Selection for Action: The Medial Frontal Cortex Is an Executive Hub for Stimulus and Response Selection

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Abstract

This EEG study investigates the electrophysiological activity underlying processes of stimulus and response selection, and their executive orchestration via long-range functional connectivity under conflict condition, in order to shed more light on how these brain dynamics shape individual behavioral performance. Participants (n = 91) performed a modified flanker task, in which bilateral visual stimulation and a bimanual response pattern were employed to isolate the stimulus and response selection-related lateralized activity. First, we identified conflict-related markers of task-relevant processes; most importantly, the stimulus and response selection were evidenced by contra–ipsilateral differences in visual and motor activity, respectively, and executive control was evidenced by modulations of midfrontal activity. Second, we identified conflict-related functional connectivity between midfrontal and other task-relevant areas. The results showed that interregional phase synchronization in theta band was centered at the midfrontal site, interpreted here as a “hub” of executive communication. Importantly, the theta functional connectivity was more robust under the condition of increased demands for stimulus and response selection, including connectivity between the medial frontal cortex and the lateral frontal and motor areas, as well as cross-frequency theta–alpha coupling between the medial frontal cortex and contralateral visual areas. Third, we showed that individual differences in the measured conflict-related EEG activity, particularly the midfrontal N2, theta power, and global theta connectivity, predict the behavioral efficiency in conflict resolution.

INTRODUCTION

Stimulus and Response Selection

Goal-oriented behavior and quick response to relevant environmental changes require a coordinated set of selection-for-action mechanisms enabling effective linking of sensory information with suitable response programs (Allport, 1987). Such a selection for action may be considered as a two-stage or two-level process. One is the mechanism of stimulus selection that acts on perceptual representations; the other is the mechanism of response selection acting on motor representations. Both mechanisms operate via simultaneous signal enhancements and distractor suppressions (Thiele & Bellgrove, 2018). Within the perceptual system, neuronal activity underlying sensory representation of a relevant object is increased, whereas the activity underlying representation of distractors is inhibited (Moore & Zirnsak, 2017; Corbetta & Shulman, 2002). Similarly, within the motor system, neuronal activity underlying the representation of a proper motor program is increased, whereas activity underlying inappropriate, reflex-like, or incorrect motor programs is inhibited, which allows us to deal with conflicting response tendencies (Carter & Krug, 2012; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

The two selection mechanisms, for stimulus and response, are therefore functionally and anatomically separate, yet they have to work together in a harmonious, coordinated manner during complex tasks of everyday life. A plausible candidate for a functional hub orchestrating these selection processes is the medial frontal cortex (MFC), including the midcingulate cortex and ACC (Cohen & Ridderinkhof, 2013; Cohen, 2011). Consistently with such a role, the MFC has long-range reciprocal structural connections with numerous cortical and subcortical brain regions (Cavanagh & Frank, 2014). A key component of this communication is an ongoing theta band oscillatory activity. It has been proposed that the MFC-generated interregional theta phase synchronization reflects the transmission of top–down control signals through which the MFC may entrain distinct task-relevant regions (Cohen, 2014a). It has also been argued that the theta band activity is a fundamental property of the stimulus selection mechanism, determining sensory sampling and reweighting functional connections between cortical and subcortical areas involved in the selection process (Fiebelkorn & Kastner, 2019). Finally, robust evidence shows that an increase in midfrontal theta power is instrumental for response selection under conditions of response conflict (Cavanagh & Frank, 2014; Cohen, 2014a).

To investigate the brain dynamics underlying such an executive orchestration of the selection processes, an experimental tool is needed that would allow for simultaneous measurement of stimulus and response selection under a condition demanding this kind of supervisory control. An example of such a procedure is the flanker task (Eriksen...
& Eriksen, 1974). In a typical arrow version of this choice-reaction paradigm, a target stimulus is either a left- or right-pointing arrow, and responses are defined as key presses with the left or right hand, respectively, to the target arrow. This establishes two fixed and ready-to-use stimulus–response (S–R) links or “event-files”: left arrow = left-hand response, and right arrow = right-hand response (cf. Verleger, Metzner, Ouyang, Śmigasiewicz, & Zhou, 2014; Hommel, 2004). In each trial of the task, the target arrow is flanked by four other arrows, which are either congruent or incongruent with the target. In the congruent condition, the target and flanker arrows point in the same direction, so that activation of the correct S–R link is easy, and responses are quick and accurate. In the incongruent condition, however, the flanker arrows point in the direction opposite to the target arrow, which causes a perceptual interference similar to the effects of visual crowding (Whitney & Levi, 2011) or grouping (Luo & Proctor, 2016). Thus, the involvement of the stimulus selection mechanism is needed for target identification. Moreover, both the target and the incongruent flankers simultaneously activate their respective S–R links (as both the left- and right-pointing arrows have established fixed links with the corresponding left- and right-hand responses), thereby triggering a response conflict between two motor programs (Egner, 2008; Gratton, Coles, & Donchin, 1992). The involvement of the response selection mechanism is therefore required. As a result, RT is longer and error rate is larger in the incongruent condition than in the congruent condition. This incongruent–congruent difference, that is, the behavioral flanker effect, reflects an accumulated, presumably additive (noninteracting; cf. Maniscalco, Bang, Iravani, Camps-Febrer, & Lau, 2012) cost of dealing with the perceptual interference and the response conflict. The cost is assumed to be inversely proportional to the efficiency of the stimulus and response selection mechanisms—the higher their efficiency, the lower is the cost. The overall performance level should therefore be, obviously, the resultant of the cumulated efficiency of both the primary S–R processing chain and its higher-order executive orchestrations.

**This Study**

In this study, we aimed to further investigate how the brain dynamics underlying the selection processes and their executive orchestration shape behavioral performance on an individual basis. To this end, we analyzed EEG data from 91 participants performing a modified version of the arrow flanker task. Our strategy was, first, to identify conflict-related electrophysiological markers of task-relevant processes; second, to identify conflict-related functional connectivity between the MFC and other task-relevant areas; and third, to examine which of and to what extent the identified markers of conflict-related brain activity and connectivity are related to the behavioral efficiency of conflict resolution.

Selective sensorimotor processing during the performance of conflict tasks is expected to involve predominantly the occipital areas—where visual selective processing is implemented (cf. Luck & Gold, 2008), the posterior parietal areas—where S–R translation processing occurs (cf. Gulbinaite, van Rijn, & Cohen, 2014; Freund, 2001), the premotor and motor areas—where response selection is implemented (cf. van Driel, Sligte, Linders, Elport, & Cohen, 2015; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988), and finally the MFC, along with the lateral frontal cortex (LFC; predominantly the dorsolateral prefrontal cortex)—from which we gain the ability to exert executive control over perceptual interference and response conflict (cf. van Driel et al., 2015; Carter & Krug, 2012). On that account, we proceeded to measure EEG markers of the listed processes at the specified sites. To discern EEG activity related specifically to stimulus and response selection, we introduced bilateral visual stimulation to the task and used a bimanual response pattern. This allowed us, by means of a double subtraction method (Coles, 1989), to isolate a lateralized (contralateral–ipsilateral) EEG activity relative to the target hemisphere and responding hand—that is to obtain a simultaneous assessment of stimulus and response selection in one task. To assess the former, we measured the posterior contralateral negativity (PCN; including the N2pc and sustained posterior contralateral negativity [SPCN] components) of the ERPs, and posterior contralateral time–frequency power and phase coherence in the alpha band. To assess the latter, we measured the lateralized readiness potential (LRPs) and lateralized beta band power over motor areas. Furthermore, to estimate the executive function-related midfrontal activity, we measured the N2 component of the ERP and theta band power. In addition, we measured the parietal P3b component of the ERP, to identify possible conflict-related modulations of the S–R translation process. Finally, to assess the hypothesized executive orchestration processes, we measured conflict-related functional connectivity in theta band between the MFC and other task-relevant sites, that is, the visual, motor, centro-parietal, and lateral-frontal areas. If any of the identified incongruent–congruent difference in the EEG activity is behaviorally relevant, it should correlate with the behavioral flanker effect. A thorough rationale for each measurement and specific performance-related hypotheses are detailed in the following paragraphs.

**Assessment of Stimulus Selection**

To obtain a comprehensive picture of the process of stimulus selection, we measured three complementary markers of selection-related lateralized EEG activity: PCN, and posterior contralateral time–frequency power and phase coherence in the alpha band. The PCN is event-related lateralization (ERL; Wascher & Wauschkuhn, 1996) of the ERPs, measured as a contra–ipsilateral difference relative to the target visual hemifield at sites located above the
occipito-temporal cortex (usually PO7 and PO8). The most prominent component of the PCN is the N2pc, occurring at about 200–250 msec after target onset at the contralateral hemisphere, and thought to reflect target selection (Eimer, 1996; Luck, Fan, & Hillyard, 1993). Another PCN component that often follows N2pc is an SPCN (Vogel & Machizawa, 2004). As suggested by Schneider, Hoffmann, and Wascher (2014), SPCN may reflect creating a stable percept of the selected stimuli “that can serve as the perceptual basis for response selection and the initiation of goal-directed behavior” (p. 1). Therefore, the PCN components should present a higher amplitude in the incongruent trials than in the congruent trials because of increased stimulus selection and discrimination demands. Assuming that larger N2pc and SPCN indicate a stronger involvement of the selection mechanism (cf. Luck, Girelli, McDermott, & Ford, 1997), the magnitude of their amplitudes should be inversely related to the behavioral flanker effect.

The lateralized power spectra (LPS) in alpha band provide an index of ipsilateral–contralateral differences calculated by the double-subtraction (as the ERLs), so that all activity unrelated to spatial selection and general hemispheric differences are subtracted out (van der Lubbe, de Kleine, & Rataj, 2019; van der Lubbe & Utzerrath, 2013; see also Zhigalov & Jensen, 2020). Thus far, the LPS index has been used for pretarget cue-evoked activity related to preparatory orienting and showed alpha suppression over the hemisphere contralateral to the cued hemifield, indicating inhibition of the irrelevant side and/or disinhibition of the relevant side (van der Lubbe et al., 2019; van der Lubbe & Utzerrath, 2013), in line with other similar methods (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). Here, however, we calculated the LPS for a target-evoked activity to examine the role of alpha suppression in stimulus selection. Recently, Bacigalupo and Luck (2019) have reported a contralateral alpha suppression evoked by uncued targets (i.e., unrelated to preparatory orienting) suggesting that “alpha also serves as an active mechanism of target processing” (p. 900). Of importance, they also found a trend for enhanced alpha suppression with increased perceptual crowding by reducing the distance between target and flanker letters. Accordingly, we expected that the LPS index would confirm the role of alpha desynchronization in target selection and show a stronger alpha suppression in the incongruent trials than in the congruent trials, as well as a negative correlation of the alpha suppression with the behavioral cost. Of interest was also the relationship between the LPS and the PCN components of the ERP, because Bacigalupo and Luck’s (2019) results have suggested that the alpha lateralization and N2pc reflect related but distinct aspects of visual selection.

Further information that is unobservable from ERPs and time–frequency power may be obtained from event-related phase coherence analysis. Indeed, it has been observed that processing of laterally presented targets is associated with a contralateral increase of phase coherence in alpha band over visual cortex, which presumably reflects the mechanism of temporal gating of visual stimuli (Keitel et al., 2019; Spaak, de Lange, & Jensen, 2014). Thus, assuming that increased involvement of the stimulus selection mechanism would entail an increase of the contralateral alpha phase coherence, we expected to observe a larger contra–ipsilateral difference in the incongruent than in the congruent flanker condition, as well as a correlation of such a flanker effect on the contra–ipsilateral alpha phase difference with the behavioral flanker effect.

Assessment of Response Selection

To isolate response-related motor activity, the LRPs and LPS were calculated from the ERPs and time–frequency power, respectively. The LRP is ERL measured over the right and left motor cortex relative to the responding hands (Smulders & Miller, 2011). Typically, a negative LRP emerges about 200–400 msec after target onset, indicating selection and activation of the correct response program. In the incongruent condition of the flanker task, the selection of the correct response is delayed because of the simultaneous activation of the incorrect response (Asanowicz, Woloszyn, Panek, & Wronka, 2019; Grent’-t’ Jong, Oostenveld, Jensen, Medendorp, & Praamstra, 2013). Inhibition of the incorrect response is thought to be a result of the implementation of executive control within motor representations (Klein, Petitjean, Olivier, & Duque, 2014; Verleger, Kuniecki, Möller, Fritzmannova, & Siebner, 2009). Assuming that the conflict is resolved prior to the execution of the correct response program, the motor processes should be delayed but not lengthened by the conflict processing. Thus, the flanker effect on the LRP latencies should only be observed relative to stimulus onset and not relative to the response. Specifically, in the incongruent trials, the motor processes should begin later—which is expected to be evidenced in the stimulus-locked LRPs—but once the correct program is selected, its execution should be as fast as in the congruent trials—hence, no latency difference should be found in the response-locked LRPs (cf. Hackley & Valle-Inclán, 1998). The same rationale and predictions apply to our measurement of the hand-movement-related oscillatory activity in beta band, which we assessed by calculating lateralized beta power spectra (beta LPS), using the same method as for the LPS in alpha band. Positive LPS will indicate beta desynchronization in motor areas contralaterally to the responding hand (cf. Siegel & Donner, 2010; Crone et al., 1998), and the time course of the beta desynchronization indicates the timing of response selection (Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Kaiser, Birbaumer, & Lutzenberger, 2001). In addition, we measured the P3b, which is a positive ERP deflection at about 300–700 msec after target onset with a maximum at the parietal midline (usually Pz). In
Assessment of Conflict-related Midfrontal Activity

The involvement of midfrontal activity in conflict processing was evaluated by measuring its two complementary signatures: the midfrontal N2 component of the ERP and midfrontal theta power. The N2 is a negative deflection occurring at about 200–400 msec after target onset with a maximum at the frontal midline (usually FCz). In the conflict trials of the flanker task, the N2 tends to display an increased amplitude (Heil, Osman, Wiegeltmann, Rolke, & Hennighausen, 2000; Kopp, Mattler, Goertz, & Rist, 1996) originating from the MFC (particularly the ACC; van Veen & Carter, 2005; Yeung, Botvinick, & Cohen, 2004). This conflict-related N2 is interpreted as a signature of the involvement of the executive system in detection and resolution of response conflict, which enables the selection and execution of the correct response (Yeung et al., 2004; van Veen & Carter, 2002). Assuming that a larger N2 amplitude indicates stronger involvement of the response selection control, we should observe a negative correlation between the N2 and behavioral flanker effects. However, this relationship has remained unclear, because Cohen and Donner (2013) found no correlation between the N2 and RT in a response conflict task (specifically, in their versions of the Simon task; see Egner, 2008, for a description of conflict tasks) and suggested that the phase-locked midfrontal activity may not be related to conflict resolution. Moreover, some studies even questioned the interpretation of the N2 as a proper index of response conflict processing in the flanker task (Kalamala et al., 2017; Tillman & Wiens, 2011). Hence, we further examined and compared the behavioral relevance of the phase-locked (the N2) and non-phase-locked (theta modulations, see below) midfrontal activities.

The conflict-related theta power is an increase of the midfrontal theta observed during response conflict, typically at about 300–600 msec after stimulus onset at frontal midline sites (usually FCz; Cohen & Cavanagh, 2011; Nigbur, Ivanova, & Stürmer, 2011). It is thought to reflect the neurophysiological oscillatory mechanism underpinning conflict detection and resolution (Cavanagh & Frank, 2014; Cohen, 2014a). As such, the theta band oscillations have been argued to have a causal role in the efficiency of conflict processing (van Driel et al., 2015; Cohen & Donner, 2013). Assuming that a larger theta power indicates increased involvement of the mechanism, we should observe an inverse relationship between the magnitude of the conflict-theta effect and the behavioral cost. Of importance, in their Simon task study, Cohen and Donner (2013) have shown that the conflict-related theta is time-locked but not phase-locked to the onset of conflict-elicitng stimuli, which indicates that this activity and the conflict-related N2 component of the ERP, despite their spatiotemporal overlap, are two distinct physiological phenomena, possibly functionally separate cogs in the executive control mechanism. Thus, here, we measured specifically non-phase-locked theta power to dissociate this activity from the N2. Alternatively, if the theta power and N2 reflect the same neuronal mechanism, not only they should be similarly related to the behavioral flanker effect but also be highly correlated with each other.

Assessment of Interregional Functional Connectivity

Understanding the interregional functional connectivity is pivotal for answering the question on how the selection processes are orchestrated within an organically connected and functionally coherent system. Such long-range connectivity seems to be mechanistically implemented by phase-locked oscillations in the communicatng neuronal groups (Siegel, Donner, & Engel, 2012; Fries, 2005). Thus, to assess the hypothesized midfrontal-centered executive orchestration, we measured the so-called intersite phase coherence (ISPC), which is an estimation of frequency-specific phase synchrony between two sources of oscillations and is interpreted as an index of functional connectivity between two brain areas.

First, we examined whether the MFC may indeed be considered as a “hub” of the executive communication in the theta band during response conflict, as predicted by the hypothesis that the MFC spreads top–down control signals through theta oscillations. Such a role of the MFC has been demonstrated for error-related processing by Cohen (2011). He used a graph theory-based method to quantify the number of functional connections of each node (electrode) with every other node over the entire scalp (i.e., all-to-all ISPC) and found out that long-range phase synchrony in the theta band was stronger at the MFC (centered at FCz) than at any other site, and this effect was larger in error trials than in the correct trials. Moreover, individual differences in this theta band functional connectivity were correlated with the strength of structural connectivity in the corpus callosum and dorsomedial prefrontal connectivity.
white matter pathways. Here, we used the same approach as Cohen (2011), expecting to find that (a) the MFC-centered theta phase synchronization degree will be significantly higher under conflict condition, reflecting a larger number of long-range functional connections between the MFC and other brain areas involved under conflict condition (cf. Cohen, 2014a), and (b) that individual differences in the degree of this MFC synchronization will be related to the efficiency of conflict resolution that is negatively correlated with the behavioral flanker effect.

Second, we examined direct functional connectivity between the MFC and specific ROIs. As mentioned before, the cortical structures functionally involved in sensorimotor conflict tasks form a network of several areas recurrently interconnected with the MFC. Theta band phase synchrony has been observed between the MFC and extra-striate visual areas, posterior parietal sensorimotor areas, motor cortex, and LFC (Cohen & Ridderinkhof, 2013; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012; van Driel, Ridderinkhof, & Cohen, 2012; Cohen & Cavanagh, 2011), which presumably reflect functional connectivity through which the MFC coordinates sensory gain control and stimulus selection, S–R integration, response selection, and action control, respectively. As alpha band oscillations play a key role in the implementation of stimulus selection in visual areas (Foster & Awh, 2019; van Diepen, Foxe, & Mazaheri, 2019), the executive communication between the MFC and occipital cortex may be carried out by coupling theta signals from MFC with alpha activity on the occipital areas (Fiebelkorn & Kastner, 2020). Thus, to assess theta–alpha coupling, we computed a cross-frequency version of ISPC (Varela, Lachaux, Rodriguez, & Martinerie, 2001; Tass et al., 1998) between midfrontal theta and occipital alpha oscillations. To access connectivity between the MFC and the other task-related regions, namely, the lateral motor areas, posterior parietal area, and LFC, we measured within-frequency coupling, that is, the theta–theta ISPC. If the MFC is an executive hub for stimulus and response selection, the task-relevant brain regions should become more strongly phase-locked to ongoing MFC theta band oscillations under the incongruent condition of the flanker task, indicating an increase of the task-related communication between MFC and these ROIs. Finally, assuming that such executive communication determines the efficiency of task performance, we should observe negative correlations between the flanker effects on connectivity strength and the behavioral flanker effect.

METHODS
Participants
Ninety-one students (62 women) of the Jagiellonian University took part in the study in return for course credits. Their average age was 20.4 years (SD = 1.5 years). The data were collected in three separate sessions (n = 27, 31, and 33; see below for further details). All participants had normal or corrected-to-normal vision and no history of neurological disorders. Informed written consent was obtained from each participant before the experiment.

Stimuli, Apparatus, and Procedure
The task is illustrated in Figure 1. Each trial of the task began with a fixation point displayed at the center of the computer screen. The time of the initial fixation varied randomly between 1000 and 2000 msec (in 150-msec steps, distributed uniformly). The fixation point was continuously displayed, except when it was replaced by visual cues (see below). The target stimulus was an arrow pointing either up or down, presented in the left or right visual field (50/50). The target arrow was flanked by four additional arrows pointing in either the same or the opposite direction, that is, the congruent and incongruent flankers (50/50). A corresponding distractor set consisted of five vertical lines without arrowheads and was simultaneously presented in the visual field opposite to the target. All these stimuli were presented for 180 msec.

For reasons not of interest to the present research questions, the target was preceded by visual cues. In one group of participants (n = 27), a predictive or neutral cue was presented 1000 msec before target onset and displayed until target offset. The cue was an increase of the fixation cross (by 0.2°) and change of its color from black to red (indicating the incongruent condition) or green (indicating the congruent condition). In the neutral cue condition, the cross remained black. In another group (n = 31), a predictive cue or no cue was presented 1000 msec before target onset. Here, the cue was a color change of the fixation cross from black to either red or green (indicating the incongruent and congruent flanker conditions, respectively), and it was also displayed until the target offset. In the third group (n = 33), the target was preceded in each trial by a spatially valid or neutral orienting cue, displayed at the center of the screen for 100 msec, with 600 msec of cue–target onset asynchrony. The valid cue was a double arrow sign pointing left or right: “<<” or “>>,” whereas the neutral cue was a square composed of the four arms of the two arrows. The valid cue always correctly indicated the target location. All these variables were counterbalanced. Condition order was randomized per participant. In the present set of analyses, only incongruent–congruent differences, that is, the flanker effects, were examined.

The target arrow and the flankers were each 8 mm (0.8°) long. The target and flanker arrowheads were 4 mm wide (0.4°). The length of all five (target and flanker) arrows in the display was 44 mm (4.4°). The arrows’ midpoints were displaced 18.5 mm (1.85°) to the left or right of the center of the screen. The fixation cross was 4 mm (0.4°), or 2 mm wide (0.2°). The height and width of the predictive cue was 4 mm (0.4°). The height and width of the orienting cue were 5 mm (0.5°). All stimuli were black and were presented on a light gray background (red, green, blue:

Downloaded from http://direct.mit.edu/jocn/article-pdf/33/8/1442/1927771/jocn_a_01727.pdf by guest on 22 August 2021
PsychoPy software (www.psychopy.org) was used for experimental control.

The participants’ task was to identify the direction of the target (middle) arrow and respond by pressing the left or right Ctrl key on the computer keyboard with the left or right index finger, respectively, to the up- and down-pointing target arrows. Speed and accuracy of responses were measured. A new trial began automatically after the response, or after 2000 msec if the participant did not respond. Participants were given written and then verbal instructions describing the task. They were asked to respond to target stimuli as quickly and accurately as possible. They were also carefully instructed to keep central fixation and explained why proper fixation is necessary during EEG measurement. The task began with two practice blocks consisting of 32 trials in total in which participants received accuracy feedback after each response. The experimental session consisted of 640 trials in five blocks (the first group), or 648 trials in three blocks (the second group), or 576 trials in four blocks (the third group). No feedback was given during the experimental trials. Between the blocks, participants were asked to take breaks to rest their eyes. The task lasted up to 1 hr. The whole session lasted up to 90 min.

EEG Data Recording and Preprocessing

EEG was recorded using a BioSemiActiveTwo system with Ag-AgCl electrodes on 64 monopolar locations according to the extended 10–20 system, and two additional electrodes, the common mode sense active electrode and the driven right leg passive electrode, used as reference and ground electrodes, respectively (www.biosemi.com/faq/cms&drl.htm). The vertical EOG was recorded from above and below the left eye, and horizontal EOG (hEOG) was recorded from the external canthi of both eyes. The data were stored at a sampling rate of 256 Hz. Brain-Vision Analyzer software (Version 2) was used for off-line data preprocessing. Data were filtered with a 0.1- to 50-Hz band-pass and a 50-Hz band-rejection filter (Butterworth zero-phase filters, attenuation of 12 dB/octave), rereferenced to linked mastoids, and split into segments from 1000 msec before target onset to 900 msec afterward. Segmented data were referred to the window from −200 to 0 msec of the segment as a baseline. Trials with an incorrect response, or with RT shorter than 200 msec or longer than 1200 msec, were automatically excluded. For response-locked analysis of the lateralized motor activity, data were segmented from 1000 msec before RT to 100 msec afterward. The same trials entered stimulus- and response-locked averages.

To exclude trials with horizontal eye movements, segments were marked if the horizontal EOG activity (right minus left EOG) exceeded ± 40 μV (which corresponds with an eye movement of approximately 2°; van der Lubbe & Woestenburg, 1997) and/or voltage steps between adjacent data points exceeded 5 μV. The marked trials were subsequently removed after inspection if a distinctive “boxcar” shape, characteristic for saccadic eye movements, was found in these marked segments within 0–800 msec after target onset. On average, 18% of segments were removed because of horizontal eye movements. Next, we calculated averaged horizontal EOG waveforms contralateral minus ipsilateral to the target hemifield, to assess whether any residual hEOG activity was present in the remaining data. The average peak amplitude of this hEOG index in the final data sample was 1.7 μV, showing that the exclusion criteria were effective and did not exceed 3 μV in individual averages of 85 participants, indicating that the residual eye movements in those participants averaged less than about 0.1° (Lins, Picton, Berg, & Scherg, 1993). In the remaining eight participants, the peak amplitude was between 3 and 5 μV. Importantly, we found no correlations between the hEOG index and any relevant contra–ipsilateral EEG difference, \( r \leq .09, p \geq .37 \), indicating that the EEG lateralizations were not contaminated by the residual eye-movement artifacts.

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Before ocular correction, gross artifacts at the scalp electrodes were first removed by rejecting segments with overall minimum–maximum voltage differences ≥ 200 μV or with voltage steps between adjacent data points ≥ 80 μV (except AF3, AFz, AF4, Fp1, Fpz, and Fp2, so that fewer segments would be rejected because of blinks). Next, the data from remaining trials were corrected for eye blinks and artifacts that had a noncortical origin using independent component analysis (Jung et al., 2000), and then, after resetting the baseline, edited for other artifacts by rejecting trials with overall minimum–maximum voltage differences ≥ 120 μV, voltage steps between adjacent data points ≥ 20 μV, and absolute amplitudes ≥ 120 μV. On average, 7% of segments (range: 1%–21%) were excluded because of artifacts. The average of accepted segments was 226 (range: 145–290) for the congruent condition and 214 (range: 131–292) for the incongruent condition.

**ERP Measurement and Analysis**

Before ERP analysis, artifact-free segments were averaged over each condition separately for each participant. All the ERP components of interest had fairly typical topographies and were measured at the sites at which their peaks were largest. The effects of flanker manipulation on the ERP measures were statistically evaluated by repeated-measures ANOVAs with the factor Flanker (congruent, incongruent) from activity recorded over visual cortex (PO7 and PO8, as the average of contra–ipsilateral differences for trials with the LVF and RVF targets, by the formula: \((\text{PO8LVF} - \text{PO7LVF}) + (\text{PO7RVF} - \text{PO8RVF})) / 2\). Thus, a negative ERL value indicates larger negativity at the hemisphere contralateral to the target visual field. Based on previous studies and inspection of the obtained grand averages, we measured the \(\text{N2pc}\) component of the PCN as mean amplitude 230–270 msec after target onset, and the sustained contralateral negativity (SPCN) as mean amplitude 360–600 msec after target onset. The latencies of the ERLs did not differ between the conditions (see Figure 3A and 3B); thus, their analysis is not reported here, for brevity. To obtain topographies of the ERLs, we subtracted all symmetrical electrodes and plotted the averaged contra–ipsilateral differences on the left hemisphere (Figure 3B).

To measure LRP, we calculated ERLs (Wascher & Wauschkuhn, 1996) from activity recorded over motor cortex at C3 and C4, as the average of activity recorded over contralateral to the target visual field.

To measure PCN, we calculated ERLs (Wascher & Wauschkuhn, 1996) from activity recorded over visual cortex at PO7 and PO8, as the average of contra–ipsilateral differences for trials with the LVF and RVF targets, by the formula: \((\text{PO8LVF} - \text{PO7LVF}) + (\text{PO7RVF} - \text{PO8RVF})) / 2\). Thus, a negative ERL value indicates larger negativity at the hemisphere contralateral to the target visual field. Based on previous studies and inspection of the obtained grand averages, we measured the N2pc component of the PCN as mean amplitude 230–270 msec after target onset, and the sustained contralateral negativity (SPCN) as mean amplitude 360–600 msec after target onset. The latencies of the ERLs did not differ between the conditions (see Figure 3A and 3B); thus, their analysis is not reported here, for brevity. To obtain topographies of the ERLs, we subtracted all symmetrical electrodes and plotted the averaged contra–ipsilateral differences on the left hemisphere (Figure 3B).

To measure the LRP we calculated ERLs from activity recorded over motor cortex at C3 and C4, as the average of the difference contra–ipsilateral relative to the responding hand: \((\text{C4Left Hand} - \text{C3Left Hand}) + (\text{C3Right Hand} - \text{C4Right Hand})) / 2\) (Coles, 1989), so that a negative value reflects activation of the correct response. In the stimulus-locked averages, the LRP amplitudes were measured as mean activity from -130 to -70 msec before the response. The LRP latencies were calculated by means of the 50% area under the curve measure, that is, by assessing the time point that divides the negative area under the LRP waveforms into two halves (Kiesel, Miller, Jolicœur, & Brisson, 2008).

The midfrontal N2 component was measured at FCz as a mean amplitude 260–320 msec after target onset. We also measured a positive component at FCz that preceded the N2, which we classified as P2, as mean amplitude 200–240 msec after target onset. The P3b component was measured at Pz. As seen in Figure 6, the P3b waves differed between the flanker conditions in terms of both its amplitude and its latency; thus, we measured both parameters. The P3b amplitude was measured as mean voltage 300–700 msec after target onset, and the P3b latency was determined using the 50% area measure in the time-window 200–800 msec after cue onset.

**Time-Frequency Analysis**

**Power and Phase Decomposition**

To obtain phase and power of ongoing EEG oscillations, the segmented artifact-free single-trial EEG data were decomposed into their time–frequency representation using custom-written MATLAB 2018a scripts based on Cohen (2014b, 2017). The power spectrum of the EEG was multiplied by the power spectrum of complex Morlet wavelets, defined as follows:

\[ e^{i2\pi f t}e^{-\tau^2/(2\sigma^2)} \]

where \(i\) is the complex operator, \(t\) is time, \(f\) is frequency (increased from 1 to 40 Hz in 40 logarithmically spaced steps), and \(\sigma\) is the width of each frequency band defined as \(n/(2\pi f)\), where \(n\) is a number of wavelet cycles. The wavelet cycles varied from four to eight in logarithmically spaced steps, to obtain an optimal tradeoff between temporal and frequency resolution (Trujillo & Allen, 2007). To avoid edge artifacts, we applied a signal reflection procedure on the segmented time-series data (Cohen, 2017). The convolution was calculated in frequency domain for each electrode and relevant experimental condition per participant. After the convolution, from the resulting analytic signal, we calculated frequency-band-specific phase and power. Phase angle values of the trial were defined as follows:

\[ \Phi(f_n,t) = \arg\{\text{Re}[y^k(f_n,t)], \text{Im}[y^k(f_n,t)]\} \]

where \(\arg\{\ldots\}\) stands for arc-tangent, \(\text{Re}\) for the real part of the signal, and \(\text{Im}\) for the imaginary part of the signal.

Power (i.e., the magnitude) of the signal \(y^k\) was estimated by averaging \(W^k\) over \(k\)-th EEG trial:

\[ W^k(f_n,t) = \text{Re}[y^k(f_n,t)]^2 + \text{Im}[y^k(f_n,t)]^2 \]
Intertrial Phase Coherence

To measure the stimulus selection-related contra–ipsilateral modulations of phase synchronization in the alpha band, we calculated frequency-band-specific intertrial phase coherence (ITPC; Benwell, Keitel, Harvey, Gross, & Thut, 2018; Cavanagh, Cohen, & Allen, 2009; or intertrial coherence, Busch, Dubois, & VanRullen, 2009; also called as intertrial phase-locked value, Wang, Goschl, Friese, Konig, & Engel, 2019; Lachaux, Rodriguez, Martinerie, & Varela, 1999). The ITPC is an estimation of consistency between phase angle values at a given electrode site for a specific frequency and time point across trials (or realizations), according to the following formula:

\[
ITPC_k(f_n, t) = \frac{1}{n} \sum_{i=1}^{n} e^{i \phi_k(f_n, t)}
\]

The ITPC values vary from 0 to 1, where 0 indicates random phase and 1 indicates identical phase values, which is the perfect phase coherence, at a given time–frequency point across trials. For statistical analysis, ITPC was measured from the PO7–8 electrode pair within a 50- to 300-msec 9- to 14-Hz frequency–time window (see Figure 3D and 3E). The ITPC was then submitted to a repeated-measures ANOVA with Flanker (congruent, incongruent) and Hemisphere (contralateral, ipsilateral to the target hemifield) as within-subject factors.

LPS in Alpha and Beta Bands

To measure stimulus selection-related contra–ipsilateral modulations of alpha power, we calculated the LPS index (van der Lubbe et al., 2019; van der Lubbe & Utzerath, 2013). First, the wavelet analysis described above was carried out for two flanker conditions, and hemispheres contralateral and ipsilateral to the target hemifield. Next, the LPS index was calculated for all symmetrical electrode pairs from the condition averaged power by a double subtraction similar to the ERL calculations. That is, a single subtraction (ipsilateral − contralateral) was calculated separately for the left and right target trials, scaled by the sum of activation of both hemispheres (ipsilateral + contralateral), and then averaged, which may be expressed by the following formula:

\[
LPS_k(f_n, t) = \frac{x_k(f_n, t) - y_k(f_n, t)}{y_k(f_n, t) + x_k(f_n, t)}
\]

where \(x_k\) is trial-averaged power from the ipsilateral channel and \(y_k\) is power from the contralateral side, both measured within the same frequency band \((f_n = f_n)\) and time-window. The LPS values vary from −1 to +1. A positive LPS value indicates a smaller power at the contralateral site relative to the ipsilateral site (which may be interpreted as desynchronization of a given frequency at the contralateral site), and zero indicates no hemispheric difference. To measure hand-movement-related contra–ipsilateral modulations of beta power, we computed LPS in the same way as the alpha LPS, but for contralateral and ipsilateral sites relative to the responding hand. For statistical analysis, the amplitudes of LPS in alpha band (9–14 Hz) were measured as mean activity 400–900 msec after target onset from the PO7–8 electrode pair, where the peaks were largest (see Figure 3G). The amplitude of motor-related LPS in beta band (18–25 Hz) was measured from the C3–4 electrode pair as the mean activity in a 300- to 900-msec time-window in the stimulus-locked averages, and in a −500- to 0-msec time-window in the response-locked averages. The LPS latencies were estimated using the 50% area measure. Flanker effects on the LPS were tested by repeated-measures ANOVAs. To improve the signal-to-noise ratio, the latencies were determined using the jackknife method: The parameters were measured in one-leave-out grand means, and the diminished error variance was corrected by dividing \(F\) values by \((n - 1)^2\) (Kiesel et al., 2008; Ulrich & Miller, 2001).

Non-phase-locked Midfrontal Theta Power

To obtain the non-phase-locked power, the phase-locked activity (i.e., the ERP, calculated as the time-domain trial average) was subtracted from the time-domain single-trial EEG signal, before the described above time–frequency decomposition (Cohen & Donner, 2013). The subtractions and then wavelet convolutions were done for each electrode and flanker condition per participant. For statistical analysis, the non-phase-locked power from the FCz site was averaged over a 400- to 600-msec, 4- to 8-Hz time–frequency window, specified based on both previous studies and inspection of the current data, and submitted into a repeated-measures ANOVA with Flanker (congruent, incongruent) as a within-subject factor.

Time–Frequency Connectivity Calculations

ISPc

Before connectivity analysis, a surface Laplacian filter (also called current source density or current scalp density; Cohen & Donner, 2013; Srinivasan, Winter, Ding, & Nunez, 2007) was applied to the artifact-free single-trial data (we used a 10th-order Legendre polynomial, and lambda was set at 1e−5) to increase spatial selectivity and minimize volume conduction. To calculate estimations of functional connectivity between the brain areas, we used the phase angles obtained from the complex wavelet convolution (as described above) and computed frequency-band-specific ISPc (Cohen, Riddelinkhof, Haupt, Elger, & Fell, 2008; also called intersite phase connectivity, Cohen, 2015; intersite phase clustering, van Driel et al., 2015; Gulbinaite et al., 2014; interchannel phase synchrony, Cavanagh et al., 2009; and between-
region phase-locking value or phase-locked value, (Fiebelkorn, Pinsk, & Kastner, 2018). The ISPC provides a measure of a difference in time–frequency phase angles between two sites (electrodes or sources of oscillations) \( x^k (f_n, t) \) and \( y^k (f_n, t) \) within the same specific frequency band \( (f_n = f_n) \) at each time point across trials, according to the following formula:

\[
\text{ISPC}_k^f (f_n, t) = \left| \frac{1}{k} \sum_{i=1}^{k} e^{j(f_n (f_n) - f_n (f_n))} \right|
\]

The ISPC value varies from 0 to 1, where 0 indicates no phase synchrony between two sites (i.e., random phases), and 1 indicates identical phase values at two sites (i.e., a perfect phase coherence between the two sites).

Graph Theory-based Estimation of All-to-all Theta ISPC

To test the hypothesis that the MFC is a hub for theta-based connectivity, we calculated the ISPC in theta (4–8 Hz) band for each pair of electrodes (all-to-all) and applied the mathematical framework of graph theory to identify the electrodes that had most robust synchronization degree with other electrodes (Cohen & van Gaal, 2013; Cohen, 2011). Graph theory has been successfully used to quantify various aspects of local and global network characteristics (Stam et al., 2009). Here, the network consisted of 64 nodes (electrodes) and 63 vertices per node (connections of each node to all other nodes). Synchronization degree (or strength) of a given node is defined as a number of other nodes with whom this node is strongly phase synchronized (i.e., the number of connections exceeding a threshold). In detail, first, we created weighted links (connections) based on pairwise ISPC connectivity vector. Second, all links have been binarized by thresholding: If a link exceeded the threshold, the value was replaced by 1; if it was below the threshold, the value was replaced by 0. Thus, the synchronization degree may be expressed as follows:

\[
SD_n^f (f_n) = \sum_{i \in N, j=1}^{n} a_{ij} (f_n)
\]

where \( n \) is the total number of relevant connections between electrodes and \( a_{ij} \) refers to the connectivity between electrodes \( i \) and electrode \( j \). For thresholding, we employed a subject-specific data-based approach and set the threshold at 1 SD above the median of each participant’s ISPC (cf. Cohen, 2011). For statistical analysis, synchronization degree was calculated separately for each theta band frequency (4–8 Hz) in a 400- to 600-msec time-window, electrode, and flanker condition, per participants, and submitted into a repeated-measures ANOVA with the factor Flanker.

MFC-to-ROI Theta Band Connectivity

To examine theta band connectivity between MFC and lateral frontal, centro-parietal, and lateral motor areas, we specified three ROIs—all based on both previous findings and data inspection—and computed ISPC between the midfrontal FCz electrode used here as “seed” and these ROIs. The AF3, AF4, F3, and F4 sites were used as lateral frontal ROI (cf. van Driel et al., 2015; Gulbinaite et al., 2014), the CPz and Pz sites were used as centro-parietal ROI (cf. Gulbinaite et al., 2014), and the C5–6 and CP5–6 electrode pairs were used as lateral motor ROI (cf. van Driel et al., 2015; Nigbur et al., 2012). After inspection of time–frequency plots (Figure 7), we decided to measure ISPC between FCz and lateral frontal and centro-parietal ROIs over two subsequent time–frequency windows: 100–400 msec 5–6 Hz, and 400–700 msec 5–6 Hz. For statistical analysis, the data were pooled across the ROI electrodes, and submitted into a repeated-measures ANOVA with Flanker and Time-window as within-subject factors. For ISPC between FCz and motor ROI, a time–frequency window of 500–800 msec and 4–6 Hz was used (see Figure 8A), the data were pooled across the ROI electrodes and submitted into a repeated-measures ANOVA with Flanker (congruent, incongruent) and Hemisphere (contralateral, ipsilateral) as within-subject factors. Although all our statistical analyses were generally specified a priori, the details of the ISPC analyses were further determined after inspection of the data. Therefore, to reduce the chance of false positives, all ISPC effects were additionally evaluated by nonparametric permutation tests with cluster-based corrections for multiple comparisons across all time–frequency points (Maris & Oostenveld, 2007). One thousand iterations of randomization were performed for each analysis. At each iteration, the ISPC values were randomly shuffled across the conditions. Next, a two-tailed \( t \) test was performed for each time–frequency point against a null-distribution of the condition difference. After all iterations, a null-hypothesis distribution was created, against which the observed \( t \)-test results were compared at \( p < .001 \). Finally, the obtained \( t \) value map was corrected at cluster level and thresholded at \( p < .01 \), so that any cluster in the real data that was equal or greater than 99% of the null distribution of clusters was considered statistically significant.

Cross-frequency Coupling

Finally, to investigate connectivity between the MFC and visual areas, we measured cross-frequency ISPC (c-ISPC) between MFC theta and stimulus selection-related occipital alpha. To quantify c-ISPC, we estimated a nonlinear phase synchronization between the lower (theta) frequency in the seed channel and the higher (alpha) frequency in the target ROI (Varela et al., 2001; Tass et al., 1998). The FCz electrode was used as “seed,” as before, and PO7–8 and O1–2 electrode pairs were used as
Values are two-tailed.

Finally, to assess the relationship between the behavioral conditions, and two hemisphere conditions (contralateral, ipsilateral, etc.), and the Pearson correlation coefficient will be referred to as the N2pc flanker effect, the EEG flanker effects (in shorthand notation, these differences will be associated with individual factors). To estimate the reliability of the RT flanker effect for individual participants, we calculated a split-half correlation between the first and second halves of the task, and an odd–even correlation between the odd-numbered and even-numbered trials (see Figure 2). The Pearson coefficient was $r = .82$, $p < .001$, for the split-half reliability, and $r = .92$, $p < .001$, for the odd–even reliability.

Overall response accuracy was near ceiling, but there was still a significant difference of 3% between the congruent (97%, $SD = 2$) and incongruent (94%, $SD = 5$) conditions, $F(1, 90) = 39.08$, $p < .001$, $\eta^2_g = .31$, which gives a RT flanker effect of 98 msec ($SD = 52$). This incongruent–congruent difference correlated with the average RT in the incongruent condition, $r = .67$, $p < .001$, and not with the RT in the congruent condition, $r = .09$, $p = .41$ (Figure 2). To estimate the reliability of the RT flanker effect for individual participants, we calculated a split-half correlation between the first and second halves of the task, and an odd–even correlation between the odd-numbered and even-numbered trials (see Figure 2). The Pearson coefficient was $r = .82$, $p < .001$, for the split-half reliability, and $r = .92$, $p < .001$, for the odd–even reliability.

Correlation Analysis

Finally, to assess the relationship between the behavioral and electrophysiological effects of the flanker manipulation, individual differences in the behavioral performance were correlated with individual differences in the electrophysiological activity. To this end, the incongruent minus congruent difference was calculated for each ERP, time–frequency, and connectivity measure, as indices of the EEG flanker effects (in shorthand notation, these differences will be referred to as the N2pc flanker effect, the P3 flanker effect, etc.), and the Pearson correlation coefficient was calculated to test for linear associations between these indices and the RT flanker effect. All reported $p$ values are two-tailed.

RESULTS

Behavioral Results

The average RT of correct responses was 580 msec ($SD = 65$) in the congruent condition and 678 msec ($SD = 87$) in the incongruent condition, $F(1, 90) = 319.08$, $p < .001$, $\eta^2_g = .78$, which gives a RT flanker effect of 98 msec ($SD = 52$). This incongruent–congruent difference correlated with the average RT in the incongruent condition, $r = .67$, $p < .001$, and not with the RT in the congruent condition, $r = .09$, $p = .41$ (Figure 2). To estimate the reliability of the RT flanker effect for individual participants, we calculated a split-half correlation between the first and second halves of the task, and an odd–even correlation between the odd-numbered and even-numbered trials (see Figure 2). The Pearson coefficient was $r = .82$, $p < .001$, for the split-half reliability, and $r = .92$, $p < .001$, for the odd–even reliability.

Overall response accuracy was near ceiling, but there was still a significant difference of 3% between the congruent (97%, $SD = 2$) and incongruent (94%, $SD = 5$) conditions, $F(1, 90) = 39.08$, $p < .001$, $\eta^2_g = .31$, which gives a RT flanker effect of 98 msec ($SD = 52$). This incongruent–congruent difference correlated with the average RT in the incongruent condition, $r = .67$, $p < .001$, and not with the RT in the congruent condition, $r = .09$, $p = .41$ (Figure 2). To estimate the reliability of the RT flanker effect for individual participants, we calculated a split-half correlation between the first and second halves of the task, and an odd–even correlation between the odd-numbered and even-numbered trials (see Figure 2). The Pearson coefficient was $r = .82$, $p < .001$, for the split-half reliability, and $r = .92$, $p < .001$, for the odd–even reliability.

Stimulus Selection-related Activity at the Visual Cortex

Introducing bilateral stimulation to the flanker task and applying the double subtraction method enabled us to isolate the stimulus selection-related lateralized signal from the overall visual activity. To thoroughly examine the effects of flanker interference on visual selection, and their relationship to behavioral performance, we analyzed three complementary features of the signal: ERPs, time–frequency power, and ITPC.

PCN (N2pc and SPCN)

Figure 3A shows grand averages of the ERPs recorded from electrodes over the visual cortex (PO7, PO8) at the hemispheres contralateral and ipsilateral to the target hemifield in two flanker conditions. The ERPs formed typical waveforms with P1 and N1 peaks, which tend to have slightly larger amplitudes at the contralateral site, followed by a conspicuous negative deflection at the contralateral site at about 250 msec after target onset, which we identified as the N2pc component. This contralateral negativity continued onward, forming an SPCN. Grand averages of the contra–ipsilateral differences in which the ERLs are isolated from the rest of the ERPs are shown in Figure 3B. The N2pc is evident as the largest negative peak, followed by the SPCN wave. All the ERLs had very similar occipito-
temporal topographies centered at PO7–8. Of importance, the N2pc amplitude was significantly larger in the incongruent condition, $F(1, 90) = 12.87, p < .001, \eta_p^2 = .12$, and so was the amplitude of the SPCN, $F(1, 90) = 77.88, p < .001, \eta_p^2 = .46$. Moreover, we found a positive correlation between the N2pc flanker effect and the RT flanker effect, $r = .29, p = .006$ (instead of the expected negative correlation; see Figure 3C), as well as between the N2pc flanker effect and the average RT in the incongruent trials, $r = .23, p = .030$. In contrast, the SPCN flanker effect did not correlate with the RT flanker effect nor the average RTs, $r \leq -0.02, ns$.

**Lateralized Alpha Power**

Time–frequency power representations of the contra–ipsilateral difference from PO7–8 electrode pair in two flanker conditions are shown in Figure 3F, and grand averages of LPS estimations for the alpha band (9–14 Hz) from PO7–8, along with their topographical maps for the relevant time-window, are shown in Figure 3G. As seen in the figures, the alpha LPS formed an early negative peak at about 140 msec after target onset and then reversed its polarity forming a positive deflection that peaked between 500 and 800 msec at the PO7–8 site. This positive LPS deflection (9–14 Hz, 400–900 msec) was significantly larger than 0 in both flanker conditions: congruent, $t(90) = 4.44, p < .001$, and incongruent, $t(90) = 9.09, p < .001$, indicating that the contralateral alpha power was significantly reduced as compared to the ipsilateral power. Of importance, this late positive LPS component was larger and had longer latency in the incongruent condition than in the congruent condition; $F(1, 90) = 37.98, p < .001, \eta_p^2 = .30$, and $F(1, 90) = 13.55, p < .001, \eta_p^2 = .13$, respectively. The correlation analysis showed no significant relationship between the alpha LPS flanker effect and the RT flanker effect, $r \leq .11, p \geq .28$. Still, we found a negative correlation between the alpha LPS flanker effect and the SPCN flanker effect, $r = -0.27, p = .010$. Correlations with the flanker effects on the other ERLs were not significant $r \leq -0.05, ns$.

**Lateralized Alpha Phase**

Figure 3D shows grand averages of ITPC in the alpha band (9–14 Hz) recorded from the PO7 and PO8 sites at the hemispheres contralateral and ipsilateral to the target hemifield in two flanker conditions. Figure 3E depicts time–frequency power representations of the contra–ipsilateral difference of the ITPC from the PO7–8 electrode pair in two flanker conditions and topographical maps of
Figure 3. Stimulus selection-related activity recorded over visual cortex (PO7–8). For all panels, Time point zero is the onset of target and flankers. Colors of lines and frames denote the conditions. (B, D, and F) The topographic maps were obtained by subtracting all the symmetrical electrodes (contra–ipsilateral) and plotting the difference on the left hemisphere. The maps are min–max scaled, with positive polarity in red and negative polarity in blue. The head view is from above. (A) Visual-evoked potentials. Grand means of the ERPs from the hemispheres contralateral and ipsilateral to the target visual field in the congruent and incongruent flanker conditions, pooled across the occipito-temporal sites PO7 and PO8. Negative voltage points upward. The gray areas indicate the time-windows in which the N2pc and SPCN components were measured. (B) ERLs. Grand means of the contra–ipsilateral differences from the PO7–8 electrode pair. Negative values (plotted upward) indicate a larger posterior negativity contralateral to the target visual field. The gray areas indicate the time-windows in which the N2pc and SPCN components were measured. The head maps depict topographies of these components within the indicated time-windows. (C) Scatter plot for correlations between the RT flanker effect and the N2pc flanker effect. The flanker effects are calculated as a difference between the incongruent and congruent conditions. (D) ITPC. Grand means of ITPC in alpha band (9–14 Hz) from the hemispheres contralateral and ipsilateral to the target hemifield in the congruent and incongruent flanker conditions, pooled across the occipito-temporal sites PO7 and PO8. The plot reveals a contralateral advantage of the alpha phase coherence. The gray area indicates the time-window in which the ITPC means were measured. (E) Lateralized ITPC. Time–frequency representations of the contra–ipsilateral difference of the ITPC from the PO7–8 electrode pair in two flanker conditions reveal the contralateral ITPC increase in the alpha band (9–14 Hz). Topographical maps show the localization of the contra–ipsilateral difference of the alpha ITPC for relevant time-windows. (F) Lateralized power over the PO7–8 electrode pair. The plots show time–frequency power representations of the contra–ipsilateral difference in two flanker conditions. Note the reduced contralateral alpha activity (9–14 Hz) peaking at about 600–700 msec after stimulus onset. (G) LPS. Grand means of the LPS estimations for the alpha band (9–14 Hz) from the PO7–8 electrode pair in two flanker conditions. The positive LPS deflection (plotted upward) indicates that the contralateral alpha power was reduced as compared to the ipsilateral power. The gray area indicates the time-window in which the alpha LPS were measured. Topographical maps show the alpha LPS in the indicated time-window.
the alpha ITPC for relevant time-windows. As evident in the figures, the occipito-temporal alpha (9–14 Hz) phase coherence peaked at about 160 msec after target onset and was significantly stronger at the contralateral site than at the ipsilateral site, $F(1, 90) = 159.70, p < .001, \eta_p^2 = .64$. Neither the main flanker effect nor the Flanker × Hemisphere interaction was significant, $F \leq 2.26, p \geq .13$. However, we found that the contra–ipsilateral ITPC difference (9–14 Hz, 50–300 msec) in the incongruent condition was negatively correlated with the RT flanker effect, $r = -0.21, p = .042$, indicating that an increase of the contralateral phase coherence was related to a lower conflict cost in RTs. The correlation of the contra–ipsilateral ITPC difference in the congruent condition with the RT flanker effect was weaker and not significant, $r = -0.18, p = .09$.

**Response-related Motor Activity**

This section describes the effects of flanker manipulation on the lateralized motor activity, measured as LRPs and LPS in the beta band. Both were calculated separately for stimulus-locked and response-locked analyses.

**Hand-movement-related LRP**

Figure 4 shows grand averages and topographies of the stimulus-locked LRPs (upper left panel) and response-locked LRPs (upper right panel) recorded over the motor cortex (C3–4) in two flanker conditions. As expected, the stimulus-locked LRPs showed a significant flanker effect on latencies, whereas the response-locked LRPs did not. Still, the response-locked LRPs had a larger amplitude in

![Figure 4](http://example.com/figure4.png)
the incongruent condition. In detail, the stimulus-locked results showed that, in the congruent trials, the LRP formed a negative peak reflecting activation of the correct response about 90 msec earlier than in the incongruent trials, which corresponds with the similar delay of behavioral responses. This latency difference was significant, \( F(1, 90) = 119.78, p < .001, \eta^2_p = .57 \), and so was, obviously, the correlation between this LRP flanker effect and the RT flanker, \( r = .31, p = .003 \). The amplitudes of the stimulus-locked LRPs did not differ between flanker conditions, \( F(1, 90) = 2.07, p = .15, \eta^2_p = .04 \), and did not correlate with the RT index, \( r = .06, p = .60 \). In the response-locked averages, the LRP amplitudes did not differ, \( F < 1.0 \), whereas the LRP amplitude was significantly larger in the incongruent condition, \( F(1, 90) = 5.06, p = .028, \eta^2_p = .05 \), indicating that, although the timing of response execution was not affected by response conflict, the strength of the activation of the correct response program was affected. Of importance, this flanker effect on the LRP amplitudes was positively correlated with the RT flanker effect, \( r = .20, p = .05 \).

**Hand-movement-related Lateralized Beta Power**

The bottom parts of Figure 4 show LPS estimates for the beta band (18–25 Hz) from the C3–4 electrode pair in two flanker conditions and their topographical maps for relevant time-windows. In the stimulus-locked averages, the beta band LPS formed a positive deflection that peaked at about 400–500 msec in the congruent condition and about 550–650 msec in the incongruent condition. Statistical analysis showed that the stimulus-locked LPS (400–900 msec) was significantly larger than 0 in both flanker conditions, \( t(90) \geq 4.05, p < .001 \); its latency was significantly longer in the incongruent condition, \( F(1, 90) = 14.35, p < .001, \eta^2_p = .14 \); and its amplitude was marginally larger in the congruent condition, \( F(1, 90) = 3.78, p = .055, \eta^2_p = .04 \). In the response-locked averages, the beta band LPS peaked at about 80 msec before response execution was significantly larger than 0 in both conditions, \( t(90) \geq 2.83, p \leq .006 \), and was significantly larger in the congruent than in the incongruent condition, \( F(1, 90) = 5.10, p = .026, \eta^2_p = .05 \). Unlike the stimulus-locked LPS, however, the latencies of the response-locked LPS did not differ, \( F < 1.0 \). Still, Figure 4 (lower right panel) suggests that their onsets might differ significantly. Thus, we estimated the onset latencies by means of the 50% of peak latency measure, which defines the onset time as the time point at which the wave reaches 50% of the peak value (Kiesel et al., 2008), and confirmed that there was no significant difference there, \( F(1, 90) = 1.52, p = .22, \eta^2_p = .02 \). The beta LPS flanker effects did not correlate significantly with the RT flanker effect, \( r \leq −.08, nS \).

**Conflict-related Midfrontal Activity**

Here, we present conflict-related and behaviorally relevant modulations of the midfrontal activity, measured as the flanker effects on the N2 component of the ERPs, non-phase-locked power, and midfrontal-centered global theta synchronization.

**Conflict-related N2 Component of the ERP**

Grand-average waveforms from FCz are depicted in Figure 5A. The second negative peak reached its maximum at about 290 msec after target onset and had the expected midfrontal topography centered at FCz, thus was classified as the N2. Importantly, the N2 amplitude was larger in the incongruent condition than in the congruent condition, \( F(1, 90) = 11.93, p < .001, \eta^2_p = .12 \), and this difference, that is, the N2 flanker effect, was negatively correlated with the RT flanker effect, \( r = −.38, p < .001 \) (see Figure 5A). We also quantified the positive peak that preceded the N2, which we classified as P2 (200–240 msec), and found out that its amplitude did not differ significantly between the flanker conditions, \( F(1, 90) = 1.97, p = .16, \eta^2_p = .02 \).

**Conflict-related Theta Power**

Figure 5B shows a time–frequency plot for the incongruent–congruent difference of non-phase-locked power (total power minus phase-locked power; cf. Cohen & Donner, 2013) from FCz along with topographical maps for relevant time-window and a scatter plot for correlation between the theta and RT flanker effects. As expected, we found a significant increase of non-phase-locked theta (4–8 Hz) power in the incongruent condition, as compared to the congruent condition, \( F(1, 90) = 34.21, p < .001, \eta^2_p = .27 \). This conflict-related theta peaked at about 400–600 msec after target onset and had the typical midfrontal topography centered at FCz. Of importance, we found a significant negative correlation between the theta flanker effect and the RT flanker effect, \( r = −.35, p = .001 \) (the correlation with the average RT in the incongruent trials was even stronger, \( r = −.54, p < .001 \)), and no significant correlation between the conflict theta (non-phase-locked activity) and the flanker N2 effect (phase-locked activity), \( r = −.05, p = .6 \).

**Conflict-related Intersite Theta Phase Synchronization**

Graph theory-based quantification of the intersite (all-to-all) phase synchronization degree showed that theta band (4–8 Hz) synchronization was strongest over the MFC (centered around FCz), as expected. This effect indicates that the midfrontal site carries out more functional connections in the theta band with all other sites than the rest of the electrodes over the scalp. Of importance, the theta synchronization degree was significantly higher in the incongruent condition than in the congruent condition, \( F(1, 90) = 37.86, p < .001, \eta^2_p = .30 \) (see Figure 5C), indicating a greater number of the MFC-centered functional connections in the conflict trials. Moreover, similar
to the power results, this incongruent–congruent difference in synchronization degree was negatively correlated with the RT flanker effect, \( r = -0.33, p = .002 \) (as well as with the average RT in the incongruent trials, \( r = -0.43, p < .001 \)).

**Conflict-related Centro-parietal Activity**

Figure 6A plots grand-average waveforms for the congruent and incongruent conditions at Pz, along with P3b topography in two flanker conditions. As evident, P3b peaked...
earlier in the congruent condition, $F(1, 90) = 40.06, p < .001$, $\eta^2_p = .31$, and this P3b latency flanker effect was modestly correlated with the RT flanker effect, $r = .24, p = .02$. Flanker congruency also had an impact on the P3b amplitude (measured as mean voltage 300–700 msec after target onset), which was in overall larger in the congruent than in the incongruent condition, $F(1, 90) = 7.03, p = .009$, $\eta^2_p = .07$, and this amplitude difference also correlated positively with the RT flanker effect, $r = .33, p = .001$ (Figure 6B).

**Conflict-related Connectivity between MFC and Task-related ROIs**

**Theta Phase Synchronization between MFC and Lateral Frontal Areas**

Figure 7A shows time–frequency plots of ISPC between FCz (“seed”) and lateral frontal ROI (AF3, AF4, F3, F4) for congruent and incongruent conditions, the incongruent–congruent difference along with theta ISPC topography for relevant time–frequency window, and a scatter plot for correlation between the theta ISPC flanker effect and the RT flanker effect. Black contours in the right panel outline time–frequency regions in which the condition difference was significant at $p < .01$, corrected for multiple comparisons using cluster-based permutation testing (also in Figures 7B and 8A). The figure reveals that theta band phase synchronization between FCz and the lateral frontal sites emerged in two stages. The first burst of synchronization occurred within 100–400 msec after target onset and the second within 400–700 msec. Although there is no difference between flanker conditions at the first stage, that second ISPC burst seems to occur only in the incongruent condition. This suggests that only the second stage reflects conflict-specific communication. Therefore, the theta ISPC between FCz and lateral prefrontal sites (AF3–4, F3–4) was evaluated with an additional factor: time-window (100–400 msec and 400–700 msec; see Methods section for details). The ANOVA yielded a significant main effect of Time-Window, $F(1, 90) = 76.05, p < .001$, $\eta^2_p = .46$, and a Time-Window × Flanker interaction, $F(1, 90) = 52.63, p < .001$, $\eta^2_p = .37$. The flanker effect was indeed present only in the second time-window, $F(1, 90) = 47.74, p < .001$, $\eta^2_p = .35$, and not in the first one, $F < 1.0$, ns. This was confirmed by the permutation test (see the right panel of Figure 7A). Moreover, the flanker effect on midfrontal—lateral frontal theta band connectivity within the second time-window (400–700 msec) correlated negatively with the RT flanker effect, $r = -.24, p = .025$ (Figure 7A), indicating that the participants who showed a stronger conflict-related increase of the theta ISPC tended to demonstrate a smaller conflict-related slowing of their RTs.

**Theta Phase Synchronization between MFC and Centro-parietal Area**

ISPC between FCz (“seed”) and centro-parietal ROI (CPz, Pz) is shown in Figure 7B. Similar to the midfrontal-to-lateral-frontal ISPC, theta connectivity occurred in two stages, with a notably stronger pronounced incongruent-congruent difference at the second stage. Thus, the analysis was also carried out with the time-window factor (100–300 msec and 400–700 msec). Both the main effect of Time-Window and the interaction between Time-Window and Flanker were significant, $F(1, 90) = 27.47, p < .001$, $\eta^2_p = .23$, and $F(1, 90) = 11.51, p = .001$, $\eta^2_p = .11$, respectively. Again, the flanker effect exceeded the level of significance in the...
Figure 7. Conflict-related midfrontal connectivity. (A) ISPC between midfrontal “seed” (FCz) and lateral frontal ROI (AF3–4, F3–4). (B) ISPC between midfrontal “seed” (FCz) and centro-parietal ROI (CPz, Pz). The left panels show time–frequency plots of the ISPC in two flanker conditions, along with time plots depicting grand means of the ISPC in the theta band (5–6 Hz). The right panels show time–frequency plots of the incongruent–congruent differences, that is, the ISPC flanker effects, and topographies of the effects’ time–frequency maxima. Black contours outline time–frequency regions in which the condition difference was significant at \( p > .01 \), corrected for multiple comparisons. The scatter plots depict correlations between the presented ISPC flanker effects and the RT flanker effect. For all panels: Time point zero is the onset of target and flankers. “Hotter” colors on the time–frequency plots and head maps indicate more robust phase synchronization. The black on white dot on head maps denotes the midfrontal “seed” at FCz, and the channels marked in black denote the selected ROI sites. ISPC is an estimation of frequency-specific phase synchrony between two sources of oscillations (sites and electrodes) and is interpreted as an index of functional connectivity between two brain areas. The depicted results show conflict-related bursts of theta communication between the medial frontal and lateral frontal cortices (A), and between the medial frontal and parietal areas (B). In both cases, the conflict-related communication occurred within 400–700 msec after target onset, and individuals with stronger conflict-related midfrontal ISPC showed a smaller behavioral cost of conflict (i.e., a smaller RT flanker effect).
Figure 8. Conflict-related midfrontal connectivity. (A) ISPC between midfrontal “seed” (FCz) and lateral motor ROI (C5–6 and CP5–6 electrode pairs). The upper left panel shows time–frequency plots of contra–ipsilateral differences of the ISPC in two flanker conditions, along with topographies of these differences in a 500–800 msec, 4- to 6-Hz time–frequency window. The lower left panel shows time plot for grand means of the ISPC in the theta band (4–6 Hz) from the hemispheres contralateral and ipsilateral to the responding hand in two flanker conditions. The upper right panel shows a time–frequency plot of the flanker effect on the contra–ipsilateral ISPC difference (i.e., contra–ipsi incongruent minus contra–ipsi congruent), and topography of this difference in the specified time–frequency window. The scatter plot depicts a correlation between the conflict-related lateralized theta ISPC and the RT flanker effect. Head maps were obtained by subtracting all symmetrical electrodes and plotting the averaged contra–ipsilateral differences on the left hemisphere. (B) cf-ISPC between midfrontal theta “seed” (FCz, 4–7 Hz) and visual alpha ROI (PO7–8/O1–2 electrode pairs, 9–12 Hz). The left panel shows grand means of the cross-frequency theta–alpha ISPC from the hemispheres contralateral and ipsilateral to the target hemifield in two flanker conditions. The right panel shows topographies of the theta–alpha cf-ISPC within 50–300 msec after target onset, separately for the hemispheres contralateral and ipsilateral to the target visual field, and for the contra–ipsilateral difference. Head maps for the contralateral averages were obtained by averaging all lateral electrodes from the left and right contralateral (to the target hemifield) hemispheres and plotting the averages on the left hemisphere. The same was done for the ipsilateral activity. Head maps for the contra–ipsilateral difference were obtained by subtracting all symmetrical electrodes and plotting the averaged contra–ipsi–ipsi differences on the left hemisphere. The results show a generally stronger cross-frequency connectivity between the MFC and visual areas at the contralateral site than at the ipsilateral site, and in the incongruent condition than in the congruent condition (although the figure suggests otherwise, a hemisphere by flanker interaction did not reach significance). For all panels: Time point zero is the onset of target and flankers. “Hotter” colors on time–frequency plots and head maps indicate more robust phase synchronization. The black on white dot on head maps denotes the midfrontal “seed” at FCz, and the channels marked in black denote the selected ROI sites. Topographies are presented on min–max scaled maps with positive values in red and negative values in blue. The head view is from above. Colors of frames denote the conditions.
second time-window, $F(1, 90) = 33.89, p < .001, \eta_p^2 = .27$, but not in the first one, $F(1, 90) = 3.41, p = .07, \eta_p^2 = .04$, which was further confirmed by the permutation test (see the right panel of Figure 7B). Also, the RT flanker effect correlated negatively with the flanker effect on the midfrontal-to-centro-parietal theta ISPC in the second time-window, $r = -.27, p = .010$ (Figure 7B), but not in the first time-window, $r = .17, p = .11$.

**Theta Phase Synchronization between MFC and Motor Areas**

The left panel of Figure 8A shows grand averages of theta (4–6 Hz) ISPC between FCz (“seed”) and lateral motor ROI (C5–6, CP5–6) for the hemispheres contralateral and ipsilateral to the responding hand in two flanker conditions, and time–frequency plots for contra–ipsilateral differences of the ISPC, along with topographies of these contra–ipsilateral differences in relevant time–frequency window (500–800 msec, 4–6 Hz). As seen in the figure, connectivity between FCz and the contralateral motor areas was stronger and lasted longer than the connectivity between FCz and the ipsilateral areas, which corresponds with the flanker effects on the RTs and the motor-related activity indexed by the LRP and beta LPS. More interestingly, the results show that although the contralateral connectivity was almost equally strong in both flanker conditions, the ipsilateral connectivity was conspicuously stronger in the incongruent condition, suggesting that better behavioral performance may be ipsilateral to target visual field in two flanker conditions, and the right panel shows head topographies of the cf-ISPC in a relevant time-window. The theta–alpha phase synchronization between FCz and the visual areas reached its maximum over the visual areas within 100–200 msec after target onset and was generally stronger at the contralateral site than at the ipsilateral site, $F(1, 90) = 13.86, p < .001, \eta_p^2 = .13$. As evident in Figure 8B, this contra–ipsilateral difference tended to be larger in the incongruent condition than in the congruent condition, although the Flanker × Hemisphere interaction did not reach significance, $F(1, 90) = 2.19, p = .14, \eta_p^2 = .02$. Of importance, the main effect of Flanker was significant, $F(1, 90) = 5.45, p = .02, \eta_p^2 = .06$, indicating generally stronger connectivity between MFC and visual areas in the incongruent trials. The ANOVA also showed a significant main effect of Frequency Pair, $F(15, 1350) = 20.20, p < .001, \eta_p^2 = .18$, but none of the remained interactions was significant, $F \leq 1.9$. Finally, we found no correlation of the overall cf-ISPC flanker effect with the RT flanker effect, $r = .08, ns$. However, such a correlation was found when we calculated the cf-ISPC flanker effect (i.e., incongruent–congruent) separately for the contralateral and ipsilateral sites: The RT flanker effect was negatively correlated with the cf-ISPC flanker effect at the contralateral site, $r = -.24, p = .021$, but not at the ipsilateral site, $r = -.12, p = .25$, suggesting that better behavioral performance may be partially related to the increased strength of cross-frequency connectivity between the MFC and contralateral visual areas.

**DISCUSSION**

**Behavioral Results**

The obtained behavioral results showed a typical flanker effect: Responses were longer and more error-prone in the incongruent condition than in the congruent condition. Importantly, the incongruent–congruent difference in RTs that is, the RT flanker effect, proved to be an accurate and reliable measure of the behavioral performance. First, the RT flanker effect was strongly positively correlated with the average RT in the incongruent condition, and not with the RT in the congruent condition, indicating that the effect indexes specifically the processes triggered by incongruent flankers, as assumed. Second, we obtained fairly high odd–even and split-half reliability estimations, which exceeded previously reported split-half reliabilities of the RT flanker effects (Asanowicz, Marzecová, Jaśkowski, & Wolski, 2012; Macleod, Lawrence, Mcconnell, & Eskes, 2010; Fan, McCandliss, Sommer, Raz, & Posner, 2002).

**Stimulus Selection- and Visual Interference-related Activity**

To assess the electrophysiological markers of visuospatial stimulus selection, we introduced bilateral stimulation into the arrow flanker task and measured selection-related lateralizations of the EEG activity (contra–ipsilateral to the
modulations may be a part of a mechanism of visuo-contralateral alpha suppression, suggesting that alpha and Luck (2019) have recently reported a target-evoked by individual differences in terms of this ability. Working memory capacity, was not significantly influenced by the SPCN (also called the contralateral delay activity; Vogel & Machizawa, 2004) is interpreted most often as a neuronal manifestation of visual working memory capacity (Luria, Balaban, Awh, & Vogel, 2016). Plausibly, the contralateral signal enhancement and, at least partially, the RT flanker effect did not correlate with the RTs, but it was negatively correlated with the ipsilateral distractor suppression. This interpretation of N2pc as an index of target selection per se (Mazza, Turatto, & Caramazza, 2009; Eimer, 1996). Nevertheless, the present results suggest that in particular circumstances like the current task (bilateral stimulation plus incongruent flankers), N2pc might reflect both the contralateral signal enhancement and, at least partially, the ipsilateral distractor suppression. This interpretation of N2pc would be in agreement with some previous findings (Luck et al., 1997; Luck & Hillyard, 1994) and an older hypothesis according to which N2pc does indeed reflect a distractor-suppression process (Luck, 2005).

The N2pc was followed by the SPCN, which also had a significantly larger amplitude in the incongruent condition. Unlike the N2pc flanker effect, however, the SPCN flanker effect did not correlate with the RTs, but it was negatively correlated with the (discussed below) lateralization of alpha power (which in turn also did not correlate with the RTs). The SPCN (also called the contralateral delay activity; Vogel & Machizawa, 2004) is interpreted most often as a neuronal manifestation of visual working memory capacity (Luria, Balaban, Awh, & Vogel, 2016). Plausibly, the flanker task performance, not particularly relying on visual working memory capacity, was not significantly influenced by individual differences in terms of this ability.

As mentioned in the Introduction section, Bacigalupo and Luck (2019) have recently reported a target-evoked contralateral alpha suppression, suggesting that alpha modulations may be a part of a mechanism of visuospatial target processing. They also inquired into the relationships of the alpha suppression with visual interference (induced by changing target–flanker distance) and the target selection-related N2pc. Here, we calculated the LPS to assess the target-related contra–ipsilateral difference in the alpha band (van der Lubbe & Utzerath, 2013). The obtained LPS estimates showed that a contralateral (vs. ipsilateral) reduction of alpha power was present from 400 msec onward, and it was larger and lasted longer in the incongruent trials than in the congruent trials. This indicates that the contralateral alpha suppression is indeed a part of the mechanisms underlying target processing, and these mechanisms are engaged to a stronger extent and for a longer time under visual interference condition. Our result confirms therefore the nonsignificant trend for enhancing alpha suppression with increased perceptual crowding found by Bacigalupo and Luck (2019). However, we neither found a correlation of the alpha LPS flanker effect with the RT flanker effect nor with the N2pc flanker effect. Still, the alpha LPS flanker effect was negatively correlated with the SPCN flanker effect (as mentioned above). Taking into account that, first, the N2pc is a marker of target selection and the N2pc flanker effect did correlate with the RTs, and second, the SPCN is a marker of visual working memory and the SPCN flanker effect did not correlate with the RTs but did correlate with the LPS flanker effect, we may tentatively conclude that the target-elicted contralateral alpha suppression reflects the same mechanisms of target processing as the SPCN, that is, sustained processing within visual working memory. This would be in line with other evidence for the role of alpha oscillations in the maintenance of visual representations over time (e.g., VanRullen & Maclonald, 2012).

Another electrophysiological aspect of stimulus selection was revealed by the difference between contralateral and ipsilateral phase coherence in the alpha band over the visual cortex. The stimulus-related alpha phase coherence peaked within 50–300 msec after stimulus onset, and the effect was notably stronger at the hemisphere contralateral to the target hemifield. This result is in line with some previous findings (e.g., Keitel et al., 2019; Spaak et al., 2014). Interestingly, the selection-related lateralization of alpha phase coherence did not differ between the flanker conditions. We did find, however, a modest negative correlation between the individual differences in the magnitude of the contra–ipsilateral bias in the incongruent condition and the individual flanker costs in RTs. This result suggests that an increase of the contralateral alpha phase may boost our selection capacity. In conclusion, phase coherence seems to reflect another detail of the mechanism of visuospatial processing that adds to the overall efficiency of target selection under flanker-induced visual interference.

Response Selection- and Response Conflict-related Activity

Response selection begins with the translation of perceptual codes into response codes and activation of the established S–R link or “event-file” (Verleger et al., 2014;
behavioral responses in the conflict trials, as expected. These P3b flanker effects did correlate with the delay of S–R link caused by the flanker-induced response conflict. These P3b flanker effects did correlate with the delay of behavioral responses in the conflict trials, as expected.

To translate an S–R link into overt behavior, the proper response program has to be selected and activated in the premotor and motor cortex, and passed on through action control. The time course of this motor-related activity is shown in measurements of the LRP and beta band LPS. The observed flanker effect on the stimulus-locked LRP is in line with the RT result showing that the selection of the correct response in the conflict condition was slowed down nearly 100 msec, compared to the congruent condition. The LPS complemented the LRP result, showing a conflict-elicited delay of beta suppression over motor areas contralaterally to the responding hand (note that the suppression is represented by positive LPS). This suppression is thought to reflect desynchronization of beta oscillations triggered by the functional cortical activation in motor-related brain areas during preparation and execution of voluntary movements (Siegel & Donner, 2010; Crone et al., 1998). The delay of the suppression reflects the timing of response selection (Kaiser et al., 2001; Tzagarakis et al., 2010). Once the conflict is resolved and the proper response program is selected, the response execution runs with no further flanker interference, as indicated by the latencies of response-locked LRP and LPS. In other words, the temporal dynamic of the process of response execution is independent from the processes of conflict resolution. Still, a trace of the conflict appeared in the amplitudes of both measures, as a slightly larger LRP and a smaller LPS in the incongruent condition. These amplitude effects may reflect a rebound-like modulation of response activation after winning the “fight” with the incorrect response program. It is unclear, though, how to parsimoniously explain the simultaneous conflict-related increase of the LRP and decrease of the LPS.

A successful S–R translation and response selection under the response-conflict condition is assumed to be orchestrated by an executive hub localized in the MFC (Cavanagh & Frank, 2014; Cohen, 2014a). Conflict-related modulations of midfrontal EEG were expected to be observed in the phase-locked activity, as an increased amplitude of the N2 component of the ERP (Heil et al., 2000; Kopp et al., 1996), and in the non-phase-locked activity, as an increased theta power (Cohen & Donner, 2013; Cavanagh et al., 2009). Our results showed that the N2 peaked at the FCz site in both flanker conditions, and its amplitude was larger in the conflict trials, as expected. Similarly, theta band power was centered at FCz and was larger in the conflict trials. Of importance, Cohen and Donner (2013), in their version of the Simon task, have found correlations of RTs with the non-phase-locked theta power, but not with the N2. Here, however, we found that the RT flanker effect was negatively correlated with both the theta flanker effect and the N2 flanker effect. In other words, both the non-phase-locked and the phase-locked components of the conflict-related midfrontal signal proved to be similarly related to the behavioral efficiency of conflict resolution: A relatively larger theta in the conflict trials resulted in participants’ better performance, reflected by a smaller cost of conflict in RTs, and similarly, the participants who had a relatively larger conflict-related N2 performed better in conflict trials. Moreover, we found no correlation between the N2 and theta power flanker effects, which suggests that they reflect two distinct processes or subsystems of the physiological mechanism of executive control.

Of importance, while the reported correlation here between the RT and theta flanker effects was negative, the aforementioned previously observed correlations between average RTs and theta power were positive (Cohen & van Gaal, 2014; Cohen & Donner, 2013). Note, however, that here, we report correlations between condition differences (incongruent–congruent) at the subject level, whereas the latter were single-trial correlations (condition-specific and/or across conditions). When we calculated the within-subject single-trial correlation on the present data set using the same method as Cohen and Donner (2013), we did obtain a positive correlation between the average RTs and theta power, closely conforming to the previous findings. The result is shown in Figure 9, and the method is described in the figure legend. This difference between the correlation results highlights two aspects of the theta–RT relationship. The across-trial positive correlation has shown that trial-to-trial fluctuations in midfrontal theta predict trial-to-trial fluctuations in behavioral task performance. This indicates that the executive system responds stronger when the task at hand becomes more demanding—either because of exogenous factors like the experimental conditions, or endogenous factors like fluctuations of the states of the visual and motor systems. Whereas the subject-level negative correlation between the condition differences shows that, generally, a more efficient conflict resolution (indicated by a smaller conflict cost) is related to a smaller involvement of the conflict-related midfrontal activity. This plausibly indicates that individuals with a more efficient executive system perform the task at hand not only more efficiently, but also with a smaller involvement of the resources, as compared to individuals with less efficient executive control. In other words, on the one hand, there is a simple
The hypothesis of midfrontal broadcasting mechanism has been said to operate via the MFC-generated theta phase top–down synchronization that entrains distinct task-relevant areas (Cavanagh & Frank, 2014; Cohen, 2014a). Here, we have confirmed that long-range theta-phase connectivity is indeed strongly centered at the MFC area, and shown that this midfrontal theta connectivity is more robust under the conflict condition. Moreover, for participants who presented a relatively stronger theta synchronization degree in the conflict trials, the behavioral cost of the conflict was smaller, which suggests they were in overall better in conflict resolution. A similar increase of the long-range theta connectivity was previously reported for motor errors (Cohen, 2011) and perceptual errors (Cohen & van Gaal, 2013), interpreted as an engagement of posterior adaptation mechanisms. The present result extends those findings in line with the idea that the MFC is an executive hub of long-range functional connectivity.

Furthermore, the present results confirm that this MFC-centered long-range executive communication includes an exchange of information with distinct task-relevant areas, that is, functional connectivity through which the MFC is thought to coordinate stimulus selection (in visual areas), sensorimotor integration (in parietal areas), response program activation (in premotor and motor areas), and executive control over response selection and execution (in lateral frontal areas). Importantly, all these MFC-centered connectivity were more robust in the incongruent condition than in the congruent one, and all those condition differences showed an inverse relationship with the behavioral cost of the flanker incongruence: The stronger the connectivity, the more efficient was the conflict resolution (although the correlations were modest).

First of all, we observed cross-frequency communication between the MFC and occipital areas. Previously, the phase-amplitude coupling between midfrontal theta phase and posterior alpha power has been demonstrated, for instance, during visual perception (Demiralp et al., 2007) and perceptual errors (Cohen & van Gaal, 2013; Mazaheri, Nieuwenhuis, van Dijk, & Jensen, 2009). More recently, it has been shown that the theta phase coordinates neural activity in the fronto-parietal selection network (Fiebelkorn et al., 2018). Here, we measured interregional connectivity by computing cross-frequency synchrony between theta-phase at the MFC and alpha-phase over the visual cortex. The results showed that the theta–alpha phase coupling was stronger for communication with occipital areas at the hemisphere contralateral to

![Figure 9. Within-subject cross-trial correlations between RT and midfrontal power (at FCz).](image-url)
the target hemifield, compared to the ipsilateral hemisphere, reflecting presumably a modulatory feedback loop from the MFC to visual cortex consolidating target processing. The theta–alpha phase coupling was also notably stronger in the incongruent condition than in the congruent condition, that is, when the target selection was more difficult because of visual interference caused by the incongruent flankers. Such theta–alpha coupling has been proposed to be one of the crucial oscillatory mechanisms of top–down control over visuospatial selection (Fiebelkorn & Kastner, 2020).

Second, the present results showed a task-related increase of the theta band synchrony between the MFC and centro-parietal area, probably reflecting processes of sensorimotor integration. This communication occurred in two bursts peaking at about 200 and 500 msec after target onset. The first one was notably stronger than the second one, but the difference between the flanker conditions was more pronounced during the second burst, reflecting enhanced connectivity in the conflict trials. Importantly, the flanker effect on the connectivity within the second burst correlated significantly with the RT flanker effect. The observed condition difference corresponds with the flanker effect on the centro-parietal P3b component of the ERPs. Similar communication between the MFC and some parietal areas has been previously reported in the Simon task (Gulbinaite et al., 2014) and error-detection task (Zhang, Chavarriaga, & Millán, 2015).

Third, our LRP and beta LPS results, showing the flanker effect on activation of correct response programs in motor areas, are complemented by observing the theta band synchronization between the MFC and motor areas contra-lateral and ipsilateral to responding hand. Specifically, communication with the contralateral areas was expectedly generally stronger than with the ipsilateral areas, and lasted longer in the incongruent condition. Interestingly, whereas the contralateral connectivity was almost equally strong in both flanker conditions, the ipsilateral connectivity was stronger in the incongruent condition than in the congruent one. This is in line with the hypothesis that the MFC not only coordinates the selection of the correct response program, but also orchestrates an inhibition of the incorrect response program that was triggered by the incongruent flankers, that is, the inhibitory projections to the ipsilateral motor site.

Finally, we observed an interesting two-phase communication between the medial and lateral frontal cortices (MFC and LFC). The first phase of the MFC-LFC communication occurred in the time-window of 100–400 msec, and here, the connectivity strength was similar in both flanker conditions. After this first burst, in the congruent condition, the communication began to fade out. In the incongruent condition, however, there was a second, even stronger burst of the theta synchronization, peaking at about 600–700 msec, plausibly reflecting the exchange of information on conflict resolution. Importantly, the increase of the MFC-LFC connectivity strength in the incongruent condition (relative to the congruent condition) within this second phase was correlated with the efficiency of conflict resolution exhibited by the speed of correct responses under the conflict condition. There is a general agreement that action control involves communication between the MFC and LFC (Petersen & Posner, 2012; Banich, 2009). According to the conflict–control loop theory (Carter & van Veen, 2007), in case of response conflict, the MFC informs the LFC about the need for control, and the LFC implements the top–down control functions to resolve the conflict and to prevent future performance decrements (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Miller & Cohen, 2001). The theta band synchrony between the MFC and LFC reflects a plausible oscillatory mechanism of information transmission between action-monitoring and action-control areas (Nigbur et al., 2012; Cavanagh et al., 2009). The current result adds another data point to this line of research on the communication within the executive network.

Conclusions

First, this study provides a comprehensive overview of the electrophysiological activity underlying selective processing under sensorimotor conflict. This includes activity at the occipital visual areas—where stimulus selection occurs, the posterior parietal area—where visual information is translated into S–R links, the motor areas—where response programs are selected and activated, and the mid-frontal area—whereas supervisory processing control is computed. Second, the obtained results show that the task-related areas are functionally connected via inter-regional oscillatory synchrony in the theta band with a central executive hub located in the MFC. Importantly, this long-range connectivity was more robust under the condition of increased demands for stimulus and response selection. Third, individual differences in the measured conflict-related EEG activity, particularly the midfrontal N2, theta power, and global theta connectivity, predict the behavioral efficiency in conflict resolution. Taken together, the present findings help to understand how the brain dynamics underlying sensorimotor processing and its executive orchestration shape individual behavioral performance.

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Funding Information

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the Journal of Cognitive Neuroscience (JoCN) during this period were M/an/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., JoCN, 33:1, pp. 3–7). Consequently, JoCN encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article’s gender citation balance.

Notes

1. The P1 and N1 asymmetry, present in the difference waves in Figure 3B as a small early positivity at 110 msec and negativity at 160 msec, did not differ significantly between the flanker conditions. These ERP deflections are caused by a slightly asymmetrical stimulus (arrows vs. vertical lines); thus, being a stimulus-driven perceptual asymmetry has been considered not relevant for the current topic and is not further discussed.

2. Note that the LPS correlations were calculated for power estimations only because the LPS latencies could not be reliably measured for individual participants; the jackknife method was used instead (see Methods section for details).

3. Given that the LRP latencies (as seen in the grand averages) correspond closely to the average RTs in two flanker conditions, one could expect a rather stronger correlation. However, the signal-to-noise ratio of LRP is typically relatively low, so that LRP latencies are generally more difficult to measure reliably for individual participants.

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