the occipital cluster ($t_{28} = 0.73, p = .23$). We next explored whether, across individuals, dimension-specific conflict-related ISPC (IC vs. C)

Figure 4. Stimulus-locked, conflict-related ISPC between FCz and parieto-occipital sites (IC vs. C; collapsed across visual dimensions). (A) Topographical display of conflict-related stimulus-locked ISPC seeded at FCz and the channels used for the parietal seed. (B) Topographical display of conflict-related stimulus-locked ISPC seeded at FCz and the channels used for the occipital seed. (C) Stimulus-locked, conflict-related ISPC between FCz and parietal sites (P3/4, P5/6) collapsed across visual features. There is significant conflict-related frontoparietal ISPC (IC vs. C) between 200 and 500 msec after stimulus presentation spanning the theta and alpha bands. (D) The conflict effect on midfrontal theta power on color trials and the conflict-related frontoparietal ISPC on color trials were significantly related across individuals. Individuals with stronger conflict-related frontoparietal ISPC preceding response showed a smaller conflict effect as reflected in midfrontal theta power. (E) Conflict-related frontoparietal ISPC on motion trials did not predict the conflict effect as reflected in midfrontal theta power on motion trials across individuals. (F) Time course of average baseline-corrected, stimulus-locked 4- to 12-Hz ISPC between FCz and parietal sites (P3/4, P5/6) separately for C and IC color trials. The black line represents ICPS on IC trials. The dotted gray line represents ICPS on C trials. Black vertical lines reflect the time window used for statistical analyses (200–500 msec after stimulus onset). (G) Time course of average baseline-corrected, stimulus-locked, conflict-related 4- to 12-Hz ISPC between FCz and parietal sites (P3/4, P5/6) on color trials. Black vertical lines reflect the time window used for statistical analyses (200–500 msec after stimulus onset). (H) Conflict-related frontoparietal ISPC on color trials did not predict the behavioral conflict effect (% correct on C vs. IC) on color trials. (I) Conflict-related frontoparietal ISPC on motion trials did not predict the behavioral conflict effect (% correct on C vs. IC) on motion trials.



between FCz and the parietal cluster was related to the dimension-specific conflict-related midfrontal theta response. To this end, we correlated conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites between 200 and 500 msec after stimulus presentation to conflict-related midfrontal theta power (in the time win-

dow that showed a significant effect of conflict; –175 to 200 msec peri response) across individuals, separately for each visual dimension (attend color vs. motion direction). This analysis revealed a negative correlation between conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites and conflict-related midfrontal theta

power when attending to color ($r_{27} = -.38, p = .04$; see Figure 4D), but not when attending to motion direction ($r_{27} = .18, p = .34$; Figure 4E). These findings may indicate that conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites selectively reduces conflict-related midfrontal theta power on IC color trials. Indeed, conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites differentially affected subsequent midfrontal conflict-related theta responses on IC color and motion trials: The correlation between conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites and midfrontal conflict-related theta power was significantly different across visual features ($z = 2.10, p = .04$). Figure 4F and G shows the evolution of conflict-related ICPS between frontal and parietal sites on attend-color trials over time.

To follow up on the correlation between conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites and midfrontal theta, we subsequently correlated conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites before response to the behavioral conflict effect for each visual dimension (accuracy of performance on C vs. IC trials) and found that conflict-related ISPC (IC vs. C) between frontal and parietal scalp sites did not predict the behavioral conflict effect on either color ($r_{27} = .14, p = .48$) or motion ($r_{27} = .31, p = .10$; see Figure 4F and G) trials. In summary, the present findings on conflict-related ISPC provide tenuous evidence for a functional relationship between pre-response interregional communication, as reflected in ISPC between frontal and parietal scalp sites, and conflict-related midfrontal theta when attending to color, but not when attending to motion direction (Zanto et al., 2010).

DISCUSSION

In this EEG study, we exploited individual differences in behavioral and oscillatory markers of color- and motion-induced response conflict to determine the extent to which response conflict is stimulus dimension dependent and to elucidate the neural mechanisms associated with the detection and resolution of dimension-based response conflict. We observed motion-induced response conflict in IC color trials on which motion direction was task irrelevant, corroborating previous research demonstrating response conflict during motion-based response activation (Galashan et al., 2008; Wittfoth et al., 2006; Bosbach et al., 2004), and additionally observed color-induced response conflict when color was task irrelevant. Time–frequency analyses of the EEG data and our individual differences approach provided three important contributions to the literature. First, time–frequency analysis of EEG data revealed that motion- and color-based response conflicts are associated with typical oscillatory signatures of response conflict, that is, increased conflict-related theta power at midfrontal scalp sites at the time of response (Cohen, 2014a; Cohen &

Donner, 2013; Cohen & Ridderinkhof, 2013; Nigbur et al., 2011, 2012).

Second, behavioral performance on IC color and motion trials was negatively correlated across individuals, indicating that the ability to perform a goal-relevant action in the presence of interfering information depends on the strength of interference, which varies across visual dimensions differentially for different individuals. These individual differences were paralleled in a dimension-specific relationship between behavioral conflict effects and conflict-related midfrontal theta power across individuals, whereas the behavioral conflict was not related to conflict-related theta power when collapsing across visual dimensions. Experienced response conflict thus does not necessarily reflect a generic phenomenon that remains constant across situations but is at least partially dimension specific.

Third and last, exploratory analyses provided evidence for a dimension-dependent relationship between early stimulus-related phase synchronization between frontal and parietal scalp sites and response conflict, as reflected in dimension-specific midfrontal conflict-related theta power. Increased interregional communication predicted a reduced conflict effect when attending to color, but not when attending to motion direction. In summary, these results provide important novel insights into the extent to which response conflict may vary depending on the degree of interference experienced by sensory information activating the incorrect response and the oscillatory mechanisms involved herein.

Feature-based Response Conflict Is Reflected in Midfrontal Theta Activity

The feature-based Simon task used in this study in which response conflict was induced by either the color or motion direction of colored moving dot patterns elicited typical response conflict, as reflected in slower and less accurate performance when the task-irrelevant visual feature activated the incorrect response hand (Lu & Proctor, 1995; Simon & Wolf, 1963), in line with the notion that conflict can arise through different sensorimotor bindings (Hommel, 2009; Hommel et al., 2001). Previous research on the neural mechanisms involved in the detection and resolution of feature-based response conflict has revealed an effect of motion-based response conflict on the P300 (Galashan et al., 2008) and BOLD activation patterns in ACC (Wendelken, Ditterich, Bunge, & Carter, 2009; Wittfoth et al., 2006). To the best of our knowledge, this study is the first to report direct evidence for the oscillatory correlates of feature-based response conflict, reflected in a typical conflict-related transient increase in midfrontal theta power (Cohen, 2014a; Lu & Proctor, 1995). This observation supports the notion that midfrontal theta power serves as a domain-general mechanism through which response

conflict is detected and subsequently resolved (Cavanagh & Frank, 2014; Cohen, 2014a; Nigbur et al., 2011).

Individual Differences in Response Conflict Depend on Feature-specific Interference

Interestingly, results from individual differences analyses indicated that response conflict and associated theta activity also depend, at least in part, on the conflict-inducing visual dimension. Performance on IC color and motion trials was negatively correlated across individuals, indicating that individuals who experienced a large conflict effect for one task-irrelevant dimension showed a smaller conflict effect when the other dimension was task irrelevant and vice versa. The inverse relationship between performance on IC color and motion trials is in line with the notion of biased competition in feature-based attention (Polk, Drake, Jonides, Smith, & Smith, 2008) and corroborates previous reports showing that individuals who exhibit improved color perception display relatively impaired motion perception (McCarthy & Caplovitz, 2014; Banissy et al., 2013). The present findings also concord with earlier work using a Navon global–local interference task showing that some individuals experienced interference when global stimulus features were task irrelevant, whereas in others, local features yielded stronger interference (Ridderinkhof & van der Molen, 1995): EEG analyses revealed that whichever was the “dominant” level incurred neural measures of response conflict at the primary motor cortex. Furthermore, a previous study on the effect of attention to stimulus color vs. motion direction on alpha power modulations (Snyder & Foxe, 2010) found that alpha power modulations sensitive to the attentional manipulation (attend color vs. motion direction) dissociated between subgroups of participants. Whereas one group of participants selectively exhibited alpha power modulations when attending to motion direction, but not color, the other group of participants showed the opposite pattern. For a given participant, the observed alpha power modulations were selective to the visual dimension that was easiest to discriminate and presumably most likely to cause interference (Snyder & Foxe, 2010). These and the present findings suggest that individuals differ greatly in the extent to which they are sensitive to stimulus color or motion direction, which in turn results in large inter-individual differences in response conflict experienced by each of these visual dimensions when irrelevant to the task at hand. The fact that, across individuals, the neural signature of response conflict was highly similar between motion- and color-induced interference suggests that such interference arises through direct sensorimotor links in both cases (Hommel et al., 2001).

The observed negative relationship between behavioral performance on IC color and motion trials across individuals in this study was mirrored in a dimension-specific cross-participant correlation between the conflict effect on behavior and midfrontal theta power, providing

further evidence that individual differences in experienced response conflict are dependent on processing of sensory information. The strength of the conflict effect is thus not only dependent on the predicted or perceived effect of a motor response associated with a particular stimulus (Hommel, 2011) but also dependent on the degree of experienced interference caused by irrelevant visual stimulation, which may vary across individuals. Our result complements previous observations of a within-participant relationship between intertrial variability in conflict-related theta dynamics and behavior (van Driel et al., 2015; Cohen & Donner, 2013; Cohen & Cavanagh, 2011). Specifically, the present findings reveal that, when taking individual differences in sensitivity to dimension-specific interference into account, the effect of response conflict on behavior and theta power is not only related within but also across individuals. Previous research has demonstrated that such individual differences in conflict-related behavioral dynamics depend on individual differences of the structure of task-relevant brain regions and pathways (van Gaal, Scholte, Lamme, Fahrenfort, & Ridderinkhof, 2011; Forstmann et al., 2008). The results reported in this study suggest that response conflict not only depends on individual differences in brain anatomy but also depends on individual differences in sensitivity to the sensory information inducing the response conflict.

Conflict-related Sensory Modulation of Interregional Communication

Exploratory analyses revealed that conflict-related phase synchronization between midfrontal and parietal sites time-locked to stimulus presentation negatively predicted midfrontal conflict-related theta power at the time of response on color, but not motion, trials (see also Zanto et al., 2010). Presumably, the observed ISPC reflects fronto-parietal synchronization, consistent with previous fMRI studies (Scolari, Seidl-Rathkopf, & Kastner, 2015; Corbetta & Shulman, 2002). To our knowledge, this study is among the first to report stimulus-locked conflict-related modulations of interregional communication that affect experienced response conflict. Existing work selectively reported increased interregional phase synchronization as a function of conflict-related adaptations after IC trials (van Driel et al., 2015; Oehm et al., 2014; Pastötter et al., 2013), but evidence for the involvement of a relationship between conflict-related modulations of interregional communication and conflict experienced on the same trial is still limited.

The observed relationship between conflict-related ISPC between frontal and parietal scalp sites and midfrontal theta power on IC color, but not motion, trials may indicate that conflict-related ISPC reflects interregional communication of goal-relevant color information: There is evidence suggesting that conflict caused by conflicting perceptual input is primarily resolved through attentional enhancement of goal-relevant information, rather than

suppression of irrelevant information (Purmann & Pollmann, 2015; Egnér & Hirsch, 2005). On the other hand, the observed conflict-related phase synchronization on color trials may also reflect diminished interregional communication of task-irrelevant information (Palva & Palva, 2011). Given the absence of a link between conflict-related ISPC between frontal and parietal scalp sites and behavioral performance, the present findings leave unclear what information is communicated through the observed conflict-related interregional phase synchronization. The precise role of the observed conflict-related interregional phase synchronization thus needs further attention in future studies. Future research using transcranial alternating current stimulation to modulate the observed frontal and parietal conflict-related ICPS may yield further insight into the precise functional role of the observed connectivity pattern.

Surprisingly, the present results revealed no relationship between conflict-related interregional communication and the effect of response conflict on midfrontal theta when participants attended to motion direction. This could be due to the fact that motion processing primarily relies on activity along the dorsal stream (Snyder & Foxe, 2010; Donner et al., 2007), which may be more difficult to measure using sensor level EEG. Furthermore, interregional communication directed at the reduction of response conflict likely also involves subcortical regions (Herz et al., 2017; Aron, Herz, Brown, Forstmann, & Zaghoul, 2016; Zavala et al., 2014). Potentially, sensory modulations after detection of conflicting sensory information are in part transmitted through subcortical routes, which complicates their measurement using scalp EEG.

Summary

This study revealed robust motion- and color-based response conflict, which was associated with increased theta activity over midfrontal scalp sites. Moreover, large individual differences were observed in the extent to which stimulus color and motion direction elicited response conflict: Individuals who experienced interference by task-irrelevant motion direction were less prone to interference by task-irrelevant stimulus color, and vice versa. These individual differences were mirrored in conflict-related midfrontal theta responses, indicating that midfrontal conflict-related theta power is involved in domain-general conflict detection and/or resolution but depends on the sensory source inducing the conflict. Finally, preliminary evidence was found for a role of early interregional communication between midfrontal and parietal scalp sites in resolving response conflict when attending to stimulus color. In conclusion, the present findings provide important insights into response conflict elicited by different visual dimensions and the oscillatory mechanisms involved.

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