



Subthreshold muscle twitches dissociate oscillatory neural signatures of conflicts from errors

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ABSTRACT

We investigated the neural systems underlying conflict detection and error monitoring during rapid online error correction/monitoring mechanisms. We combined data from four separate cognitive tasks and 64 subjects in which EEG and EMG (muscle activity from the thumb used to respond) were recorded. In typical neuroscience experiments, behavioral responses are classified as “error” or “correct”; however, closer inspection of our data revealed that correct responses were often accompanied by “partial errors” – a muscle twitch of the incorrect hand (“mixed correct trials,” ~13% of the trials). We found that these muscle twitches dissociated conflicts from errors in time-frequency domain analyses of EEG data. In particular, both mixed-correct trials and full error trials were associated with enhanced theta-band power (4–9 Hz) compared to correct trials. However, full errors were additionally associated with power and frontal–parietal synchrony in the delta band. Single-trial robust multiple regression analyses revealed a significant modulation of theta power as a function of partial error correction time, thus linking trial-to-trial fluctuations in power to conflict. Furthermore, single-trial correlation analyses revealed a qualitative dissociation between conflict and error processing, such that mixed correct trials were associated with positive theta-RT correlations whereas full error trials were associated with negative delta-RT correlations. These findings shed new light on the local and global network mechanisms of conflict monitoring and error detection, and their relationship to online action adjustment.

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Introduction

Several cognitive control processes, including response conflict monitoring and error processing, rely on brain structures within the medial prefrontal cortex (Nachev, 2006; Ridderinkhof et al., 2004b; van Veen and Carter, 2006). Response conflict arises when multiple response options are activated and only one must be selected, whereas error processing occurs when an incorrect response is made. Some have argued that conflict and errors are processed by the same neural system (van Veen and Carter, 2006; Yeung et al., 2004), on the basis of cognitive models and similar topographical distributions of EEG during conflict and error trials, and spatially overlapping patterns of activation in fMRI studies (Ridderinkhof et al., 2004a). Others have argued that errors and conflicts are processed by different neural systems (Falkenstein et al., 2000; Swick and Turken, 2002) and may recruit somewhat dissociable spatial regions within the medial frontal cortex (Mathalon et al., 2003; Nee et al., 2011; Ullsperger and von Cramon, 2001).

Whether errors and conflict lead to the same neurocognitive process can be difficult to test empirically, because errors often occur when conflict is already present. Conflict, on the other hand, should be easier to isolate from errors. Typically, conflict effects are examined by comparing trials in which conflict is induced by the experiment with trials in which conflict is not induced by the experiment. This occurs, for example, in the Stroop task, when the word RED is printed in blue ink. A valid interpretation of condition differences relies on the assumption that subjects experienced response conflict in one condition and not in the other. Although there are clear behavioral condition differences that support this assumption—reaction times (RTs) are generally longer and error rates higher in conflict conditions—there is also thought to be conflict during conditions that supposedly contain no conflict (Coles et al., 2001), and there are fluctuations in cognitive control that affect how much conflict is experienced on each trial, depending on previous trial and other contextual events (Egner, 2007; Gratton et al., 1988). Thus, a more ideal way to test for conflict would be to measure it directly. One approach is to perform trial-to-trial brain-behavior analyses, wherein trial-varying brain activity is correlated with trial-varying RTs. However, RTs can vary across trials for a number of reasons unrelated to conflict, including general attention and other non-specific cognitive factors (Carp et al., 2011; Esterman et al., 2012; Weissman et al., 2006). Comparing

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brain activity-RT correlations between conditions helps minimize some of the general contributors to RT variance (Cohen and Cavanagh, 2011), but still, RT does not directly measure response conflict.

Here we sought to measure conflict more directly, and dissociate it from full errors, by recording subthreshold muscle twitches (measured via electromyography; EMG) from the thumbs that subjects used to indicate responses. The idea is that if the subject twitches the muscle of the incorrect hand but then pressed the correct button, then both responses were partially activated, but only one was fully engaged (Coles et al., 1995). This arguably provides a more accurate measure of endogenous conflict compared to averaging all trials in which the experimenter hopes that the subject experienced conflict. Furthermore, the EMG data provide a single-trial estimate of the amount of conflict experienced, as measured either by the time lag between the onset of the muscle twitch of the incorrect response and the onset of the muscle used to press the correct button (hereafter: correction time), or by the strength of the EMG response.

Subthreshold muscle twitches during correct trials are termed “partial errors” (Allain et al., 2009; Gratton et al., 1988). We here call the correct trials in which partial errors occur “mixed correct” (MC) trials, and contrast them with “pure correct” (PC) trials, in which only the thumb corresponding to the correct response was activated, and with “full error” (FE) trials, in which only the thumb corresponding to the incorrect response was activated. Without measuring EMG activity, subthreshold muscle twitches go undetected, and partial errors are classified as correct responses. Surprisingly few investigations have studied partial errors, although they are known to be slow (Coles et al., 1995; Szucs et al., 2009), elicit post-trial slowing (Allain et al., 2009), and elicit some electrophysiological activity associated with error processing (Burle et al., 2008; Carbonnell and Falkenstein, 2006; Endrass et al., 2008; Masaki et al., 2012). Partial errors have also been used to probe memory (Seymour and Schumacher, 2009).

EEG studies of brain circuits that support conflict and error processing typically focus on the error-related-negativity (ERN) or the stimulus-locked N2 (Nieuwenhuis et al., 2003; Yeung et al., 2004) or on a conflict-modulation of the correct-trial-related ERN (called the CRN). Others have highlighted that activity in a broad theta-band range (~2–8 Hz), maximal over midfrontal scalp sites (typically maximal at electrode FCz), increases with conflict and errors, correlates with RT, and predicts post-error adjustments (Cavanagh et al., 2009; Cohen, 2011b; Cohen and Cavanagh, 2011; Hanslmayr et al., 2008; Nigbur et al., 2011; Trujillo and Allen, 2007; Yordanova et al., 2004). In fact, although the error-related activity is often labeled as theta-band, visual inspection of time-frequency plots often suggests that the error-related activity extends lower, into the delta band (Yordanova et al., 2004). This might simply reflect frequency smoothing resulting from time-frequency decomposition (Cohen, 2014), or it could reflect the errors actually being processed by neural networks that operate in the delta band (Yordanova et al., 2004). This is an important distinction because different but temporally overlapping cognitive processes might be dissociable in frequency bands (Cohen, 2011b). In other words, a frequency-band dissociation between conflicts and errors would provide evidence in favor of distinct neurocognitive processes for conflict processing versus error processing. A time-frequency approach to EEG data is particularly well suited for making this distinction, because different neurocognitive processes that occur in the same brain region could produce distinct patterns of temporal-frequency dynamics, while producing the same or similar BOLD response and ERP (Cohen, 2011a). Indeed, it appears that much of the time-frequency power related to conflict and error processing is non-phase-locked (Nigbur et al., 2011), and is only weakly correlated with ERP indices of conflicts and errors (Cavanagh et al., 2012; Cohen and Donner, in press; Trujillo and Allen, 2007).

Thus, the purpose of this paper was to examine EEG oscillatory dynamics related to mixed correct trials (indexing conflict without errors) and full error trials (indexing a combination of errors and

conflict). We pooled data from four different experiments, including 64 subjects. The same analyses were applied to all datasets in order to highlight commonalities in conflict and error processing across a range of cognitive control and perception tasks (Riesel et al., 2013). Our analyses focus on features of time-frequency dynamics that have been observed in previous conflict and error studies, including frequency band-specific power, phase synchronization (a measure of frequency-resolved functional connectivity), and trial-to-trial correlations between EEG dynamics and behavior dynamics.

Methods

Subjects

Seventy-eight subjects from the University of Amsterdam community participated in these studies in exchange for course credit or 14 Euros. Each study was approved by the local ethics committee and subjects signed an informed consent document. Subjects had normal or corrected-to-normal vision and were self-reported free of neurological disorders and history of physical head trauma.

EEG data collection

EEG/EMG acquisition and analysis procedures were the same across all four studies. EEG data were acquired using at least 512 Hz from 64 channels placed according to the international 10–20 system, and from both earlobes. Electromyographic (EMG) recordings were taken from the flexor pollicis brevis muscle of each thumb using a pair of surface electrodes, placed on a subject-by-subject basis approximately 5 mm apart on the thenar eminence. Offline, EEG data were high-pass filtered at 0.5 Hz and epoched from -1.5 to $+2$ s surrounding stimulus onset of each trial. All trials were visually inspected and those containing facial EMG or other artifacts not related to blinks were manually removed. Independent components analysis was computed using eeglab software (Delorme and Makeig, 2004), and components containing blink/oculomotor artifacts or other artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. All data were scalp Laplacian transformed prior to analyses (Kayser and Tenke, 2006). Scalp Laplacian is a band-pass spatial filter (effectively a high-pass spatial filter for 64 electrodes) that minimizes volume conduction by removing spatially broad and therefore likely volume conducted activities. This approach has been validated for investigating inter-electrode synchronization (Srinivasan et al., 2007; Winter et al., 2007), and is an appropriate method for examining synchronization dynamics of large-scale cortical networks during error/conflict monitoring (Cohen, 2011b; Nigbur et al., 2011; van de Vijver et al., 2011). The units of the data after this transform are $\mu\text{V}/\text{cm}^2$, although time-frequency power data here were converted to decibel (see below).

Tasks

Data from four tasks were pooled together. In Task 1 (Cohen and van Gaal, 2013), subjects performed a visual discrimination task in which they had to report whether a briefly presented target stimulus was a square or a diamond by pressing a left or right response button (counterbalanced across subjects). The target (17 ms) was followed by a metacontrast mask (200 ms, 67 ms after target offset). Auditory performance feedback was given at button press. Tones were presented on both correct and error trials, and the mapping of tone pitch to correct/error was counter-balanced across subjects. The inter-trial-interval was fixed at 1017 ms. In Task 2 (Vissers et al., 2013), subjects performed a color-motion variant of a Simon task, in which a dot kinetogram with low-coherence moving blue or green dots was presented. Subjects responded to motion direction or dot color in blocks of trials, signaled by instructions. Conflict arises when, for example, blue dots that require a right-hand response are moving leftward.

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