Layers of latent effects in cognitive control: An EEG investigation

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ABSTRACT

Recent research demonstrates that two components of reaching behavior – initiation time (the time elapsed from stimulus presentation to movement initiation) and reach curvature (the degree to which a reach movement deviates from a direct path to the selected response) – exhibit distinct cross-trial dynamics in cognitive control tasks, indicating that these components of behavior reflect two dissociable processes underlying cognitive control: a threshold adjustment process involving the inhibition of motor output and a controlled selection process involving the recruitment of top-down resources to support goal-relevant behavior. The current study investigates the extent to which the cross-trial dynamics previously observed in reaching behavior in the Eriksen flanker task are reflected in event-related potentials during standard button-press responses. Candidate EEG measures of the threshold adjustment process (N2 and Pre-LRP amplitudes) failed to reveal the cross-trial dynamics previously observed in initiation times. Slow wave amplitudes exhibited a close correspondence to the cross-trial dynamics observed in reach curvatures, indicating that the measure is sensitive to some functions of the controlled selection process. Further, LRP slopes presented a close correspondence to the cross-trial dynamics observed in response times, indicating that this measure reflects the combined output of the threshold adjustment process and controlled selection process. The implications of these findings for future research examining the links among behavioral and neural dynamics are discussed.

1. Introduction

Human beings exhibit a remarkable capacity for cognitive control – the ability to re-align one's thoughts and actions with one's ever-changing goals. A central component of cognitive control is the ability to detect and resolve conflict stemming from the co-activation of competing responses (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004; Egner, 2008; Greene, Nystrom, Engell, Darley, & Cohen, 2004; Kim, Kroger, & Kim, 2011; Larson, Clayson, & Clawson, 2014; Shenhav, Botvinick, & Cohen, 2013; Yeung, Botvinick, & Cohen, 2004). Varied theoretical perspectives propose that conflict detection and resolution are supported by a number of dissociable processes, including a *threshold adjustment* process that inhibits motor output when signals of conflict are detected and a *controlled selection* process that resolves conflict between co-active responses by directing top-down support in favor of the response that is most closely aligned with one's current goal (Erb, Moher, Sobel, & Song, 2016;

Shenhav et al., 2013).[1] However, little work has been done to confirm if the latent processes proposed via cognitive accounts share common features with the latent features supposedly identified with neural imaging.

Given the important role that cognitive control plays in supporting flexible and adaptive behavior in everyday life (for a discussion, see Diamond, 2013), a central focus of research in the psychological and brain sciences is to determine how the various processes proposed to underlie cognitive control unfold over the course of a response (*within-trial dynamics*) and are modulated by recent experience (*cross-trial dynamics*). Targeting these processes with traditional behavioral measures poses certain challenges, however, given that button-press measures of accuracy and response time reflect the summation of multiple processes (Erb & Marcovitch, 2018a; Erb, Moher, Song, & Sobel, 2018). It is therefore difficult to identify how individual processes such as the threshold adjustment process or controlled selection process contribute to the behavioral effects observed across different tasks, individuals, or

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[1] Our usage of the term "threshold" in reference to the threshold adjustment process is intended to capture the notion that the level of motoric inhibition generated at the initiation of a response can be adjusted in response to signals of conflict. The term "threshold" should not yet be interpreted as a direct correspondence to decision thresholds featured in bounded-accumulation models of decision making (e.g., Ratcliff & McKoon, 2008). While these concepts could be empirically contrasted, such an undertaking is beyond the scope of the current study.

groups.

To address this limitation of button-press measures, Erb and colleagues (Erb et al., 2016, 2018; Erb & Marcovitch, 2018a, 2018b; Erb, McBride, & Marcovitch, in press; Erb, Moher, Song, & Sobel, 2017) investigated the extent to which the threshold adjustment process and controlled selection process could be targeted behaviorally by recording the spatial and temporal characteristics of participants' hand movements (*manual dynamics*). Participants completed cognitive control tasks such as the Eriksen flanker task (Eriksen & Eriksen, 1974) by reaching to touch response targets on a digital display while their hand movements were measured using an electromagnetic position and orientation recording system. In the flanker task, participants are presented with a stimulus array consisting of central target and surrounding distractors also known as flankers. For example, participants may be instructed to generate a left response when the central target is an "M" and a right response when the central target is an "N". On congruent trials, the target and flankers cue the same response (e.g., "MMMMM"). On incongruent trials, the target and flankers cue competing responses (e.g., "NNMNN"). A *congruency effect* is typically observed in the task, with higher error rates and slower response times (the time elapsed between stimulus onset and response completion) on incongruent relative to congruent trials.

In addition to accuracy and response time, the reach-tracking technique used by Erb and colleagues (Erb et al., 2016, 2017, 2018; Erb & Marcovitch, 2018a, 2018b) provided measures of *initiation time* (the time elapsed between stimulus onset and movement onset) and *reach curvature* (the degree to which a movement deviates from a direct path to the selected target). Erb et al. (2018) proposed that initiation times could be used to target the threshold adjustment process, with slower initiation times reflecting higher thresholds and longer periods of motor inhibition. Consistent with this proposal, the researchers observed main effects of current congruency and previous congruency in the flanker task, with slower initiation times on incongruent trials and trials preceded by incongruent trials, resulting in the following pattern of effects: cC < iC < cI < iI (lowercase letters denote the congruency of the previous trial and uppercase letters denote the congruency of the current trial; see Fig. 1A). This pattern of effects supported the researchers' claim that conflict detected at the outset of a trial results in heightened response thresholds which, in addition to generating slower initiation times on the current trial, are carried over into the subsequent trial. Notably, this same pattern of effects was previously observed in single-unit recordings of the dorsal anterior cingulate cortex (dACC) – a region that has been implicated in threshold adjustments (e.g., Cavanagh et al., 2011; Wiecki & Frank, 2013) – during performance of a button-press version of a Stroop-like task (Sheth et al., 2012).

Erb and colleagues (Erb et al., 2016, 2017, 2018; Erb & Marcovitch, 2018a, 2018b) further proposed that reach curvatures could be used to target the controlled selection process by indexing how active competing responses were over the course of a movement. On this view, larger reach curvatures indicate that participants were more pulled toward an inappropriate response option before sufficient top-down support was recruited to bias response activations in favor of the goal-relevant response. Consistent with this proposal, Erb et al. (2018) found that reach curvatures exhibited a very different pattern of effects than initiation times in the flanker task (see Fig. 1B). Trials that featured a different response than the previous trial (*response switch trials*) revealed a main effect of current congruency alone (cC-s = iC-s < cI-s = iI-s; where -s denotes a response switch), whereas trials featuring the same response as the previous trial (*response repeat trials*) revealed a significant interaction between the congruency of the current and previous trial. No effect of previous congruency was observed on congruent trials featuring a response repeat but reach curvatures were significantly larger on incongruent trials preceded by a congruent trial relative to those preceded by an incongruent trial (cC-r = iC-r < iI-r < cI-r; where -r denotes a response repeat).

Erb et al. (2018) interpreted the reach curvature difference observed

between cI-r and iI-r trials in terms of the *feature integration account* of trial sequence effects, which proposes that transient associations are formed between stimulus and response features on each trial (Hommel, 2004; Hommel, Proctor, & Vu, 2004; Nieuwenhuis et al., 2006). In versions of the flanker task that involve only two responses and a limited number of stimuli, cI-r trials generate conflict during stimulus-response (S-R) binding because the response of the current trial (e.g., "LEFT") is associated with the stimulus of the previous trial (e.g., "MMMMM"). Consequently, the association formed on the previous trial must be broken before the stimulus of the current trial (e.g., "NNMNN") can be paired with the appropriate response (e.g., "LEFT"). This conflict during S-R binding delays the ability of the controlled selection process to bias response activations in favor of the goal-relevant response, resulting in particularly large reach curvatures on cI-r trials.

Importantly, the pattern of effects observed in initiation times and reach curvatures by Erb et al. (2018) combined to generate the same pattern of response time effects previously been observed in button-press versions of the flanker task, including a pattern of effects in response repeat trials known as the *Gratton effect* (e.g., Mayr et al., 2003; Nieuwenhuis et al., 2006; see Fig. 1C).[2] This finding indicates that reach tracking can be used to disentangle different patterns of effects linked to the threshold adjustment process and controlled selection process that may otherwise be obscured in button-press measures. Taken together, the results of Erb and colleagues (Erb et al., 2016, 2017, 2018; Erb & Marcovitch, 2018a, 2018b) present a framework for linking the behavioral and cognitive dynamics of control by demonstrating that different components of reaching behavior can be used to isolate distinct patterns of effects that (a) are obscured in both reaching response times and button-press response times and (b) appear to reflect dissociable processes underlying cognitive control.

1.1. The current study: neural indicators of latent states

The current study evaluates the extent to which electroencephalography (EEG) can be used to target latent neural states underlying cognitive control during performance of a button-press version of the flanker task. Although we do not measure reaching behavior, a central aim of the current study is to explore the extent to which the dynamics of control observed in prior reach-tracking investigations of the flanker task are reflected in the neural dynamics registered with EEG. Given that simultaneously measuring reaching behavior and neural dynamics presents a number of practical and computational challenges (e.g., minimizing and removing unwanted movement artefacts in the EEG signal), the current study represents the early steps of a larger research effort to link the behavioral and neural dynamics of control.

Erb et al. (2016) explored the link between the behavioral and neural dynamics of cognitive control by comparing the patterns of effects observed in initiation times and reach curvatures to those observed in previous fMRI and electrophysiology research that utilized button-press measures of behavior. For example, the researchers found that reach curvatures in a three-response version of the Stroop task generated the same pattern of effects observed in ACC activation in an fMRI investigation using a button-press version of the same task (Kerns et al., 2004): cC = iC < iI < cI. Initiation times, on the other hand,

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[2] A large body of research has emerged in recent decades concerning the cognitive and neural underpinnings of the Gratton effect. Debate is ongoing concerning the extent to which the effect stems from various top-down and bottom-up factors in different congruency tasks and under different testing conditions (see Egner, 2007, 2017; Schmidt, 2018). For a detailed discussion of how the Gratton effect observed in two-alternative forced-choice versions of the flanker task can be understood to reflect two dissociable trial sequence effects, see Erb and Marcovitch (2018a).

Erb et al. (2018) – Reaching Behavior
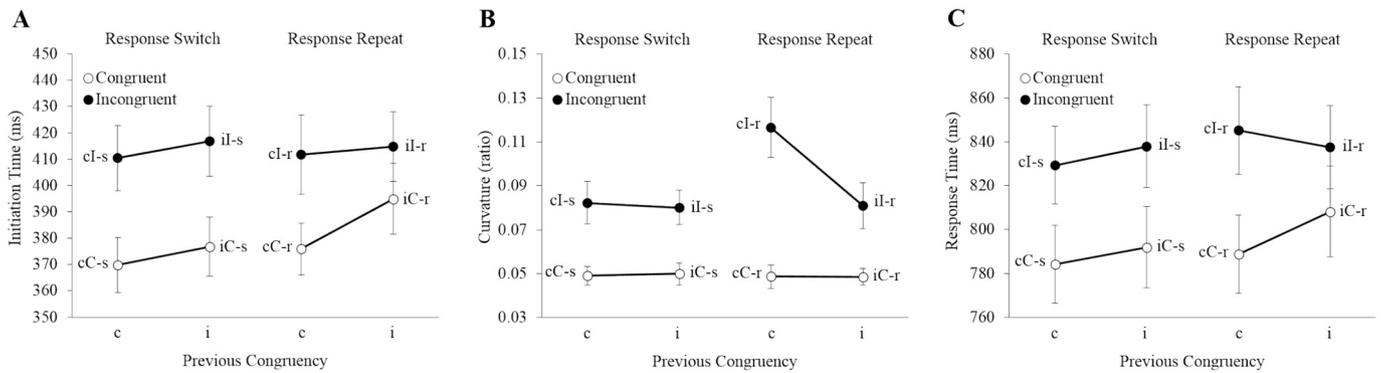
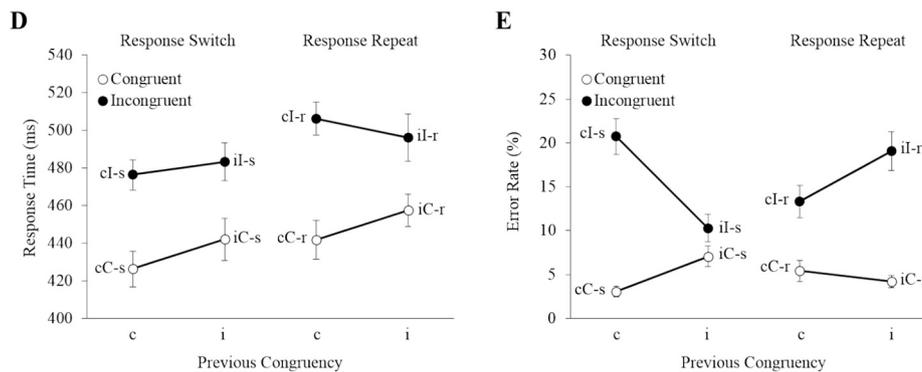## Current Study – Behavioral Results

Fig. 1. The pattern of trial sequence effects observed in (A) initiation times, (B) reach curvatures, and (C) response times by Erb et al. (2018). The pattern of trial sequence effects observed in (D) response times and (E) error rates in the current study. Error bars display standard errors. The pattern of effects observed in response times in the current study and in the study of Erb et al. matches the pattern of effects observed in button-press response times in previous investigations of the flanker task (e.g., Mayr, Awh, & Laurey, 2003; Nieuwenhuis et al., 2006).

presented the same pattern of effects observed in single-unit recordings of the dACC in alert human participants completing a button-press version of a Stroop-like conflict task (Sheth et al., 2012): cC < iC < cI < iI.

Although the results of Erb et al. (2016) present some evidence that the behavioral dynamics observed in hand movements can be linked to neural dynamics, ideally researchers would be able to target the neural dynamics associated with the threshold adjustment process and the controlled selection process within the same task and participants. Given that collecting single-unit recording data from alert human participants is quite uncommon, invasive, and expensive, and given that fMRI lacks the temporal resolution necessary to track rapid threshold adjustments, neither of these techniques are ideally suited to target the two processes simultaneously. EEG, on the other hand, presents a high temporal resolution and sensitivity to canonical neural computations offering novel insight into the dynamics of cognitive processing. In contrast to reach tracking, EEG also enables researchers to investigate a multitude of processes leading up to and following an overt behavioral response.

Candidate EEG events related to threshold adjustment include the stimulus-locked N2 component, a fronto-central response that is specifically enhanced by response conflict ~250 ms following stimulus presentation (Folstein & van Petten, 2008; Yeung et al., 2004). The N2 has a spectral representation in the theta band (Cavanagh, Zambrano-Vazquez, & Allen, 2012), which is highly sensitive to conflict (Cohen & Donner, 2013), and has previously been linked to an increased decision threshold in the context of drift diffusion modeling (Cavanagh et al., 2012). Response-locked activity prior to action selection may also offer an index of conflict at the motor cortex; such activity has been observed

early in the Lateralized Readiness Potential (LRP), an ERP component created by subtracting contralateral motor cortex areas (relative to the response hand) from ipsilateral motor cortex areas (Coles, 1989; Xu, Sommer, & Masaki, 2015). If the N2 or early LRP can be used to target the threshold adjustment process in a manner similar to initiation times in reaching tasks, then these components should reveal main effects of both current congruency (C < I) and previous congruency (c < i).

Candidate EEG events possibly linked to controlled selection are less readily apparent. P3 amplitude appears to reflect a domain-general decision process, suggesting that it may be a good candidate for the integration of control, sensory, and motor processes (O'Connell, Dockree, & Kelly, 2012; Verleger, 1997). Slow wave activities occurring after the P3 have also been shown to exhibit a sustained effect of conflict (West, 2003), including an interaction between current and previous congruency (cC = iC < iI < cI; Larson, Clayson, Kirwan, & Weissman, 2016) that has been proposed to reflect regulative control (i.e., the controlled selection process). If P3 amplitude or slow wave activity can be used to target the controlled selection process in a manner similar to movement curvatures in reaching tasks, then the measures should reveal an interaction between current congruency and previous congruency on response repeat trials but not response switch trials.

Finally, a number of EEG events should be directly related to the combined manifest RT outcome, including the Gratton effect observed in response repeat trials (see Fig. 1C). Similar to the domain-general final decision process indexed by P3 amplitude, P3 peak latency has long been directly associated with response times (Johnson, 1986). In addition, the LRP activities immediately preceding the response may be expected to faithfully reflect the motor cortex disinhibition directly

linked to responses, thus conforming closely to patterns observed in RT.

1.2. Linking behavioral and neural dynamics

In this study, we evaluate the extent to which the patterns of within- and cross-trial dynamics previously observed in reaching behavior are observable in the neural dynamics captured by EEG in a standard button-press version of the flanker task. If EEG features do reveal similar patterns of effects to those observed in manual dynamics, this would suggest that EEG can also be used to target the functioning of the threshold adjustment process (N2, pre-LRP) and controlled selection process (P3 amplitude, slow wave), which interact to elicit a combined output (P3 latency, LRP). If the patterns of effects observed in these features do not resemble the effects observed in reaching behavior, this would suggest that the behavioral dynamics observed in reaching movements might be uniquely well-suited for targeting the functioning of the threshold adjustment and controlled selection processes. Such a finding would also raise important questions concerning how future research might proceed in the effort to link the behavioral and neural dynamics of cognitive control.

2. Experiment

2.1. Participants

All participants gave written informed consent and the study was approved by the research ethics committee of the University of Arizona. All participants had normal or corrected-to-normal vision. Participants were awarded course credit for their participation. Data from these participants have been reported before in a study investigating Obsessive-Compulsive Disorder (Gründler, Cavanagh, Figueroa, Frank, & Allen, 2009). Note that only the group scoring under the clinical cut-off for obsessive-compulsive symptoms in the Obsessive-Compulsive Inventory (< 21) are reported here, resulting in the inclusion of 23 participants (12 males; $M = 19$ years, $SD = 0.78$). The average OCI-R score of these participants was 8.8 ($SD = 6.6$), a value consistent with previous research evaluating non-anxious controls from undergraduate populations (Foa et al., 2002; Hajcak, Huppert, Simons, & Foa, 2004).

2.2. Task

Participants completed a modified Eriksen flanker task (Eriksen & Eriksen, 1974). Ten blocks of 40 trials were presented, for a total of 400 trials. On each trial, participants were required to press one of two hand-held response buttons with their thumbs to identify the center letter in a string of five letters (e.g., by pressing the left button for the letter "M" and the right button for the letter "N"). Half of the trials in each block were congruent, with all five of the letters cueing the same response (e.g., "MMMMM" or "NNNNN"). The remaining half of the trials in each block were incongruent, with the center letter cueing a different response than the flankers (e.g., "NNMNN" or "MMNMM"). Different letter pairs were used for different blocks (E & F; I & T; N & M; Q & O; U & V). The target–hand mappings were reversed between consecutive blocks to increase response conflict.

Each trial began with a blank screen for 100 ms, followed by a fixation cross for 700 ms. The fixation was replaced with the flanker stimuli, which were presented 135 ms before the target letter to increase conflict. The whole string was presented for another 135 ms and was followed by a fixation cross for 600 ms. Participants had 1000 ms to respond; otherwise a negative feedback ("WRONG") was displayed for 500 ms.

The first trial of each block was excluded from analysis given that these trials were not preceded by another trial. To control for post-error performance adjustments (e.g., Danielmeier & Ullsperger, 2011), all error responses and trials following an error response were also excluded from analysis for each of the measures reported, as were any trials with an RT under 200 ms or a missed response.

2.3. EEG

EEG was recorded continuously across 0.1 to 100 Hz with a sampling rate of 500 Hz and an online CPz reference on a 64-channel Neuroscan system. Data were then epoched around the cues (−2000 to 2000 ms). Epochs were coded based on the congruency of the current and previous trial (cC, iC, cI, iI) as well as if they featured the same response as the previous trial (e.g., right-right) or the opposite response as the previous trial (e.g., right-left).

Cerebellar (CB) electrode sites were removed due to unreliability, and data were re-referenced to linked mastoids, leaving 60 total EEG channels. Bad channels and bad epochs were identified using the FASTER algorithm (Nolan, Whelan, & Reilly, 2010) and were subsequently interpolated and rejected respectively. FASTER identifies artefacts based on 3 standard deviations of the absolute z-score of a variety of correlation and variance measures (see Nolan et al., 2010). Eye blinks and horizontal eye movements were removed following independent component analysis (ICA) (Delorme & Makeig, 2004). ICA components were algorithmically identified as potentially ocular if they were strongly correlated with vertical electroencephalogram (> 3 standard deviations from all absolute z-scored ICA component correlations). All algorithmic suggestions were verified by visual inspection of the ICA topography prior to removal.

All ERPs were filtered at 20 Hz and baseline corrected (−200 to 0 ms). Response-locked activities were then calculated by shifting each cue-locked epoch by the response time. Electrodes C3 and C4 were used to monitor motor cortex activities. The LRP was calculated as ipsilateral cortex electrode minus contralateral cortex electrode, where ipsilateral and contralateral were defined relative to the response hand. Major cue-locked components were defined as the mean activity over the following windows and electrodes: N2 (FCz: 275 ± 20 ms), P3 (Pz: 450 ± 150 ms), Slow wave (Pz, 700 ± 250 ms), additionally P3 peak times were quantified at the P3 window and electrode. Topographical plots are idiosyncratically scaled but zero centered and they show the difference of the mean activity for each of these components between experimental conditions. Response-locked LRP components were defined as the pre-LRP (−300 to −150 ms) and the LRP slope (−50 ms minus −150 ms). Figs. 2 and 3 present select ERPs as a function of current congruency (C vs. I) and response type (Switch vs. Repeat), respectively. Fig. 4 presents stimulus- and response-locked plots of the lateralized readiness potential.

2.4. Statistical analysis

The data were analyzed using a series of 2 (Previous Congruency: c vs. i) x 2 (Current Congruency: C vs. I) x 2 (Response Type: Switch vs. Repeat) repeated measures Analyses of Variance (ANOVAs). Given the strong a priori hypotheses based on Erb et al.'s (2018) findings and the large number of factors to interpret, we present the statistical results from our behavioral measures in Table 1 and the statistical results from our EEG measures in Table 2. While use of p-values to infer prior probabilities is statistically crude, the existence of a single prior study limits the utility of formal priors and the indication of the range of p-values does directly relate to statistical confidence given that all prior analyses were from a single repeated-measures sample. The data for this study are available at https://osf.io/t9w2r/?view_only=332784370e5248ad8d3c2b8ac55cf45a.

3. Results

3.1. Behavioral results

We first confirmed that that response times in the current study conformed to the same pattern of effects observed in previous
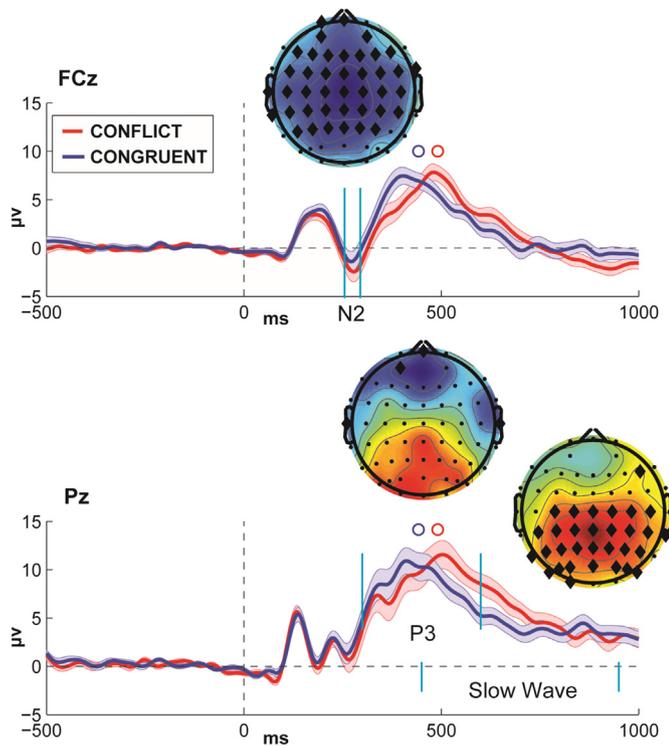
Fig. 2. Stimulus-locked ERPs split by conflict. Shading around the ERPs are ± SEM. Dots are average RTs. Vertical cyan bars reflect the analysis window. Topographical plots represent the conflict-congruent difference in this window; significant effects are indicated by large diamonds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Stimulus-locked ERPs split by response requirements between consecutive trials. Shading around the ERPs are ± SEM. Dots are average RTs. Vertical cyan bars reflect the analysis window. Topographical plots represent the switch-repeat difference in this window; significant effects are indicated by large diamonds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
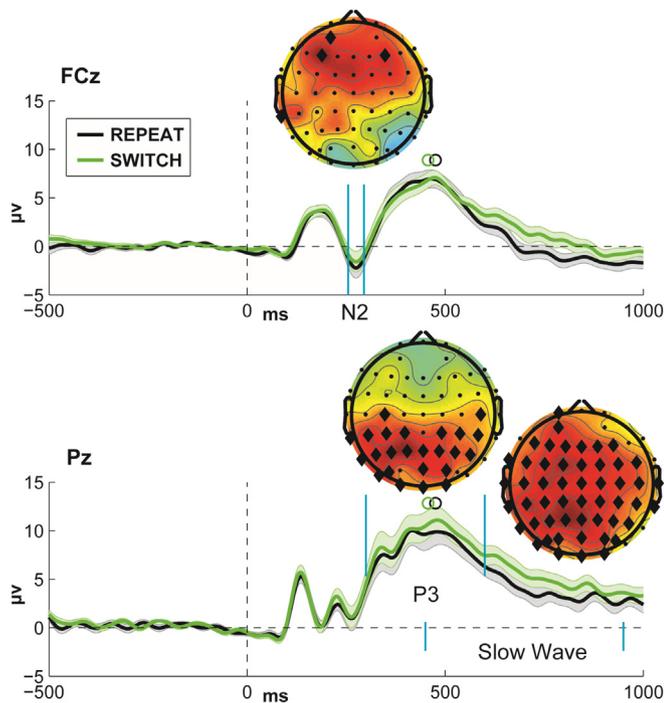
behavioral work with button-press measures. Consistent with the results of Mayr et al. (2003) and Nieuwenhuis et al. (2006), response times revealed main effects of Current Congruency (C < I) and Previous Congruency (c < i) on Response Switch trials, and a Gratton effect on Response Repeat trials (cC < iC < iI < cI; see Fig. 1D). These results confirm that the behavioral task used in the current study produced the same pattern of cross-trial dynamics observed in response times in the reaching task used by Erb et al. (2018), despite the difference in response modality.

Given that the error rates observed by Erb et al. (2018) in their reach-tracking version of the flanker task were at floor for adult participants (< 1%), we did not have a priori hypotheses for error rates. Error rates revealed a main effect of Current Congruency (C < I) and a number of interactions, including a three-way interaction between Previous Congruency, Current Congruency, and Response Type (Fig. 1E; Table S2 in the Supplementary materials). Higher error rates were observed on cI-s relative to iI-s trials and on iI-r relative to cI-r trials. This pattern of effects is consistent with the effects observed in response times, as cI-s and iI-r trials featured faster response times relative to iI-s and cI-r trials, respectively. These findings indicate that errors were more likely to occur on the trial types that featured relatively faster response times or that the exclusion of a higher number of trials featuring an error led to lower average response times on select trial types. Given that errors were unevenly distributed across the trial types, we performed two additional sets of analyses that equated the number of trials in each of the trial types by (1) identifying the condition with smallest number of trials and randomly removing trials from the other conditions until all epoch counts were identical and (2) including error trials along with accurate trials in the analyses. The results of these additional analyses are available in Tables S3 and S4 of the Supplementary materials and were substantially similar to the results of the primary analyses reported below.

3.2. Electrophysiological scalp data

3.2.1. Candidate components for threshold adjustment process

Next, we evaluated whether candidate EEG events possibly linked to the threshold adjustment process exhibited the same cross-trial dynamics observed in initiation times by Erb et al. (2018); namely, main effects of both Current Congruency (C < I) and Previous Congruency (c < i) (see Fig. 5A). N2 amplitudes were greater on Incongruent trials relative to Congruent trials (see Fig. 5B). The main effect of Previous Congruency did not approach significance ($p = .64$), indicating that the N2 failed to capture the pattern of effects linked to the threshold adjustment process in initiation times. Theta band power was also tested. Like the N2, it had a main effect for current congruency as well as a mix of findings with response type, but none of these outcomes provided additional support for the threshold adjustment process (see Supplementary materials).

Response-locked Pre-LRP amplitudes revealed a main effect of Current Congruency, with greater amplitudes on Incongruent trials relative to Congruent trials, and a main effect of Response Type, with greater amplitudes on Response Repeat trials relative to Response Switch trials (see Fig. 5C). This main effect of Response Type appears to be influenced by a long-duration slow shift in relative excitability between motor cortices (similar to the effect described later in stimulus-locked voltage across the scalp). The main effect of Previous Congruency did not approach significance ($p = .30$), indicating that Pre-LRP amplitudes also failed to capture the pattern of effects linked to the threshold adjustment process in initiation times.

3.2.2. Candidate components for controlled selection process

We then evaluated whether P3 and slow wave amplitudes exhibited the same cross-trial dynamics observed in reach curvatures by Erb et al. (2018); namely, a significant effect of Current Congruency on Response Switch trials and a significant interaction between Current Congruency
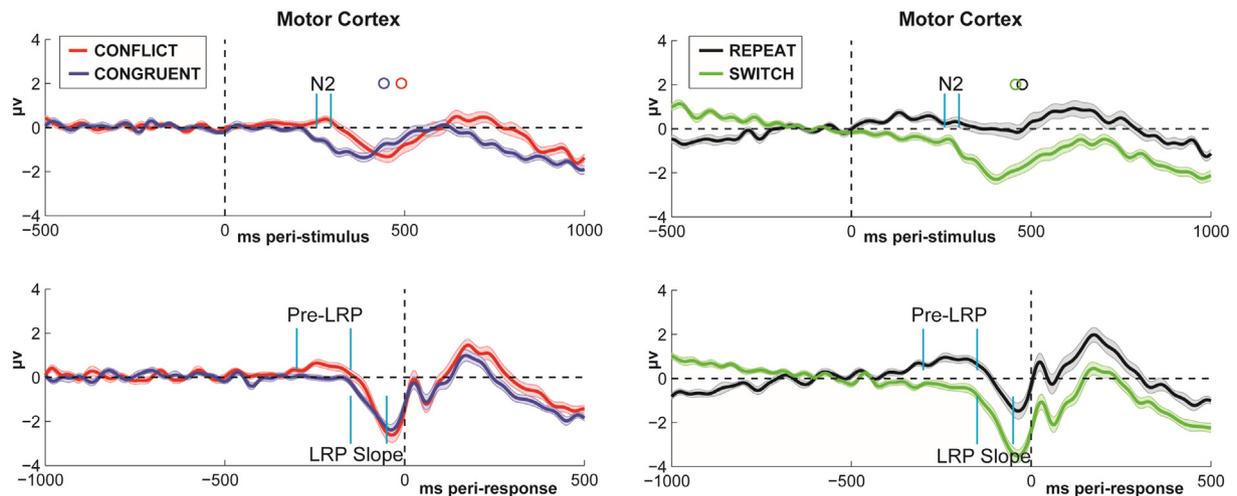
Fig. 4. Stimulus and response-locked plots of the lateralized readiness potential (LRP: contralateral motor cortex minus ipsilateral motor cortex). Shading around the ERPs are ± SEM. Dots are average RTs. Vertical cyan bars reflect the analysis windows. Conflict effects were expected in the response-locked Pre-LRP time window; this appears to overlap substantially with the stimulus-locked N2 time window which had a notable conflict-related modulation in the LRP. The slope within the LRP window was investigated as an index of motor readiness during response selection. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
ANOVA results from behavioral data. CI = current congruency, ci = previous congruency, SR = response type (switch vs. repeat).

		F	η_p^2	p	Predicted effect	Match?
Combined output						
Response time	CI	182.14	0.89	< .001		
	ci	8.27	0.27	.009		
	SR	16.76	0.43	< .001		
	CI*ci	13.55	0.38	.001		
	CI*ci*SR	3.47	0.14	.076		
Switch						
	CI	187.47	0.89	< .001	C < I	Yes
	ci	10.57	0.32	.004	c < i	Yes
	CI*ci	3.64	0.14	.069		
Repeat						
	CI	109.45	0.83	< .001		
	CI*ci	10.34	0.32	.004	cC < iC; iI < cI	Yes
Error rate	CI	56.88	0.72	< .001		
	CI*ci	9.33	0.30	.006		
	ci*SR	20.35	0.48	< .001		
	CI*ci*SR	59.96	0.73	< .001		
Switch						
	CI	52.17	0.70	< .001		
	ci	7.80	0.26	.011		
	CI*ci	59.87	0.73	< .001		
Repeat	CI	43.12	0.66	< .001		
	ci	14.83	0.40	< .001		
	CI*ci	14.41	0.40	< .001		

Note. dfs = 1, 22 for all analyses. All effects with p < .1 are displayed.

and Previous Congruency on Response Repeat trials, with no difference between cC-r and iC-r trials and a significant difference between iI-r than cI-r trials (cC-r = iC-r; iI-r < cI-r; see Fig. 5D). P3 amplitudes revealed a main effect of Previous Congruency, with greater amplitudes on trials preceded by a congruent trial relative to trials preceded by an incongruent trial (i < c), and a main effect of Response Type, with greater amplitudes on Response Switch trials relative to Response Repeat trials. Response Switch trials did not reveal a significant effect of Current Congruency (see Fig. 5E). The predicted interaction between Current and Previous Congruency on Response Repeat trials did, however, approach significance (p = .086).

Slow wave activity had main effects of Current Congruency and Previous Congruency on Response Switch trials, with greater amplitudes on Incongruent trials than Congruent trials, but smaller amplitudes on trials preceded by an incongruent trial relative to those preceded by a congruent trial (see Fig. 5F). Thus, the effect of Previous Congruency observed in slow wave activity (i < c) on Response Switch trials was the inverse of the effect observed in response times (c < i). On Response Repeat trials, late activity revealed the same pattern of effects previously observed in reach curvatures on Response Repeat trials by Erb et al. (2018), with significantly greater activation on cI-r than iI-r trials, but no difference between cC-r and iC-r trials.

3.2.3. Candidate components for combined output

Next, we evaluated whether P3 latencies and LRP slopes conformed to the same cross-trial dynamics observed in response times in the current study (Fig. 5A) and in Erb et al. (2018) (see Fig. 5G); namely, main effects of Current Congruency (C < I) and Previous Congruency (c < i) on Response Switch trials, and a Gratton effect (interaction between Current and Previous Congruency) on Response Repeat trials (cC < iC; iI < cI). P3 latencies revealed a main effect of Current Congruency alone, with longer latencies occurring on Incongruent relative to Congruent trials (C < I; see Fig. 5H). No effect of Previous Congruency was observed on Response Switch trials, p = .45, nor was a Gratton effect observed on Response Repeat trials, p = .47.

LRP slopes revealed a main effect of Current Congruency, with greater steepness on Incongruent trials relative to Congruent trials (C < I), and a main effect of Response Type, with greater steepness on Response Switch trials relative to Response Repeat trials (see Fig. 5I). LRP slopes also revealed the Gratton effect, as demonstrated by a significant interaction between Current Congruency and Previous Congruency. Consistent with our predictions, this Gratton effect was specific to Response Change trials. No effect of Previous Congruency was observed on Response Switch trials, p = .48.

3.3. Follow-up to novel findings of response switch effects

The simple act of switching from a left to right response (or vice versa) between trials elicited a surprisingly large, temporally extended, and spatially diffuse increase in amplitude in the P3 and slow wave time windows (Fig. 3). Since this effect begins at the same approximate time that the response occurs (~P3 peak), we examined response-locked plots split by Response Type (and Current Congruency for contrast), see Fig. 6. This a posteriori contrast revealed a punctate beginning to this large, temporally extended, and spatially diffuse amplitude deflection

Table 2
ANOVA results from EEG data. CI = current congruency, CI = previous congruency, SR = response type (switch vs. repeat).

		F	η_p^2	p	Predicted effect	Match?
Threshold adjustment process						
N2 amplitude	CI	14.46	0.40	< .001	C < I	Yes
	ci	0.22	0.01	.642	c < i	No
Pre-LRP amplitude	CI	28.48	0.56	< .001	C < I	Yes
	ci	1.13	0.05	.299	c < i	No
	SR	31.52	0.59	< .001		
Controlled selection process						
P3 amplitude	ci	10.73	0.33	.003		
	SR	7.36	0.25	.013		
Switch	CI	1.62	0.07	.217	C < I	No
	ci	12.94	0.37	.002	None	No
Repeat	CI*ci	3.23	0.13	.086	cC = iC; iI < cI	Trending
Slow wave amplitude	CI	17.78	0.45	< .001		
	ci	12.57	0.36	.002		
	SR	23.42	0.52	< .001		
	CI*ci*SR	4.74	0.18	.040		
Switch	CI	15.97	0.42	< .001	C < I	Yes
	ci	9.17	0.29	.006	None	No
Repeat	CI	8.23	0.27	.009		
	ci	3.34	0.13	.081		
	CI*ci	6.47	0.23	.018	cC = iC; iI < cI	Yes
Combined output						
P3 latency	CI	31.53	0.59	< .001		
Switch	CI	13.32	0.38	< .001	C < I	Yes
	ci	0.58	0.03	.453	c < i	No
Repeat	CI	12.67	0.37	.002		
	CI*ci	0.54	0.02	.469	cC < iC; iI < cI	No
LRP slope	CI	15.23	0.41	< .001		
	SR	5.33	0.19	.031		
	CI*ci	8.91	0.29	.007		
Switch	CI	5.33	0.19	.031	C < I	Yes
	ci	0.52	0.02	.478	c < i	No
Repeat	CI	3.34	0.13	.081		
	CI*ci	8.06	0.27	.010	cC < iC; iI < cI	Yes

Note. dfs = 1, 22 for all analyses. All effects with p < .1 are displayed.

beginning about 200 ms post-response. A posteriori analysis windows of 200 to 500 ms at FCz revealed a main effect of Response Type, $F(1, 22) = 35.81, p < .001$, as well as a main effect of Current Congruency, $F(1, 22) = 10.64, p = .004$. Interestingly, these appear to be different phenomena.

The Response Type effect observed in the stimulus-locked slow wave is observed in this response window, which is not surprising since these windows overlap considerably. However, the punctate beginning of this shift following the response suggests that this phenomenon may be triggered by post-motor adjustments. It remains unclear what this means, but the insight from the conflict-specific effect may help illuminate this finding. The conflict effect in this post-response time window was unexpected, and showed a greater negative deflection following conflict in frontal midline areas. This could be a candidate for a conflict-specific eligibility trace that alters pre-motor activities, particularly when experiencing upcoming conflict (e.g., a candidate mechanism for the Gratton effect). In contrast to this post-response pre-motor phenomenon, we examined cue-locked ERPs split by prior conflict (see Fig. S2 in the Supplementary materials) and found no evidence

for a slow wave modulation of neural activity between trials. Thus, this explanation for motor-locked plasticity linking trial-to-trial response conflict adaptations appears more plausible than a continuously occurring modulation of neural activity, which would be observed prior to the cue.

This interpretation of post-conflict pre-motor plasticity changes may help interpret the response switch effect in this same time window; it is possible that large-scale visuo-motor binding is continuously occurring following each stimulus-response presentation and that continuous switches constantly re-map this binding. Akin to the obligatory trial-to-trial adaptation observed in the Gratton effect, there may be a similar obligatory trial-to-trial adaptation of stimulus-response binding, each reflected by post-response amplitude deflections. This novel a posteriori hypothesis should be empirically tested.

4. Discussion

This report aimed to compare the latent behavioral and neural dynamics thought to reflect two dissociable processes underlying cognitive control in the flanker task; namely, a threshold adjustment process involving the inhibition of motor output and a controlled selection process involving the recruitment of top-down resources to support goal-relevant behavior. Although points of overlap did emerge between the behavioral dynamics observed in reaching behavior in previous research (Erb et al., 2018) and the neural dynamics observed with EEG in the current study, no simple one-to-one mappings were observed, suggesting that these techniques are differentially sensitive to the functioning of the processes. In the following, we discuss each of the proposed candidate EEG measures in turn.

4.1. Threshold adjustment

Candidate EEG measures of the threshold adjustment process did not contain any information about prior trial congruency and were thus only sensitive to trial-specific immediate pre-motor demands. This is in contrast to the single-unit recording measurements taken from neurons in the dorsal anterior cingulate cortex of humans (Sheth et al., 2012), which are characterized by enhanced firing rates on trials following conflict. These single neuron activities may reflect a simple hysteresis for the purpose of maintaining an eligibility trace of demand over time, but that effect is not present in the N2, theta band response, or early motor cortex activity.[3] However, enhanced single unit activity may contribute to the post-response adaptation to conflict observed in Fig. 5. These findings suggest a novel testable hypothesis: measuring movement initiation may be particularly effective for targeting the functioning of the threshold adjustment process, and may reveal a distinct neural signature in the EEG.

4.2. Controlled selection

In contrast to the response-specific N2 and Pre-LRP effects, P3 amplitude was specifically modulated by trial history (previous congruency and response type), but these main effects did not interact. The predicted interaction between previous congruency and current congruency on response repeat trials did approach significance in P3 amplitudes, indicating that this measure exhibits some degree of sensitivity to the controlled selection process. Later amplitude modulation of the slow wave appeared to accumulate the separate main effects contributing to P3 amplitude, coming much closer to faithfully reflecting the controlled selection processes observed by Erb and colleagues (Erb et al., 2016, 2018). Notably, slow wave amplitudes revealed the

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[3] Similarly enhanced single neuron activities in rodent have also been suggested to maintain the eligibility trace following errors (Narayanan & Laubach, 2008).
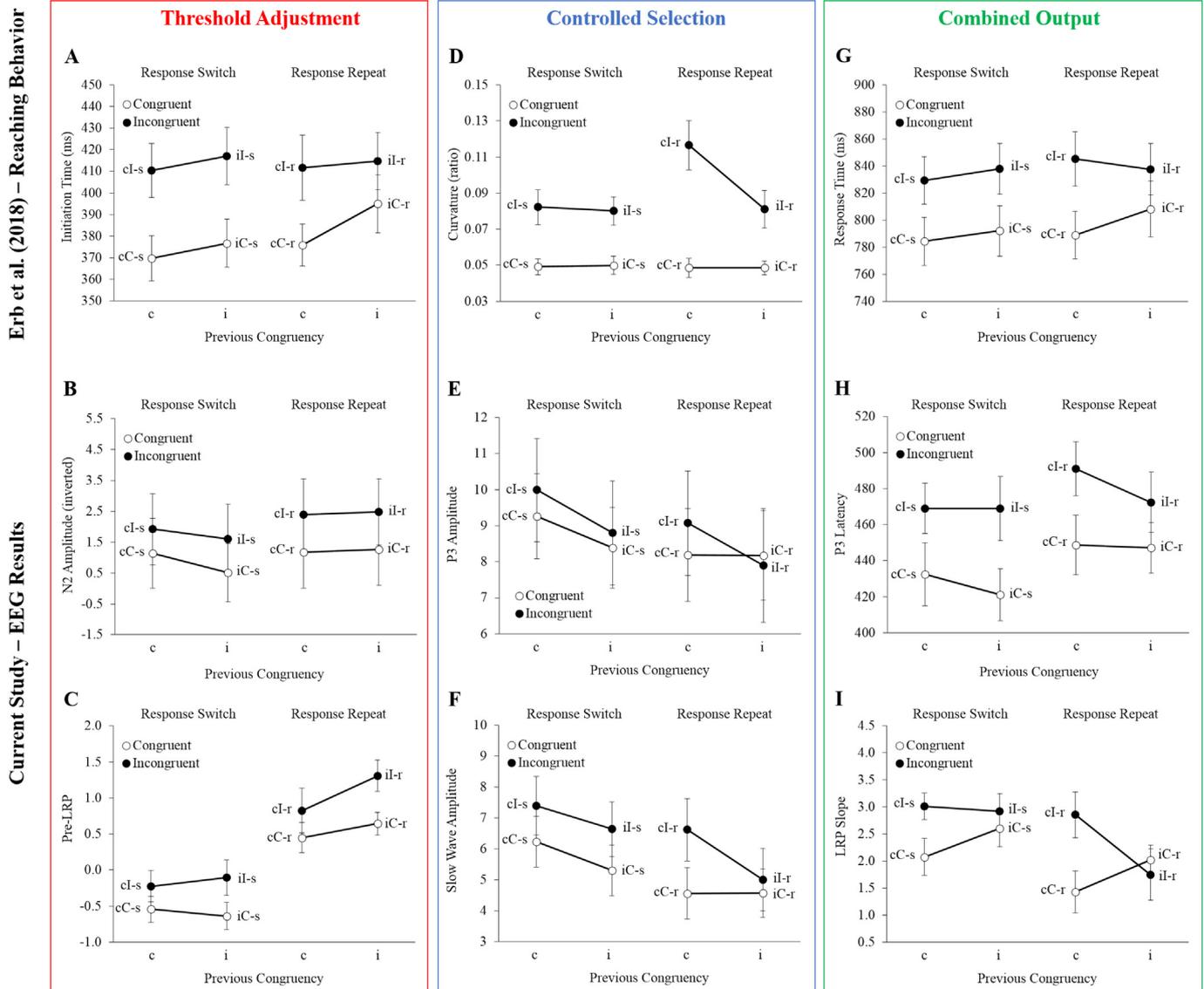
Fig. 5. Prior behavioral data from Erb et al. (2018) is presented in the top row as point of comparison with the EEG data presented in the bottom two rows. Colored columns indicate hypothesized similarity between latent constructs inferred from Erb et al.'s results and the measures of the current study. Error bars display standard errors.

predicted interaction between previous congruency and current congruency on response repeat trials, with no difference between cC-r and iC-r trials and significantly larger amplitudes on cI-r than iI-r trials. Although this interaction between previous congruency and current congruency has been observed in the slow wave previously (Larson et al., 2016), the effect has not been tied to the pattern of effects observed in reach curvatures. This novel theoretical extension provides a compelling avenue for understanding the significance of this often-overlooked EEG feature.

Both P3 and slow wave amplitudes also revealed major and unexpected main effects of response type (switch vs. repeat), wherein the simple act of switching from left to right responses (or vice versa) yielded globally increased amplitudes starting at P3 and evolving to nearly all sites later in time (Fig. 3). This is a surprisingly large and late effect for a response that has already been executed, suggesting that the interactive process reflected by slow wave activity is important for non-conscious trial-to-trial adaptations that may underlie obligatory sensorimotor learning.

The effect of previous congruency observed in P3 and slow wave amplitudes on response switch trials was unanticipated. It is possible

that the effect of previous congruency anticipated in N2 and Pre-LRP amplitudes may have instead manifest in P3 and slow wave amplitudes as the inverse of the effect observed in RTs on response switch trials. Although further research is necessary to test this possibility, such an interpretation is consistent with the conclusion that the reaching behavior and EEG measures appear to reflect latent processes differentially, suggesting layers of inference that are specific to each measure.

4.3. Combined output

The identification of EEG responses that faithfully reflect response times seems trivially simple and thus possibly unimportant, but the lack of perfect correspondence observed here suggests that even the most closely-linked EEG activities contain different information content than RTs. P3 latency was surprisingly uninformative, only providing a trial-specific indication of the largest RT effect: current congruency. The fact that this did not parallel the rest of the RT effects of trial history suggests that P3 latency is either too difficult to reliably quantify (a definite possibility) or that it reflects the combination of a multitude of different stimulus-response processes which may not separate along simple lines
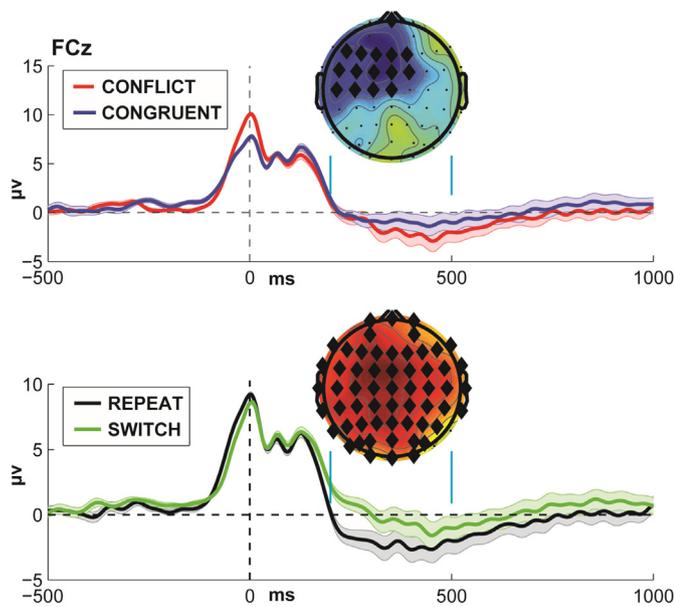
Fig. 6. Response-locked ERPs (FCz electrode) split by conflict or response requirements between consecutive trials. Shading around the ERPs are ± SEM. Vertical cyan bars reflect the a posteriori analysis window. Topographical plots represent the condition difference in this window; significant effects are indicated by large diamonds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of conflict and response repetition type (Verleger, 1997; Verleger, Grauhan, & Śmigasiewicz, 2016).

Even direct measurement of scalp activities related to relative motor activation (LRP slope) did not correspond to the full pattern of RTs observed here, given that LRP slopes failed to reveal a main effect of previous congruency on response switch trials. LRP was sensitive to current conflict with a large baseline shift due to response repeats or switches. Interestingly, the LRP also contained information about the congruency of the previous trial, faithfully reflecting the Gratton effect observed in RTs. This is particularly notable given the null effects of trial history observed in pre-motor (N2, Pre-LRP) conflict-specific processes.

4.4. Limitations and future directions

It is important to note that some of the predicted patterns of effects may not have been observed in the current study because the predictions were derived from the reaching task used by Erb et al. (2018) rather than the button-press task used in the current study. For example, neither of the candidate EEG measures of the threshold adjustment process revealed a main effect of previous congruency, raising the possibility that the threshold adjustment process described by Erb and colleagues may be enhanced (or perhaps only present) in reaching tasks. A number of considerations suggest that such a possibility is unlikely, however. First, the overall pattern of response time effects observed in the current study matched the pattern observed in reaching behavior by Erb and colleagues (including the main effect of previous congruency on response switch trials), indicating that the two behavioral tasks were fundamentally similar. Second, Sheth et al. (2012) observed main effects of conflict from the previous trial (c < i) and the current trial (C < I) in single-unit recordings of the dACC in a button-press task, indicating that the cross-trial dynamics proposed to reflect the threshold adjustment process can be detected by other neural measures in button-press tasks. There are also a variety of other candidate markers of latent control processes not investigated here. For instance, Fischer, Nigbur, Klein, Danielmeier, and Ullsperger (2018) recently described beta-band activities that correspond strongly with

drift diffusion parameters involved in controlled response selection. Interestingly, a recent study by Von Gunten, Volpert-Esmond, and Bartholow (2018) found that EEG features may habituate even though response time patterns remain stable. This finding suggests that effects of interest may fade over time in EEG measures, making it particularly difficult to target distinct patterns of effects underlying cognitive control.

Given the limitations associated with interpreting behavioral and neural dynamics from different tasks and participants, future research should seek to combine hand-tracking techniques (e.g., reach tracking or mouse tracking) with EEG. This would allow for EEG measures to be assessed in relation to events other than stimulus onset and response completion, including movement initiation or "changes of mind" in which individuals begin their movement in a manner characteristic of a reach to one target but subsequently redirect their movement to touch an alternate target (e.g., Erb & Marcovitch, 2018b; Resulaj, Kiani, Wolpert, & Shadlen, 2009). Such a combination of techniques could also enable researchers to evaluate the links among continuous movement parameters (e.g., velocity profiles) and unfolding EEG components. Although the simultaneous acquisition of behavioral and neural dynamics does raise important methodological and interpretational challenges (e.g., unwanted movement artefacts in EEG signals), the results of the current study highlight the promise of evaluating the links among behavioral and neural dynamics and underscore the importance of addressing these challenges.

5. Conclusion

This study aimed to bridge two research literatures that have remained largely isolated despite their shared focus on the dynamics of cognitive control: an extensive and well-established literature exploring the neural dynamics of control with EEG (e.g., Badzakova-Trajkov, Barnett, Waldie, & Kirk, 2009; Cavanagh, Cohen, & Allen, 2009; Cavanagh & Frank, 2014; Folstein & Van Petten, 2008; Gratton, Coles, & Donchin, 1992; Larson et al., 2014; Yeung et al., 2004), and a relatively smaller body of research targeting the behavioral dynamics of control with hand-tracking techniques such as mouse tracking (e.g., Incera & McLennan, 2017; Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011; Scherbaum, Frisch, Holfert, O'Hora, & Dshemuchadse, 2018) and reach tracking (e.g., Buetti & Kerzel, 2009; Erb et al., 2016, 2017, 2018; Erb & Marcovitch, 2018a, 2018b). We sought to identify the extent to which the cross-trial dynamics previously observed in initiation time, reach curvature, and response time in the flanker task (Erb et al., 2018) corresponded to the effects observed in established EEG measures. These measures failed to reveal a close correspondence with the cross-trial dynamics observed in initiation times, indicating that reaching behavior may be particularly well-suited for targeting the functioning of a threshold adjustment process involving motor inhibition. Slow wave amplitudes revealed a close correspondence with the pattern of effects previously observed in reach curvatures, indicating that this EEG component is sensitive to the functioning of a controlled selection process that supports goal-driven response selection. LRP slopes exhibited the closest correspondence to response times, revealing a significant Gratton effect in response repeat trials alone. Surprisingly large-amplitude effects of response repetition type are hypothesized to reflect obligatory stimulus-response adaptations, which may be similar, but still distinct from post-conflict adaptation in pre-motor areas. These and other hypotheses will be best tested by advancing beyond *status quo* tasks with limited degrees of freedom and examining EEG and behavioral dynamics concurrently in more naturalistic tasks.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actpsy.2019.02.004.

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