Received: 6 September 2016 | Revised: 7 August 2017 | Accepted: 17 August 2017

DOI: 10.1111/psyp.13011

ORIGINAL ARTICLE

WILEY PSYCHOPHYSIOLOGY SPR SOCIETY FOR PSYCHOPHYSIOLOGICAL RESEARCH

Occipital alpha power reveals fast attentional inhibition of incongruent distractors

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Funding information
Research Council of Ghent University (fellowship grant) (to C. J.), (grant BOF17-GOA-004) (to T. V.)

Abstract

Recent associative models of cognitive control hypothesize that cognitive control can be learned (optimized) for task-specific settings via associations between perceptual, motor, and control representations, and, once learned, control can be implemented rapidly. Midfrontal brain areas signal the need for control, and control is subsequently implemented by biasing sensory representations, boosting or suppressing activity in brain areas processing task-relevant or task-irrelevant information. To assess the timescale of this process, we employed EEG. In order to pinpoint control implementation in specific sensory areas, we used a flanker task with incongruent flankers shown in only one hemifield (congruent flankers in the other hemifield) isolating their processing in the contralateral hemisphere. ERPs revealed fast modulations specifically in visual processing areas contralateral to the incongruent flankers. To test whether these modulations reflect increased or decreased processing of incongruent flankers, we investigated alpha power, a marker for attentional inhibition. Importantly, we show increased alpha power over visual areas processing incongruent flankers from 300 to 500 ms poststimulus onset. This suggests fast cognitive control by attentional inhibition for information disrupting goal-oriented actions. Additionally, we show that midfrontal theta earlier in the trial is also modulated by incongruency, and that theta power predicts subsequent alpha power modulations. This supports the hypothesis that midfrontal incongruency detection leads to control implementation, and reveals that these mechanisms take place on a fast, within-trial timescale.

KEYWORDS

attention, cognitive control, EEG, ERPs, oscillation/time frequency analyses

1 | INTRODUCTION

Routine activities, such as driving a car, are often performed automatically, without consciously deciding which actions to perform. However, when a cyclist suddenly crosses the street, the flow of automatic functioning is broken, and we are forced to focus attention on relevant stimuli in the environment to guide deliberate actions. Such goal-directed behavior relies on cognitive control, a set of top-down mechanisms employed to regulate more basic processes (Botvinick, Cohen, & Carter, 2004). Since cognitive control is vital for everyday functioning, it has been extensively studied in psychology, often with congruency tasks (Eriksen & Eriksen, 1974; Hazeltine, Poldrack, & Gabrieli, 2000; MacLeod, 1991; Stroop, 1935).

Classical theoretical models assume cognitive control to be a rather slow process (Posner & Presti, 1987; Shiffrin & Schneider, 1977). Consistently, computational models (e.g., conflict monitoring theory; Botvinick, Braver, Barch, Carter, & Cohen, 2001) have typically implemented relatively slow (trial-to-trial) cognitive control. The conflict monitoring theory (Botvinick et al., 2001) proposes that response conflict occurs when several potentially relevant responses are active simultaneously. On the neural level, response conflict is thought to trigger control representations in midfrontal brain areas (e.g., anterior cingulate cortex, ACC). These representations in turn activate sensory cortical areas responsible for stimulus processing. This purported pathway has gained some support from fMRI, where incongruency boosts BOLD activity in task-relevant sensory areas (Egner & Hirsch, 2005; Weissman, Warner, & Woldorff, 2004) or suppresses activity in irrelevant sensory areas (Polk, Drake, Jonides, Smith, & Smith, 2008).

In contrast to more classical control theories, recent associative models of control predict that control adaptation can occur rapidly, within trials. Such models state that control is implemented via associations between perceptual, motor, and control representations (Abrahamse, Braem, Notebaert, & Verguts, 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009). Perceptual or motor input quickly activates associated control representations, which in turn influence perceptual or motor processes. Also, reward representations are known to enhance control (Stürmer, Nigbur, Schacht, & Sommer, 2011). In a behavioral study, Janssens, De Loof, Pourtois, and Verguts (2016) already show the fast associative nature of this process by demonstrating rapid control implementation in response to a reward cue.

The primary aim of the current study was to investigate the time course of cognitive control implementation, testing if control can occur rapidly, as predicted by associative control models. More specifically, we were interested to see how and on what timescale control occurs in cortical areas responsible for sensory processing. Due to the slow resolution of the BOLD signal, fMRI studies cannot reveal the timescale of sensory adaptations and thus cannot directly show the fast associative nature of these modulations. EEG is a temporally much more precise technique and has been used to investigate fast control processes. Scherbaum, Fischer, Dshemuchadse, and Goschke (2011) applied EEG with frequency tagging and showed that attention focused on the target stimulus increased during stimulus processing, whereas attention to distractors decreased. Importantly, these changes occurred continuously throughout the trial, supporting the notion of fast dynamics of cognitive control.

In the visual attention literature, the contralateral organization of the visual system is often used to characterize spatially specific sensory and attentional processes. This is done by separating different stimuli (or attentional operations) of interest across lateral hemispaces, which allows for a clear distinction in the EEG signal that is otherwise spatially resolved rather poorly. A similar strategy to investigate cognitive control in sensory specific brain areas was introduced by Appelbaum, Smith, Boehler, Chen, and Woldorff (2011). They administered a lateralized Eriksen flanker task, in which incongruent flanker letters appeared in only one visual hemifield (congruent flankers always appeared in the other hemifield). They used ERPs to study distractor processing in sensory brain areas during a trial. When comparing occipital activation for left versus right hemifield incongruent flanker trials, they obtained a lateralized incongruency difference (LID), showing differential ERP activity to incongruent versus congruent flankers. The LID can be interpreted as a positivity in the signal on occipital sites contralateral to incongruent flankers compared to ipsilateral ones. In visual search paradigms, a similar component—the distractor positivity (P_D)—has been observed. The P_D is interpreted as reflecting the suppression of unattended distractor stimuli during visual search (Hickey, Di Lollo, & McDonald, 2009). The LID in the study by Appelbaum et al. (2011) thus might also reflect reactive suppression of incongruent information. However, a more pronounced LID was correlated with a larger behavioral interference effect, and thus the authors interpreted the LID as reflecting increased distraction by and thus attention for incongruent flankers, rather than a control process. In the current study, we aimed to clarify if the LID component reflects increased or decreased attention for distractors, by investigating alpha power, a reliable marker for attention allocation.

In visual attention, alpha oscillations in the EEG (approximately 8 to 14 Hz) have been used as a reliable marker of attention allocation. Suppression of attention for irrelevant visual information has been reliably linked to power in the alpha frequency band. Power in the alpha band is increased in sensory areas processing distracting stimuli in sustained attention tasks (Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). It is thought that such alpha power enhancements are used for active inhibition of cortical areas (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010). Furthermore, alpha power is negatively correlated with brain activity (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Laufs et al., 2003; Ritter, Moosmann, & Villringer, 2009). Visual attention studies have mainly focused on relatively slow, proactive attentional shifts occurring before target onset. For example, in the seminal paper by Thut et al. (2006), alpha power was measured in the 2,600-ms interval before stimulus onset. In contrast, rapid target-triggered (i.e., reactive) alpha modulations marking fast and sensory-specific cognitive control have been studied far less in the literature, and studies have yielded mixed results, showing opposing alpha modulations (Fukuda, Kang, & Woodman, 2016; Sauseng et al., 2009; Vissers, van Driel, & Slagter, 2016) or no reactive modulations at all (Van Diepen, Miller, Mazaheri, & Geng, 2016). In the current study, we aim to investigate how fast reactive alpha modulations can be used for control implementation.

Another interesting aspect of time-frequency analysis is that it allows us to study power in the theta band

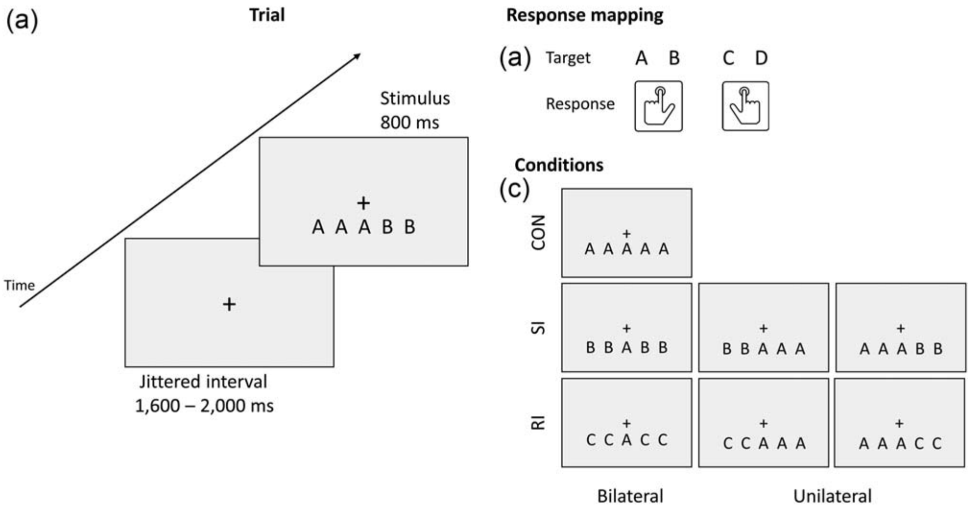

FIGURE 1 Overview of the flanker paradigm. (a) A stimulus was presented (800 ms) consisting of one central target letter and two flanker letters on each side of the target. Stimuli were interspersed with a jittered interval (1,600–2,000 ms). (b) There were four possible targets, linked to only two responses. (c) There were congruent (CON, 50%), stimulus-incongruent (SI, 25%), and response-incongruent (RI, 25%) trials in the experiment. SI and RI trials could have bilaterally incongruent flankers (33%) or unilaterally incongruent flankers (left or right hemifield, both 33%)

(approximately 4 to 8 Hz). Frontal theta power is increased in a wide variety of cognitive control tasks (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen, van Gaal, Ridderinkhof, & Lamme, 2009), suggesting that frontal theta is crucial for conflict and error detection, or cognitive control more generally (Cavanagh & Frank, 2014). We therefore also investigated the relation of frontal conflict detection areas with posterior sensory modulations by linking frontal theta power to occipital alpha power.

A second aim of our study was investigating whether the LID was caused by the response incongruency or instead by a visual discrepancy between target and flankers. Since the LID study of Appelbaum et al. (2011) only included congruent (CON) and response incongruent (RI) trials, differences could not be unambiguously attributed to the response incongruency. The importance of the distinction between response and stimulus incongruency (RI and SI) is illustrated by fMRI and EEG research demonstrating ACC activation for RI, but not for SI trials (Van Veen & Carter, 2002; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001, but see Wendt, Heldmann, Münte, & Kluwe, 2007). To address this issue, we introduced SI stimuli, in which there is a visual discrepancy between target and flanker, but no response incongruency. This allows an unambiguous attribution of the effects of differences between flankers and targets.

In sum, the current study combined lateralized incongruency with time-frequency analysis to investigate the time course of control in visual sensory areas. The LID ERP (Appelbaum et al., 2011) showed that incongruent flankers are rapidly processed. To clarify the interpretation of the LID, we investigated alpha power. If flankers visually distinct from the target draw attention, we predicted less alpha power (more attention) in areas processing these flankers (i.e., both SI and RI) than in areas processing flankers identical to the target (CON). On the other hand, if cognitive control operates by inhibiting attention for response-conflicting flankers, we predicted a very different pattern, namely, more alpha power (less attention) in areas processing incongruent flankers relative to congruent ones. In this study, alpha power was compared across CON, SI, and RI conditions to pit these predictions against one another.

2 | METHOD

2.1 | Experimental design

Twenty paid subjects participated in this experiment. Participants performed a flanker task similar to the one used by Appelbaum et al. (2011). An overview of the paradigm and stimuli is presented in Figure 1. A total of 384 trials were presented in 16 blocks of 24 trials, interspersed by self-paced breaks. Stimuli consisting of five letters were presented for 800 ms, mixed with jittered interstimulus intervals sampled from a uniform distribution (1,600–2,000 ms). The presented stimulus consisted of one central target letter and four flanker letters, two to the left and two to the right of the central target (see Figure 1a). Participants viewed the screen at a distance of 60 cm. Letter height was 0.48° (font: Courier New Bold). The two flanker stimuli were presented at 3° and 6° left and right of the center of the screen, and letters were presented 2.39° below the fixation cross (which was centered, both horizontally and vertically on the screen). Stimulus letters came from a set of four letters. There were two possible sets of letters (Set 1 = ABCD, Set 2 = WXYZ). Sets were counterbalanced across participants, so each participant received letters from only one set. Participants were

TABLE 1 Mean, standard deviation, minimum and maximum number of trials per condition after artifact rejection

Condition	Left flankers SI	Left flankers RI	Right flankers SI	Right flankers RI	Congruent
Mean number of trials ($n = 20$)	32.05	28.90	28.80	28.85	115.60
SD of number of trials	2.04	1.41	1.99	1.66	5.97
Minimum number of trials	29	27	22	26	102
Maximum number of trials	36	32	30	32	124

instructed to respond to the identity of the central target letter with a button press as soon as possible. Two letters mapped onto one response (see Figure 1b). Since the experiment took place following another similar experiment (same experiment for each participant; outside the scope of this paper) with the same response mapping, this mapping was well learned by the beginning of the experiment. Stimuli were congruent (CON, 50%), stimulus incongruent (SI, 25%), or response incongruent (RI, 25%). For both types of incongruent stimuli, incongruent flankers were presented on both sides of the central target (33%) or on only one side of the central target (33% only left and 33% only right). If incongruent flankers were presented on one side of the target, congruent flankers were presented on the opposite side (see Figure 1c).

2.2 | EEG data acquisition, processing, and analysis

Continuous EEG activity was acquired at 512 Hz using a 64-channel (pin-type) BioSemi ActiveTwo system (http://www.biosemi.com) referenced to the CMS-DRL ground and positioned according to the extended 10/20 International EEG system. Six additional electrodes were attached to the head: left and right mastoids, two electrodes for vertical and horizontal electrooculogram.

EEG data were analyzed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (http://erpinfo.org/erplab) software, running on MATLAB. The data were rereferenced offline to linked mastoids. Independent component analysis (ICA) was performed on continuous EEG data to correct data for eyeblinks. Noteworthy, we only removed ICs that were clearly related to eyeblinks. Horizontal eye movements occurred in only 1.6% of trials on average (ranging over subjects from 0% to 4.9%) and were not removed or corrected. Note that targets were always presented centrally, so maintaining central fixations was the best and most natural strategy for participants. We concluded that not controlling for these movements did not affect the results in an important way. Epochs of −200 to +1,000 ms locked to stimulus onset were selected. Semiautomatic artifact rejection was applied to the data using a 200 μV threshold (deviation from baseline) for initial artifact marking and visual inspection for final artifact removal. Trials containing high frequency noise as well as sudden amplitude shifts were removed. In Table 1, an overview is given of the mean number of trials per condition after artifact rejection.

For ERP analysis, the epochs were baseline corrected to the prestimulus period. Next, the epochs were averaged per condition per participant, and a grand average across participants was created resulting in one average ERP per condition. To enhance spatial resolution, these averages were transformed using the CSD toolbox for Laplacian transformation (Kayser & Tenke, 2006; http://psychophysiology.cpmc.columbia. edu/software/CSDtoolbox). Current source densities (CSDs) were calculated according to the spherical spline algorithm of Perrin, Pernier, Bertrand, and Echallier (1989), using a 10-cm head radius and a smoothing constant of 1 − 5.

Previous research by Appelbaum et al. (2011) used the LID to show activity specific to incongruent flankers. The LID was computed by subtracting the signal for trials with incongruent flankers in the right hemifield (e.g., AAA**; here, * can be any SI or RI flanker in the stimulus set, e.g., AAABB or AAACC) from the signal for trials with incongruent flankers in the left hemifield (**AAA). Note that the LID topographical plot shown by Appelbaum et al. (2011) in their figure 3C was defined as contra – ipsilateral flanker presentation. We used the same presentation for ERP and alpha power waveforms. The LID topographical plot by Appelbaum et al. (2011) is symmetrical by definition. In our study, to show the specific spatial distribution of differences, we defined the LID as left–right flanker presentation in the topographical plots, resulting in a typically nonsymmetrical difference. The LID was quantified at electrodes PO7 (left hemisphere) and PO8 (right hemisphere) for further analysis. These electrode sites were selected based on Appelbaum et al. (2011) and on previous literature showing that these electrode locations index lateralized visual attention processes (Eimer, 1996; Hickey et al., 2009). To investigate the LID, the interaction of electrode site (left vs. right hemisphere) and side of the incongruent flankers (left vs. right visual hemifield) was tested. To determine differences in LID for SI versus RI conditions, congruency type was also added to the analysis, resulting in a repeated measures analysis of variance (ANOVA) performed for ERP amplitudes

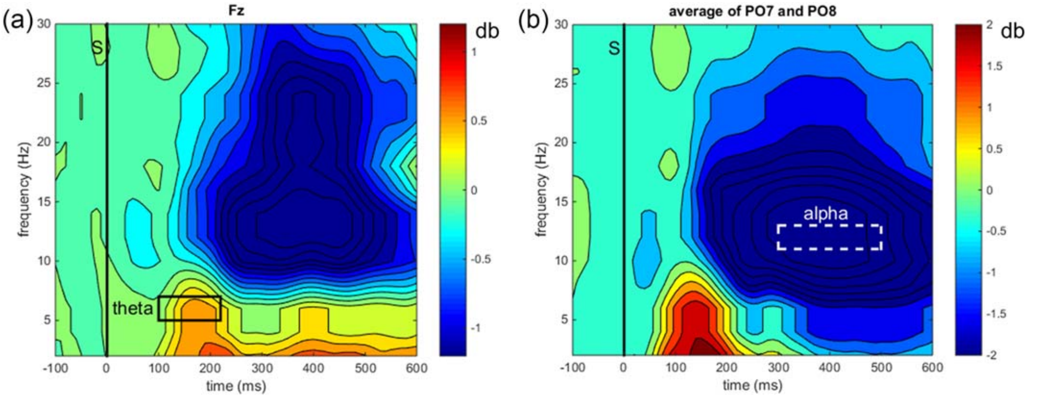

FIGURE 2 ERSP (power) locked to stimulus presentation (at time 0) at (a) frontal (Fz) and (b) occipital (average of PO7 and PO8) sites. A power increase in the theta band (4–8 Hz) peaking around 160 ms was followed by a power decrease in the alpha band (8–14 Hz) peaking between 300 and 500 ms. TF-ROIs were based on this pattern of power changes

with three factors: (a) congruency (RI vs. SI), (b) electrode site (left hemisphere vs. right hemisphere), and (c) incongruent flanker side (left hemifield vs. right hemifield). This analysis was done for a number of different time windows, ranging from 100 to 600 ms poststimulus onset in steps of 50 ms (selected times based on Appelbaum et al., 2011).

For the time-frequency analysis, fast Fourier transform was applied to the selected epochs in a moving window (width: 250 time points/488 ms, with Hann tapering), resulting in power estimates ranging from −100 ms to 600 ms (step 10 ms) locked to stimulus onset. Single trial event-related spectral perturbation (ERSP; i.e., power) estimates were acquired using the *newtimef* function from EEGLAB. Estimates were obtained at 15 uniformly distributed frequencies ranging from 2 to 30 Hz. Obtained output of the function was baseline corrected to the prestimulus period (baseline per subject, frequency, electrode, and condition), and then converted to decibels. Note that baselining did not take place at the trial level (approach based on Cohen, 2014). For this reason, in combination with the decibel conversion, the sum of the baseline data points is not necessarily zero, and therefore there may appear to be slight amplitude differences between conditions at stimulus onset. We defined our time-frequency regions of interest (TF-ROIs) based on the grand-average time-frequency analysis (as in Cavanagh et al., 2012, see Figure 2), and hence independent of the specific research question. Visual inspection reveals a power increase in the theta band (4–8 Hz) followed by a power decrease in the alpha band (8–14 Hz). For the purpose of the research question, we selected occipital regions PO7 for the left hemisphere and PO8 for the right hemisphere. These same electrodes were used to determine the LID and are commonly used when investigating occipital alpha (e.g., Kelly et al., 2006). For frontal regions, electrode Fz was selected. This electrode has a location similar to that used by Appelbaum et al. (2011).

Both occipital alpha and frontal theta power were analyzed. Based on the TF-ROIs (see Figure 2), occipital alpha power was defined as mean power at 12 Hz in the interval 300–500 ms poststimulus onset, representing the observed alpha power decrease. Frontal theta was defined as the mean amplitude around the peak of the initial theta power increase (peak at 160 ms, interval 100–220 ms). Power estimates were standardized per subject, and outliers were removed (more than four standard deviations from the mean) prior to statistical analyses.

3 | RESULTS

3.1 | Behavioral results

For reaction time (RT) analysis, error trials and post-error trials were removed. First, a linear mixed effects (LME) model was fitted for RTs with congruency (CON vs. SI vs. RI) as a fixed factor and a random intercept per subject. Results show a main effect of congruency, $F(1, 6573) = 26.8$, $p < .001$. Follow-up contrasts revealed that RTs on CON trials were significantly faster than on SI trials, $t(6573) = 4.16$, $p < .001$, and faster than on RI trials, $t(6573) = 7.06$, $p < .001$. Also RTs on SI trials were faster than on RI trials, $t(6573) = 2.52$, $p = .01$.

Second, we also wanted to investigate the effect of unilateral versus bilateral flankers. A LME model was fitted for RTs with lateral incongruency (congruent vs. unilaterally incongruent vs. bilaterally incongruent) as a fixed factor and a random intercept per subject (see results in Figure 3d). This revealed a significant effect of congruency type, $F(1, 6573) = 29.36$, $p < .001$. Post hoc t tests revealed a significant difference between congruent and unilaterally incongruent trials, $t(6578) = 4.63$, $p < .001$, between congruent and bilaterally incongruent trials, $t(6578) = 7.26$, $p < .001$, and between unilaterally and bilaterally incongruent trials, $t(6578) = 3.40$, $p < .001$.

Mean accuracy was 92.5%. First, a generalized LME model for binary responses was fitted for accuracy with congruency (congruent vs. SI vs. RI) as a fixed factor and a

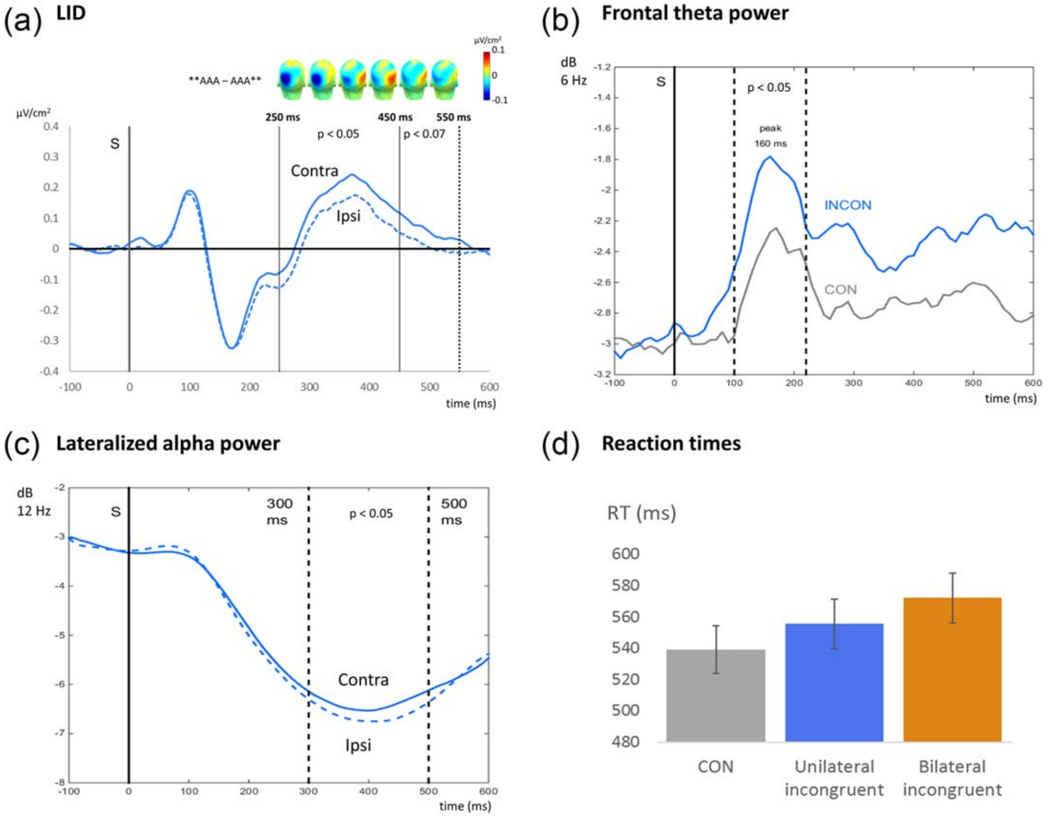

FIGURE 3 Results. (a) ERP lateralized incongruency difference (LID). ERP waveforms are shown for occipital electrodes located over the contralateral (full line) and the ipsilateral (dotted line) hemisphere (for plotting purposes, trials with left and right incongruent flankers are collapsed here). This shows a contralateral positivity for incongruent trials, maximal between 250 and 450 ms. Topographical plots for the difference between left hemifield incongruent-flanker trials (**AAA) and right hemifield incongruent-flanker trials (AAA**) are shown. Note that here the LID is not defined as contra versus ipsi to retain spatial specificity. For each topographical plot, the mean amplitude in a 50-ms time window is plotted, ranging from 250–550 ms poststimulus onset. A lateralized pattern of activation (negative difference in the left hemisphere, positive in the right hemisphere) shows the distribution of the contralateral positivity on the scalp. (b) Alpha power (12 Hz) over time, measured at contra- and ipsilateral hemisphere electrodes. For plotting purposes, trials with left and right presentation of incongruent flankers are collapsed here. Incongruent flankers elicited more alpha power in the contralateral hemisphere (full line) than in the ipsilateral hemisphere (dotted line), indicating that attention for the hemifield where incongruent flankers were presented was inhibited. (c) Frontal theta power (6 Hz) in electrode Fz, time-locked to stimulus presentation. Following stimulus presentation, theta power increases (peaks around 160 ms). Theta power (mean amplitude in the 10–220 ms interval) is significantly increased for incongruent trials (blue) compared to congruent trials (gray). (d) Reaction times. RTs were significantly slower in the unilateral incongruent condition (blue) than in the congruent condition (gray) and were again significantly slower in the bilateral incongruent condition (orange) than in the unilateral incongruent condition (blue). Error bars reflect standard errors

random intercept per subject. There was no effect of congruency, $\chi^2(2, N = 20) = 0.42$, $p > .05$. Second, to investigate the effect of number of incongruent flankers, a model was fitted with number of incongruent flankers (congruent vs. unilaterally incongruent vs. bilaterally incongruent) as a fixed factor and a random intercept per subject. This revealed no effect of number of incongruent flankers, $\chi^2(1, N = 20) = 0.97$, $p > .05$.

3.2 | EEG results

3.2.1 | Lateralized incongruency difference

To investigate the LID and the effect of congruency type, a repeated measures ANOVA for mean amplitudes was performed with three factors: (a) congruency (RI vs. SI), (b) electrode site (left hemisphere vs. right hemisphere), and (c) incongruent flanker side (left hemifield vs. right hemifield). The LID (interaction of electrode site and flanker side) was significant in all 50-ms windows from 250 to 450 ms ($p < .05$) and was marginally significant in windows from 450 to 550 ms ($p < .07$). In all other time windows, it was not significant ($p > .10$). The LID did not differ for SI versus RI conditions in any of the tested time windows, as was shown by a nonsignificant three-way interaction of electrode site, flanker side, and congruency type ($p > .10$). We therefore collapsed the SI and RI condition in the figure (see Figure 3a).

3.2.2 | Occipital alpha power is increased for irrelevant flankers

The effect of incongruent flankers on alpha power in lateral occipital electrodes was tested. Lateralized alpha power, the difference in alpha power for left versus right hemisphere (power at PO7 minus power at PO8), was determined on every trial. A LME model was fitted for this hemispheric difference in alpha power with presentation side of the incongruent flankers (left vs. right hemifield) as a fixed factor and a random intercept per subject. Importantly, this revealed a significant effect of incongruent flanker side on alpha power lateralization, $\chi^2(1, N = 20) = 6.47$, $p = .01$. Figure 3b shows the time course of alpha power. There is more alpha power in the hemisphere contralateral to incongruent flankers, indicating less attention for the visual hemifield containing distractors. Figure 3b also shows that this difference in alpha power occurs between 300 and 500 ms poststimulus onset. This pattern of results was similar for SI and RI trials; the interaction of distractor hemifield and congruency type (SI vs. RI) was not significant, $\chi^2(1, N = 20) = 0.78$, $p = .38$. We therefore collapsed the SI and RI conditions in the figure (Figure 3b). There was also no main effect of congruency type, $\chi^2(1, N = 20) = 1.15$, $p = .28$.

To test if the observed alpha power modulations predict behavior, a LME model was fitted for RTs with alpha lateralization (alpha contralateral minus alpha ipsilateral to incongruent flankers) as a predictor and a random intercept per subject. Lateralized alpha power was not significantly predictive of RTs, $\chi^2(1, N = 20) = 0.01$, $p = .97$.

3.2.3 | Frontal theta power is modulated by stimulus incongruency

To examine frontal control mechanisms that might influence these sensory processes, the effect of congruency on frontal theta power was examined (see Figure 3c). A LME model was fitted for theta power around the peak (160 ms) of the theta increase with congruency (CON vs. SI vs. RI) as a fixed factor, and a random intercept per subject. Results show a main effect of congruency, $\chi^2(2, N = 20) = 15.09$, $p < .001$. Follow-up contrasts revealed a significant difference between CON and RI trials, $t(4532) = 3.84$, $p < .001$, a marginally significant difference between CON and SI trials, $t(4532) = 1.82$, $p = .07$, and a marginally significant difference between SI and RI trials, $t(4532) = 1.75$, $p = .09$. Since we observed no clear difference between SI and RI trials, these conditions were collapsed in the figure (Figure 3c). To test if theta power predicts behavior, a LME model was fitted for RTs with theta power as a predictor and a random intercept per subject. Theta power was not significantly predictive of RTs, $\chi^2(1, N = 20) = 0.41$, $p = .52$.

3.2.4 | Theta power predicts alpha power on single trial level

To test our hypothesis of frontal theta leading control through alpha power modulations, we also fitted a LME model for alpha lateralization (alpha power contralateral minus alpha power ipsilateral to incongruent flanker presentation) with theta power as a predictor and a random intercept per subject. We found evidence for a direct influence of theta power on alpha power modulations, $\chi^2(1, N = 20) = 4.54$, $p = .03$, with higher theta power predicting more pronounced lateralized alpha modulations. Importantly, this effect was found on a single-trial level; trials with higher theta power earlier in the trial showed stronger alpha power modulations later in the same trial.

4 | DISCUSSION

We capitalized on the high temporal resolution of EEG to investigate within-trial modulations of cognitive control, specifically in sensory processing areas. To localize activity in sensory areas, we applied a lateralized flanker paradigm. The LID showed early processing differences for congruent versus incongruent flankers. More specifically, we observed a positivity contralateral to incongruent flankers, consistent with the P_D component reflecting distractor suppression described in visual attention literature (Hickey et al., 2009). We used alpha power to determine whether this LID signifies increased or decreased attention for distracting information. We hypothesized that, if visually distinct flankers capture attention, there should be less alpha power in areas processing incongruent flankers. If, on the other hand, incongruent flankers elicit cognitive control, there should be more alpha power in areas processing these incongruent flankers, reflecting active inhibition of attention. We observed higher alpha power in areas processing incongruent flankers, which strongly supports the cognitive control hypothesis. This alpha modulation did not significantly differ for SI and RI trials, suggesting that stimulus incongruency might have been the main driver of control. Frontal theta power earlier in the trial, marking conflict detection, was also modulated by incongruency. Moreover, (trial-to-trial) theta power predicted alpha modulations, suggesting that incongruency was detected in frontal regions, and, subsequently, control was implemented in specific sensory areas processing irrelevant information. Crucially, the data show that these control mechanisms operate on a fast, within-trial timescale.

An important argument of the current study was that incongruent flankers might in principle decrease alpha power (indexing increased attention). Indeed, visual search literature shows that stimuli that differ from their surroundings “pop out” and draw attention (Treisman, 1985). This phenomenon is known as attentional capture (Posner, 1980) and is strongly stimulus driven (Jonides & Yantis, 1988; Yantis & Hillstrom, 1994). In a static array of visual stimuli, a discontinuity involuntarily captures attention (Burnham & Neely, 2008; Burnham, Neely, Naginsky, & Thomas, 2010).

Consistently, when stimuli are presented serially, neural responses gradually decrease for repeating visual stimuli, a phenomenon called repetition suppression (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Similarly, alpha power increases across repetitions (Engell & Mccarthy, 2014). Taken together, studies with both simultaneous and serial stimulus presentation predict decreased attention for repeated stimuli but increased attention for discrepant stimuli. In the current study, we use a static array of visual stimuli where the target is repeated in one visual hemifield and a visual break between target and incongruent flankers is created in the other visual hemifield. Based on the attention literature (Burnham & Neely, 2008; Burnham et al., 2010), one would predict that such a discontinuity might capture attention. However, we find exactly the opposite, namely, less alpha power for repeating (congruent) flankers and more alpha power for discrepant (incongruent) flankers. This points to an active top-down control mechanism inhibiting the incongruent flankers rather than stimulus-driven attentional capture.

Our interpretation of increased alpha for incongruent flankers as a marker for increased cognitive control depends on the notion that alpha oscillations have an active inhibitory function. Initially, alpha oscillations were thought to reflect cortical inactivity (Pfurtscheller, Stancák, & Neuper, 1996), but strong evidence currently supports the hypothesis that alpha oscillations mark active inhibition of irrelevant information, to promote the processing of relevant information (gating by inhibition; for a review, see Jensen & Mazaheri, 2010). For instance, a number of studies show that alpha power is decreased in brain regions that are actively involved in task performance, and that alpha modulations predict task performance (Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). Decreased alpha power has also been clearly linked to increased BOLD activity measured by fMRI (Laufs et al., 2003; Ritter et al., 2009). Finally, intracranial recordings in monkeys during task performance demonstrate that neural firing is locked to the troughs of alpha oscillations in the local field potentials (Haegens et al., 2011). This strongly links alpha power modulations to the engagement and inhibition of specific brain areas and supports our interpretation of increased alpha as reflecting increased cognitive control.

As described above, the inhibitory role of alpha oscillations in visual attention has been made abundantly clear for relatively slow, strategic attention allocation. In most paradigms, a cue is presented before target presentation, proactively directing attention to a relevant location on the screen (Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000). In contrast, fast, reactive alpha power modulations following target onset have been studied far less, and mixed results have been obtained. Some studies reported reactive alpha power modulations (Fukuda et al., 2016; Sauseng et al., 2009), but others challenged this idea and showed only slow, proactive attention shifts but no evidence for similar reactive mechanisms operating on a fast timescale (Vissers et al., 2016). Van Diepen et al. (2016) report reactive alpha power modulations, with more alpha power contralateral (vs. ipsilateral) to distractors around 500–750 ms posttarget onset. Interestingly, these authors observed fast modulations in the least challenging condition (where target and distractor are clearly distinguishable), but not in the most challenging one (where target and distractor are highly similar). Therefore, alpha modulations in this study could not be interpreted as top-down cognitive control signals but were seen instead as bottom-up markers for successful distractor suppression. Our study importantly adds to this previous work by showing that alpha modulations can be used in a top-down fashion to implement control by suppressing distractors. Additionally, we show that such top-down modulations can occur on a fast, within-trial timescale and are not limited to slow and proactive mechanisms, as suggested by previous studies (Kelly et al., 2006; Thut et al., 2006; Vissers et al., 2016; Worden et al., 2000).

Both classical (Botvinick et al., 2001) and more recent associative (Abrahamse et al., 2016; Egner, 2014; Verguts & Notebaert, 2008, 2009) accounts of cognitive control predict that control is guided by frontal regions that are activated when a challenging event, such as an incongruency or an error, occurs. This initial detection of conflict is reflected in a midfrontal theta power increase for incongruent or error trials (Cavanagh et al., 2012; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). Earlier work observed an increased synchrony between frontal theta and occipital alpha on posterror trials, supporting the connection between error detection and control implementation (Cohen et al., 2009). Another study reported a correlation between frontal theta increases and occipital alpha decreases following errors (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009). Consistently, we observed that theta power at 160 ms poststimulus onset predicts alpha power modulations later in the trial, from 300 to 500 ms. Higher theta power was linked to a more pronounced inhibition of attention for irrelevant information. The timing of these events and their correlation at the single trial level strongly suggest that initial incongruency detection reflected in theta power leads control implementation in sensory areas later during the trial. Importantly, this happens on a very fast (within-trial) timescale, before the response is given.

In the current study, theta and alpha power seem to be modulated equally in the SI and RI conditions, suggesting that visual stimulus incongruency may be sufficient to initiate control implementation in this task. However, insufficient statistical power due to a limited number of trials might also explain why no significant differences could be detected between the SI versus RI condition. It is theoretically plausible that response incongruency may add to the visual stimulus effects and elicit more pronounced control processes. Future work should thus determine more conclusively whether response incongruency has an effect above stimulus incongruency. From the current study, we can, however, already safely conclude that incongruency does trigger alpha for inhibition of irrelevant flankers. That stimulus incongruency might suffice to trigger control is in line with previous work (Nigbur et al., 2012) and can be interpreted from an associative control model perspective. From this perspective, control would be gradually learned while solving a task, depending on current task demands, and can occur at different levels. Subjects in an experiment search for and learn strategies that are useful for the particular task that is given to them, taking into account the stimuli and stimulus contingencies at hand (for a similar argument, see Brown, 2009; Pansky & Algom, 2002; Schmidt & De Houwer, 2012). In classical cognitive control tasks (where only CON and RI conditions are presented), response conflict is the most relevant and obvious feature that predicts task performance and is picked up by participants. In the current context, we propose that subjects might learn a different aspect of the task that predicts task performance. They learn that information in one or both hemifields can hinder performance. They consequently develop task-specific and location-specific (left and right hemifield) representations that detect whether target and flankers are different. When these representations are activated by an experimental stimulus, they trigger control mechanisms and inhibit processing of incongruent flankers. These representations are formed based on visual discrepancy, so they are triggered by both SI and RI trials, inhibiting incongruent flankers in both SI and RI conditions. Any possible surplus effects of response incongruency could be explained by a similar logic, since multiple environmental cues can be used to optimize task performance. Although currently speculative, the account can lead to testable predictions. For example, future studies with more power to detect changes across trials can investigate the evolution of alpha during the experiment.

In conclusion, the current study shows that task-specific control is implemented by inhibiting sensory processing of irrelevant stimuli, in sensory areas specific to these stimuli. This control process is guided by midfrontal brain areas detecting the need for control, which is also task specific. Crucially, this occurs on a fast, within-trial timescale. The current study thus supports associative models for control that predict such fast and task-specific control mechanisms.

ACKNOWLEDGMENTS

C. J. was a Ph.D. fellow supported by the Research Council of Ghent University while performing this research. T. V. was supported by grant BOF17-GOA-004 from the Research Council of Ghent University.

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How to cite this article: Janssens C, De Loof E, Boehler CN, Pourtois G, Verguts T. Occipital alpha power reveals fast attentional inhibition of incongruent distractors. *Psychophysiology*. 2017;00:000–000. https://doi.org/10.1111/psyp.13011