

Modulation of somatosensory cortex underlying error compensation in a
tactile speeded-response task

By

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Author's Declaration

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Abstract

There is a lack of empirical evidence that the dorsolateral prefrontal cortex (DLPFC) is exerting control over post-error selective attention adjustments. This is an error compensation mechanism that is hypothesized by the conflict monitoring theory of error processing.

Understanding the error detection and compensation system enables the easily detectable error-related negativity (ERN) EEG signal, which reliably occurs approximately 100 ms after an erroneous action/response, to be utilized in brain-computer interfacing (BCI) systems effectively. An error-aware BCI has many promising applications and advantages, including error mediation in critical tasks such as piloting, error tracking in training programs, as well as allowing more responsive interpretation of commands for disabled users.

This thesis focused on utilizing a speeded-response task in the somatosensory modality to determine whether sensory processing is modulated post error commission, specifically at the stages controlled by the DLPFC. Additionally, we investigated whether the ERN, cognitive control, and temporary behavioural adjustments are linked. We hypothesized that a customized version of the flanker task that applies vibrotactile stimuli could effectively generate the ERN and characteristic post-error behavioural adjustments; and that the early somatosensory event-related potentials (ERPs) will be modulated in post-error trials compared to post-correct trials; additionally, larger ERNs would correspond to a greater degree of modulation and greater reduction of interference in post-error performance. The current results demonstrate that error commission does induce a clear modulation of early somatosensory processing components, which reflect the DLPFC's influence of spatial selective attention. Furthermore, this effect is conditional on the interpretation of error: ambiguity dampens the sensory cortical modulations.

Subject-wise correlations showed that in the pre-error state, the size of somatosensory ERPs did not predict performance, but post error commission, the temporarily modulated P100 amplitude became correlated with individual performance. Furthermore, post-error P100 amplitudes correlated with participant ERN amplitudes. The degree of *change* in performance following error commission, however, only correlated (in one aspect) with individual ERN size, and not with the selective attention related signals. These findings suggest that perhaps error detection circuits directly induce some compensatory adjustments onto the current behaviour; while it also recruits the DLPFC, which heightens optimization of selective attention and influences the general strategy to the task.

In general, the combined paradigm of speeded-response flanker task and vibrotactile discrimination task was an effective method to probe the error system. There is potential for more trends to be detected, which could be achieved with a larger participant group, for example, by dividing data into subgroups based on individual compensatory strategy.

In addition to providing support to theories of error processing, a directly utilizable finding of the current study is that people cannot effectively compensate for errors if the circumstances are ambiguous, even if internal error detection was successful. Hence, if a BCI training tool monitors the ERN, it can enhance the user practice experience by explicitly displaying parameters and highlighting errors as they occur.

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List of Abbreviations

BCI	Brain-computer interfacing
cTBS	Continuous theta burst (transcranial magnetic) stimulation
DLPFC	Dorsolateral prefrontal cortex
EEG	Electroencephalography
ERN	Error-related negativity
ERP	Event-related potential
fERN	Feedback error-related negativity
PEBA	Post-error behavioural adjustment
PERI	Post-error reduction of interference
PES	Post-error slowing
PIA	Post-error improvement in accuracy
rERN	Response-locked error-related negativity
SI	Primary somatosensory cortex
SII	Secondary somatosensory cortex

Introduction

Over the last 20 years a huge amount of experimental evidence has revealed the human error processing system to be complex and involving/affecting a multitude of functional systems such as motor preparation, sensory processing, and reward/expectation handling. Furthermore, the error system generates a clear electrophysiological marker of error detection, the error related negativity signal (ERN), that associate with (if not predict) subsequent adjustments invoked by the error system. For the emerging field of brain-computer interfacing (BCI), the ERN offers a reliable and prompt means to detect user erroneous operation, or recognition that the computer has misinterpreted a command. This offers an unparalleled means/opportunity to circumvent negative consequences of operator error in critical scenarios (such as aircraft piloting). However, proper utilization of the ERN will rely on knowledge of the conditions that trigger the signal and its properties. Equally importantly, a highly responsive BCI application should be designed with anticipation of how other aspects of cognitive/sensory/motor processes are affected during the period after error occurrence. This includes which regions are invoked by error compensation mechanisms, how those regions then affect downstream motor and sensory processing areas, and the behavioural implications.

What has been shown in literature is an increase in dorsolateral prefrontal cortex (DLPFC) activity in post-error trials, and in some studies, direct correlation with the degree of certain post-error behavioural adjustments. Also in the literature are findings of down-regulations in motor regions and task-relevance based modulations in sensory encoding areas; these activation changes correlated with specific forms of behavioural adjustments such as post-error slowing, and post-error reduction of interference. Such evidence support theories of error processing -- the conflict monitoring theory, in particular, postulates that the anterior cingulate cortex (generator

of ERN) recruits the DLPFC to exert cognitive control to help reduce motor excitability, and improve attentional focus on relevant stimuli and suppress irrelevant/distracting stimuli. There is specifically a lack of empirical data that fully substantiate the chain of links between the ERN, DLPFC activation, differential modulation of sensory input, and post-error reduction of interference; as the indirect evidence and theories would suggest.

The purpose of the current study was to find more evidence of the theorized mechanisms via an error investigation using somatosensory inputs. Early processing of tactile stimuli in particular can be monitored at high temporal resolution as event related potentials (ERPs) via electroencephalography (EEG). Characteristics of the ERPs (e.g. latency, amplitude) are easily quantifiable indicators of sensory cortex modulation. More importantly, there exist in depth literature on the role of the DLPFC in somatosensory selective attention and how it is reflected in ERP modulations (detailed in Section 2.7.2). Hence, the current study sought the specific modulations that are known to implicate the DLPFC post error commission, and any correlations with subsequent performance changes. The findings of this thesis would help elucidate error compensation mechanisms, and inform future researchers the utility of the tactile domain and somatosensory ERPs for error research.

Chapter 1: Review of relevant literature

1.1 Electroencephalography and event related brain potentials

In general, electroencephalography (EEG) is a brain imaging technique that detects cortical electrical activity at electrodes distributed on the scalp. When many post synaptic potentials occurring at apical dendrites of pyramidal cells are synchronized, of common orientation, and in close proximity, the ionic currents across the cell membranes generate voltage fluctuations that are large enough to reach the scalp surface (Misulis & Head, 2003). EEG is less effective for detecting activity in deeper structures, and gives poor spatial resolution when compared with imaging techniques such as fMRI. It does however provide high temporal resolution measurements, which are useful for evaluating fast consecutive stages in the sensory information processing and motor preparation pathways.

Event related brain potentials (ERPs) are positive and negative EEG components (peaks) that occur at relatively predictable time delays before or after an event, such as after perceiving external stimuli, after committing an error, or before generating an action (Luck, 2005). Sensory ERP components reflect information processing/association stages that the sensory information travels through. Stimuli in different modalities generate different characteristic ERPs; this thesis focuses on analyses of somatosensory ERPs and the error related negativity signal (detailed in Section 2.2).

Somatosensory inputs, in particular from cutaneous mechanoreceptors, travel through the dorsal column-medial lemniscal pathways to reach the thalamus, which relays the signal to the primary somatosensory cortex (SI) for processing, which passes signals to association areas including secondary somatosensory cortex (SII) for higher level processing such as recognition and discrimination. EEG recordings over central to parietal lateral regions typically reveal the

following somatosensory evoked potentials: P50, N70, P100, and N140. (The letters denote polarity and numbers denote approximate delay from the stimulus event in milliseconds). The P50 and N70 are believed to represent SI activation and are influenced typically by attributes of the external stimulus, the P100 is SII related, while the N140 likely has many generators; the P100 and N140 can be more significantly influenced by top-down control, such as spatial selective attention (Desmedt & Tomberg, 1989).

1.2 Error related negativity

The electrophysiological indicator of error commission is an ERP known as the error related negativity (ERN). In order to utilize the ERN in an application, it is necessary to understand the conditions under which it is generated. This section describes how the ERN is commonly observed/elicited under experimental conditions, as well as its localization, which is significant to proper capturing of the signal. Studies have shown that the amplitude (and in some cases latency) of the ERN is influenced by many experimental parameters. These are reviewed to facilitate interpretation of the ERN, as well as shed light on a complex underlying error detection mechanism.

1.2.1 Eliciting the rERN

The classic ERN, also known as response-locked ERN (rERN), is generated in frontal central sites when a person commits a simple error / slip: the individual must know the correct response for a given stimulus, yet make an unintentional response, to elicit the clearest rERN (Scheffers & Coles, 2000). Hence rERN experiments often involve speeded-response tasks to rush the subjects to commit “slips” (distinguished from “mistakes” where a person followed an erroneous intent). The rERN typically onsets with the EMG of the erroneous motor response and

peaks 100 ms after, and is isolated in EEG by time locking to response onset (Gehring et al., 2012). Since the rERN occurs for a variety of tasks, the signal may coincide with different EEG activity related to task performance itself. To overcome this issue studies frequently work with the difference wave obtained by subtracting error trial signals from correct trial signals (Dehaene et al., 1994; Nieuwenhuis et al., 2001).

Several studies have found a correlation between rERN amplitude and the severity of the error commission. Burle et al. (2008) and Vidal et al. (2000) observed larger rERN in trials with greater amplitude of the error EMG. Although the direction is not conclusive as Gehring et al. (1993) found smaller error force associated with larger rERNs.

The rERN appears affected by the consequence of the error. According to Hajcak et al. (2005), trials with 5pt rewards yielded smaller rERNs than 100pt rewards. Consistently Gehring et al. (1993) and Ganushchak & Schiller (2008) observed larger rERNs in cases with bigger penalties/rewards respectively. This effect extends even to non-tangible error consequences, demonstrated by Hajcak et al. (2005), where subjects produced larger rERNs when told their performance was being evaluated online by a research assistant and compared to others.

In varying ways rERN amplitude correlates with the amount of similarity between error and correct responses. Bernstein et al. (1995) represented four responses with two fingers on each hand, and reported that wrong finger with wrong hand responses gave the largest rERN. However, when Gehring & Fencsik (2001) represented four responses with two hands and two feet, the wrong side plus wrong limb responses gave the smallest rERN.

Additionally the rERN is influenced by subject certainty of the correct response. Scheffers & Coles (2000) found that by reducing visibility of the stimuli, rERN amplitudes were smaller as subjects were more unsure of their correctness. Consistent with these findings,

Holroyd & Coles (2002) showed that for a probabilistic learning task, as subjects learned the stimuli-response mapping the rERN amplitudes became larger.

In terms of the underlying detection mechanism, error investigations reveal that it is highly generic. Most notably, Luu et al. (2000) found that when both error trials and late response trials (missed deadline) were treated as failed trials, the late responses generated rERNs even if correct. This indicates that the definition of error is highly adaptable, including temporal criteria.

It has been repeatedly shown that the rERN can be elicited regardless of modality of stimuli: a variety of visual cues (Dehaene et al., 1994; Gehring et al., 1993; Nieuwenhuis et al., 2001), auditory words (Falkenstein et al. 1991), tactile position discriminations (Forster & Pavone 2008) etc. As well, the rERN characteristic is consistent across different modalities of response (though in some cases requiring the difference wave method), including bimanual finger response (Bernstein et al., 1995), use of feet (Gehring & Fencsik, 2001), eye movement (Nieuwenhuis et al., 2001), even verbal response of the colour in a Stroop test (Masaki et al., 2001). Very interestingly, the rERN is generic over aware and unaware errors. Nieuwenhuis et al. (2001) performed an anti-saccade study aimed to investigate impact of error perception on the rERN, leveraging the subcortical nature of saccades that produced many unaware errors (according to subject report after each trial), and observed that the rERN occurs regardless of conscious error awareness. The rERN was not compromised here by uncertainty of error commission because subjects could perceive the stimuli clearly and knew the required action (but did not always know their own action). This result seems to suggest a subconscious error detection system.

1.2.2 Neurogenerator of the rERN

It is generally agreed that the rERN is generated in the anterior cingulate cortex (ACC). Dehaene et al. (1994) were able to find a single dipole solution in the ACC using BESA techniques that accounted for over 88% of data variance, for both numeric and semantic choice reaction-time tasks. fMRI studies generally support this result (Carter et al., 1998); some implicated additional structures, such as pre-SMA (Garavan et al., 2002); others isolated the source to the cingulate motor area (BA 24c', Ullsperger & von Cramon, 2001) and the rostral cingulate zone (Debener et al., 2005). Furthermore, when ACC is compromised the rERN becomes abnormal in unpredictable ways, e.g. groups with ACC lesions either always exhibit large rERNS or have no rERN at all (Stemmer et al., 2004; Swick & Turken, 2002); and when inhibitory rTMS was applied to the ACC, the rERN was attenuated as did the percentage of corrected errors (Rollnik et al., 2004). The dorsolateral prefrontal cortex, involved in higher error processing, did not prove to hinder the rERN when inhibited by rTMS in this study.

1.3 Post-error behavioural adjustments

The final output of human error processing is not the error signal (an intermediate stage) but corrective actions and strategic adjustments in subsequent trials. An accurate understanding of error processing systems should explain/predict these adjustments. This section reviews the known types of post-error behaviour changes, and how they are affected by task parameters. Three main forms of post-error behavioural adjustments (PEBA) have been observed: post-error slowing (PES), post-error reduction of interference (PERI), and post-error improvements in accuracy (PIA).

1.3.1 Post-error slowing and post-error improvements in accuracy

PES is perhaps the most investigated form of PEBA. In general, most error commissions, e.g. choice reaction time, go/no go, and extending to typing tasks (Crump & Logan, 2012); can exhibit significantly longer reaction times in the trial immediately following an error trial. Traditionally, PES was regarded as a sign of caution in order to improve performance (Rabbitt, 1981; review see Gehring et al., 2012). This interpretation is supported by concurrent occurrences of PES and PIA in experiments (Danielmeier et al., 2011; Maier et al., 2011; Marco-Pallarés et al., 2008), and Laming (1968) in particular showed both measures slowly return to study mean over several post-error trials. Though poorer performance (or lack of significant PIA) may also accompany PES (Carp & Compton, 2009; Dudschig & Jentsch, 2009; Fiehler et al. 2005; Hajcak et al., 2003; Houtman et al., 2012; King et al., 2010). It is therefore inconclusive whether the role of slowing is directly related to improving accuracy. In fact, PES and PIA may be independent and both depend on the duration of rest between trials (the response-stimulus interval (RSI)). Dudschig & Jentsch (2009) found that short RSIs of less than a half second gave rise to severe post-error slowing and a drop in post-error accuracy; while long intervals (half second and one second cases) reduced PES to minimal and resulted in superior rather than typical accuracy.

PES is affected in a complex manner by task conditions, giving insight to error processing/performance monitoring mechanisms. For example, Fiehler et al. (2005) observed that while a control group showed post-error speed and accuracy effects, the group instructed to correct errors exhibited none. The authors suggest that PEBA are absent when subjects perceive errors as acceptable. In fact, corrective action can result in post-error speeding (typing task by Crump & Logan, 2012). Importantly, Logan & Crump (2010) found that when typists were

unknowingly deceived by computer manipulation of typed words (to arbitrarily appear correct or erroneous), their PES behaviour still reflected real typos committed by the typist. This finding suggests an inner mechanism of error detection distinct from conscious perception is linked to PES. Another key characteristic of PES is that it only occurs when errors are the minority (Houtman et al., 2012; Notebaert et al., 2009). In colour discrimination tasks where overall accuracy rates were manipulated (75%, 55%, 35%), subjects exhibited post-error slowing, no slowing, and post-*correct*-slowing respectively. Hence the authors argued that PES is not related to error processing at all, but rather an orienting response to infrequent conditions. Taken together with other evidence however, PES is still a behavioural outcome of performance monitoring.

1.3.2 Post-error reduction of interference

PERI is associated with experiments that have an interference effect. In protocols where the subject receives multiple concurrent stimuli (target and distractor), performance is typically worse on trials where the distractor contradicts the target (the incompatible/incongruent case), than when stimuli match each other (the compatible/congruent case). The difference in reaction time or error rate between compatible and incompatible cases constitutes the interference effect. For example, in a flanker task trial the flanking arrows may be identical to the central arrow or point the other way, causing slower and more erroneous responses in these trials. Simon tasks are also used to study interference effect (or Simon effect), where a single stimulus has multiple “dimensions” of information, and the irrelevant dimension is made to resemble a response choice. For example, subjects could be required to push a left vs. right button according to the colour of a visual cue, while the cue appears on the left or right side of the screen.

PERI, first described by Ridderinkhof et al. (2002), is the phenomenon that the interference effect is diminished temporarily after error commission. I.e. incompatible trials immediately post error have better reaction time or accuracy than typical incompatible trials. However, PERI is not observed in all error experiments, even when PES and accuracy effects occur (Carp & Compton, 2009). In an attempt to explain inconsistent PERI effects, Maier et al. (2011) isolated errors caused by the distractor stimulus from errors due to other causes (i.e. premature responding and motor failure). In this study, four response options are given in a flanker test with letters and symbols such that there is one correct choice, one matching the flanker, and two additional irrelevant choices. As the authors hypothesized, PERI was significant only post flanker errors, but not post random errors. They postulated that PERI, interpreted as enhanced attentional selectivity, took place only when errors are caused by its failure.

These results indicate that several distinct processes may occur after error commission: recovery from a performance anomaly (PES); focusing better on the target (PERI); and if conditions are conducive, improved accuracy in the next trial (PIA).

1.4 Theories on the error processing system

Having a significant volume of observations on a versatile error processing system, which involves detection (reflected by the ERN), correction, and compensation (reflected by PEBA), researchers have consolidated these data into several contending models/theories.

1.4.1 Error comparator theory

According to the error comparator theory, errors are detected by comparing an efference copy of the actual response with the correct response that is determined by continued processing of an input stimulus. This theory implies that errors occur upon impulsive acting, and that further

opportunity to perceive the stimulus will aid error detection and correction, which are supported by empirical evidence (Dudschig & Jentsch 2009; Rabbit & Vyas 1981; respectively). The concept of using an efference copy is based on the short latency of the rERN, approximately 100 ms post response, which is too quick for peripheral/sensory feedback. The ACC is suggested to function as a comparator and output an error signal when a mismatch is detected. Coles et al. (2001) theorized that the rERN is generated upon the arrival of the error signal to the remedial action system, while Falkenstein et al. (2000) suggested the rERN could represent the comparison process itself – in order to explain the correct response negativity (CRN, a small rERN like peak that occurs on correct trials). The former idea is still feasible however if the CRN represented the completion of the comparison process but is below threshold for activating remedial systems.

The error comparator theory has the criticism that if the brain already knows the correct response at the time of muscle activity onset, then why not execute it? As well, the rERN as the trigger to all remedial action is challenged by the finding that the lateral readiness potential (an ERP believed to reflect motor preparation) of error correction movements tends to occur before or asynchronous to the rERN itself (Rodriguez-Fornells et al., 2002).

1.4.2 Conflict monitoring theory

The conflict monitoring theory is more computationally elaborate and differs significantly from the comparator theory on how errors are detected. The conflict model theorizes that the ACC merely detects conflict between competing responses (not knowing which is correct), and if this conflict continues – and exceeds a threshold – after the response is made, then an error has occurred. This is because by the time a response is made, the output of stimulus processing should be sufficiently accurate, thus if this output and the actual response are still

conflicting, then the executed response must have been in error (Yeung et al., 2004). The essential model is composed of several logical layers: an *input layer* (with units to represent each stimulus), a *response layer* (with units to represent each response alternative), and a *conflict monitoring unit*, which computes conflict as the Hopsfield energy due to any co-activations in the response layer (Botvinick et al. 2001). Additionally, the model includes an *attention layer* or a *response priming layer* depending on simulation purpose. The attention layer excites/inhibits units in the input layer depending on stimulus relevance, while the response priming layer can prime the response layer to adjust speed-accuracy trade-off. Proponents of the conflict monitoring theory emphasize the evidence that the ACC is active for general conflict situations (e.g. response override, underdetermined responding) as well as error processing (Botvinick et al., 2004). The theory also incorporates the concept that detection of conflict in the ACC could serve as a trigger to more cognitive control from prefrontal areas, which would reduce conflict and improve performance on following trials. Accordingly, Kerns et al. (2004) showed that on both error & incongruent correct trials ACC activation will heighten, and lead to subsequent trials with increased DLPFC activation, proportional behaviour adjustments, and less ACC activation. The theory could also justify a relevant finding by Gehring & Knight (2000), where damage to PFC causes the rERN to appear on correct trials. Cohen et al. (2000) provided an explanation that since PFC suppresses distractor stimuli via selective attention, when it is hindered the distractor related responses will be more active and persist after a correct response has been made, inducing a rERN. In general, Yeung et al. (2004) were able to match simulation results to various empirical observations, e.g. larger rERN on congruent errors (Scheffers & Coles, 2000), trends for accuracy vs. speed conditions on the rERN (Gehring et al., 1993), even the contradictory correlations of error force vs. rERN size in these two studies; and Botvinick et al.

(2001) were able to match simulation results to Laming (1968) where lower error rates and slower reaction time occurred after errors, which slowly drifted over next trials toward the study mean.

Challenges to this theory include: Burle et al. (2008) found corrective EMG that occurred slower (i.e. has less temporal overlap/conflict) to produce larger rERNs. Bernstein et al. (1995) reported that erroneous actions more dissimilar to the correct action (e.g. both hand and finger choices were incorrect – this is lower conflict from a motor command perspective) produced larger rERNs. Lastly the conflict monitoring model does not justify the CRN (Yeung et al., 2004).

1.4.3 Reinforcement learning theory

The reinforcement learning theory of the ERN (RL-ERN) aims to explain both the rERN and the fERN, which is a negative ERP that occurs upon receiving error feedback (typically in tasks where the correct choice is unknown at time of action, such as gambling). This model consists of two large components: a *task module* (“actor”), and a *monitoring module* (“critic”).

Holroyd et al. (2005) described the computational model in detail with respect to a flanker experiment with unequal target frequency of 4:1 ratio, and equal (50%) probability of flanker congruence. In this implementation the task module has four layers: *perception* (to encode stimuli), *categorization* (to identify stimuli), *response* (to activate the response mapped to the identified stimulus), and *attention*. The attention layer contains two types of units: *attention-perception*, which modulates the perception layer based on stimulus relevance, and *attention-response*, which modulates the response layer based on likelihood of response occurrence (creating response biases based on stimulus frequency). Errors are predicted to occur in two ways: when a response-bias-heightened response unit, coupled with noise, crosses threshold before stimulus processing was complete; or when an incongruent flanker generates a response

before this irrelevant stimulus is inhibited by attention-perception. Both predictions matched experiment data: for the infrequent target, errors occurred much earlier than correct responses, due to impulsive responding with bias; for the frequent target, errors occurred in the middle of a dual peak of correct response latencies (after the impulsive responses, and before proper stimuli processed responses).

The monitor module has three layers: *state*, *value*, and *temporal difference* (TD). The state layer has units to detect and represent every possible stimulus, response, and feedback alternative, more importantly, units to represent every stimulus-response combination. The value layer contains corresponding units, and assigns a value to each combination depending on how favourable that scenario is for the organism. In the value layer, when an incorrect stimulus-response combination is active, a negative value is output to indicate an error. The TD layer finally compares the current value to the previous and outputs a rERN/fERN if a negative change occurs. And the compensatory adjustment of PES is achieved when the ERN signal reduces the connection strength between attention-response and response layers, thus lowering the impact of response bias. (Note this does not explain PES in protocols with equal stimulus frequency across different targets.) Computational results matched the experimental finding that errors on the frequent target produced larger ERNs and longer PES.

Physiologically, the RL-ERN theory suggests the monitoring module lies in the basal ganglia and the ERN is the disinhibition of motor neurons in the ACC, via the TD signal that is transmitted by the mesencephalic dopamine system. This idea is somewhat supported by e-amphetamine's enhancement on ERN size (de Bruijn et al., 2004), and reduction effect of alcohol on ERN size (Ridderinkhof et al., 2002).

1.4.4 Comparison

In summary, the models differ in a few key areas: how errors are detected, what ERNs are, and how the signal is utilized. For error detection, the comparator and conflict models both work with response presentations: comparing correct response and actual response, or detecting competition between several contending responses, respectively. The RL-ERN model instead works with both response and stimulus information to evaluate if the right combination is occurring. As for the purpose of the ERN, in the comparator model the signal is the amount of mismatch between correct and actual responses; in the conflict model, the degree of conflict between contending responses; and in the RL-ERN it is any negative change in the merit of ongoing events. Generally however, the ERN appears linked to the degree of error in all three models. Regarding the utility of the signal, the latter two theories are more specific: the conflict monitoring theory predicts the ERN reduces priming of all response units to adjust speed-accuracy trade-off, as well as signals DLPFC to improve focusing of attention and reduce influence of distractors, while the RL-ERN theory predicts the ERN proportionally reduces excitation on specific response units to decrease response biasing.

1.5 Interactions between ACC and DLPFC

As the ACC is the generator of the rERN and the DLPFC is associated with error compensation (in theory and by some empirical evidence), it is helpful to consider their relationship. The ACC, particularly the cingulate motor areas, is sometimes considered a pre-motor region due to its projections to the motor cortex and spinal cord (Gates & Goldman-Rakic 1993). As well, reciprocal connections exist between cingulate areas and prefrontal areas (including BA46 and BA9). The influence of arousal and drive state also reaches the ACC due to

afferents from midline thalamus and brainstem nuclei (Paus 2001). Hence the cingulate motor areas can serve as an interface between sensorimotor, executive and limbic systems (Habas 2010).

Both the ACC and DLPFC are suspected to be involved in managing response competition, which may arise from distracting stimuli features (e.g. flanker and Stroop tasks), explicit priming via cues/secondary stimuli features (e.g. Simon tasks), or subliminal priming that bypasses conscious processes. Some studies have observed clear division of responsibility between the two regions: MacDonald et al. (2000) reported only a DLPFC activation difference after cues indicating high vs. low attention demands, and only an ACC activation difference between congruent vs. incongruent targets.

1.6 Neurocorrelates of PEBA

Recent PEBA literature offers new evidence on the exact mechanism underlying the behavioural adjustments. This section reviews these findings and implications to the error processing models, as well as highlights the aspects that require further investigation.

King et al. (2010) aimed to determine whether post-error adjustments in control by the LPFC is achieved by suppressing motor responses, or by redirecting attention to relevant features. The study applied a Simon task of distinguishing the gender of faces presented on either side of the screen. The authors found both a reduction of activity in medial motor structures (SMA, paracentral lobule, bilateral SMC), as well as elevation of activation in task relevant sensory area (bilateral fusiform face area (FFA)). The two modulations however, appeared independent, as did the PEBA measures. Subjects fell into two groups exhibiting either more PES or more PERI. The former, labeled “slowers”, showed reduced SMC activity but negligible FFA modulation;

and the latter “speeders” (who maintained or increased reaction time following errors), showed increased FFA activation and no SMC changes. The authors suggested that people adopted either a proactive / early selection, or reactive / late correction strategy to handle errors, which manifests as PERI and PES respectively. Accordingly, Danielmeier et al. (2011) also observed that activity decrease in the motor area correlated with PES; and Maier et al. (2011) demonstrated that only errors due to failure in selective attention (flanker errors) will cause PERI in the subsequent trial. Together the evidence suggests that PES and PERI are distinct, arising from motor/premotor area suppression and attentional selectivity mechanisms respectively.

Overall, the conflict monitoring theory is generally consistent with experimental evidence on PEBA, and is presently the most complete error processing theory that accounts for mechanisms behind PEBA. Hence it will be utilized to guide the development of this thesis.

According to the conflict model, the ACC performs error detection, and generates the rERN to signal the DLPFC to modulate both the speed-accuracy trade-off (producing PES) and selective attention to task-relevant stimuli (producing PERI). Some of these links have empirical support: fMRI studies have shown that ACC/pMFC activation during error trials predict DLPFC activation in subsequent trials, which correlate with amount of PES (Kerns et al. 2004, Garavan et al. 2002). Some data suggest however the ACC/pMFC can directly enable PEBA without relying on the DLPFC. In a fMRI study of a Simon task with coloured dots (relevant dimension) that also moved left or right (distracting dimension), Danielmeier et al. (2011) reported direct pMFC correlation with all post-error activity changes: increases in the colour processing cortical area, decreases in the motion processing area, as well as decreases in motor area activity that correlated with PES. In this study while DLPFC did exhibit heightened activity in post-error trials, there was no correlation with the aforementioned adjustments.

There lacks evidence that post-error modulation of selective attention is, at least in part, exerted by the DLPFC. This however, is in general not an unexplored topic; literature on selective attention has considerable emphasis on the role of the DLPFC.

1.7 Selective attention

To investigate the link between DLPFC and post-error selective attention adjustments, it is helpful to leverage knowledge and protocols associated with selective attention in general.

1.7.1 Effect of selective attention

The processing of sensory information can be modulated to boost certain stimuli and suppress others based on what is relevant to the task at hand. Examples of selective attention include selectivity by stimulus modality or location. In a multimodal choice reaction time task, Spence & Driver (1997) found that stimulus in the expected modality produced significantly faster and more accurate responses, as well as distinct effects of spatial cuing. In a study on spatial attention Scharlau (2004) applied temporal judgement tasks and showed that perceptual latency of a stimulus is shortened when attending to the target location. Hillyard & Anllo-Vento (1998) regarded the impact of spatial attention 80-200 ms after visual stimuli (reflected as larger P1/N1 components) to be associated with enhancement of reaction times and target signal detection. The effect of selective attention on early somatosensory processing has been demonstrated with electrophysiological data: amplitudes of ERPs of task-relevant vs. task-irrelevant vibrotactile stimuli differ significantly at the P100 and N140 components (Bolton & Staines, 2011). Occasionally modulations have been shown to occur as early as the P50 (Schubert et al., 2008).

1.7.2 Role of prefrontal and medial frontal regions

Studies have revealed a critical role for the DLPFC in the selective attention system. Bolton & Staines (2011), in a study of somatosensory ERPs to vibrotactile stimuli, demonstrated that cTBS inhibition of right DLPFC reduces sensory gating in early stages of somatosensory processing, as reflected by poorer inhibition of P100 for irrelevant stimuli. Gehring & Knight (2002) also observed increased effects of distractor stimuli in lateral PFC damaged groups. As well, fMRI evidence (Staines et al., 2002) showed heightened DLPFC and SI activation when applying selective attention. The authors have provided some theories on the underlying pathways and mechanisms: Staines et al. (2002) supported the possibility of a prefrontal-thalamic inhibitory system, where excitatory projections from DLPFC to the thalamic reticular nucleus applies intermodality inhibition to the thalamic sensory relay nuclei and hence impacts the sensory processing system at an early stage; as well, relevant ascending sensory paths can be facilitated by the same mechanism via disinhibition. Another possibility discussed is the direct modulation via reciprocal connections of DLPFC with the parietal cortex. There is also evidence that ACC contributes to selective attention. Weissman et al. (2005), in an fMRI study, cued subjects on whether to attend to local or global features of the target stimulus. The authors found that consistent with the understanding that local features are more attentionally demanding than global, dorsal ACC activation was also significantly higher after cues for local attention. This difference in activation level, which followed closely with trends in DLPFC activity, showed that dACC may also have a role in modulating attentional resources.

1.8 Experiment design considerations

Studies on error commission and selective attention have elucidated conditions that impact these systems. Some considerations for experiment design are highlighted here, to facilitate minimizing confounds and better manipulating target variables.

- 1) Error awareness: rERN and error correction remain intact in unaware errors, but PES is lost (Nieuwenhuis et al., 2001). Experimenting on unperceived errors would isolate purely rERN related mechanisms, but may eliminate aspects of error processing gated by awareness.
- 2) Probability of error occurrence: low error rates produce stronger rERN signals (Gehring et al., 2012), e.g. 15-25% is commonly used. 50% error rate is a special condition that prevents conflict processing due to novelty / expectation violation (Van Veen et al., 2004); as well, PES does not occur at this error rate (Notebaert et al., 2009). Error probability may be controlled by periodically advising subjects to either speed up or to be more careful, or by applying custom timeouts based on individual practice data (Rodriguez-Fornells et al., 2002; Rollnik et al., 2004).
- 3) Stimulus repetition: if two consecutive stimuli happen to be identical, it has a significant impact on reaction time related performance measures. Such stimulus repetitions occur often in flanker tests, i.e. congruent – congruent and incongruent – incongruent progressions have a 50% likelihood of repeating the same stimulus. This scenario results in “stimulus specific repetition priming” and will skew experiment results (Mayr et al., 2003).
- 4) Stimulus frequency: if unequal proportions of targets are given, e.g. a flanker test with 80% “H” targets and 20% “S”, response biasing can be induced, where impulsive responding mechanisms will favour the frequently occurring stimulus. There is a chance some transient response bias occurs even when stimuli frequencies are globally equal, and shifting the stimulus frequency may help make the bias predictable and facilitate relevant investigations.

- 5) Congruence ratio (also known as trial-type frequency): interference effects are stronger when congruent trials are prevalent, as reported by Ridderinkhof (2002b), where a 75/25 ratio of congruent vs. incongruent stimuli was necessary to induce PERI.
- 6) Accidental overt and spatial attention shifts: orienting receptors, e.g. eyes or head, when only required to attend to a target internally will inadvertently facilitate processing. Likewise attending to a different area around the body when only required to divert attention to another modality will confound results with spatial attention effects (Spence 2002). Thus precise protocol, e.g. specifying where to look and keeping stimuli sources close together, is necessary.
- 7) Intrinsic priority of modalities in multi-modal designs: response determination to auditory stimuli, for example, takes significantly longer than visual stimuli (Hohnsbein et al., 1991).
- 8) Error categorization: compensatory activity may be a function of error type. For example, separating “flanker errors” from “random errors” in analysis can reveal subtle PERI effects (Maier et al., 2011).
- 9) Compensatory strategies: subjects may exhibit either PERI or PES due to adopting a proactive or reactive strategy to error compensation (King et al., 2010). Subjects can be divided into two groups based on post-error speeding vs. slowing and analysed separately.
- 10) Error correction: PES may be linked to the inhibition of natural corrective instincts, as it is absent in corrected trials (Crump & Logan 2012). Hence error correction should be explicitly encouraged or made infeasible to isolate the different types of error – remediation sequences.
- 11) Response-stimulus interval: following an error, a processing/recovery period may exist. Dudschig & Jentsch (2009) reported a half second delay to be a turning point – shorter RSI causes significant PES and reduction in accuracy. Thus it is important to design timing that either deliberately investigates this process or clearly falls outside of it.

Chapter 2: Research Questions and Hypotheses

This thesis has three main aims: investigate whether a vibrotactile based protocol is effective for activating the error system; detect any changes in cortical sensory processing after error commission (particularly components influenced by the DLPFC), and look for relationships between the electrophysiological markers of error detection and selective attention, and between these markers and behavioural trends. The specific objectives and hypotheses are:

1. Determine if a speeded-response flanker-task in the somatosensory modality produces similar interference effect as visual tasks. (Interference effect is measured as reduction in reaction speed and accuracy when flankers are incompatible to the target.) Determine if a clear rERN is produced in error trials. Additionally, look for PES, PIA, and PERI effects.

Hypothesis: A) Performance in the incompatible case, where flanker stimuli and target stimuli are different amplitudes, will take significantly longer reaction time and be significantly less accurate than the compatible case, where flanker and target are identical amplitudes.

B) A discernible rERN signal will be exhibited in the frontal central areas, in the difference wave between response-locked EEG signals of error and correct cases.

C) After error commission, the subsequent trial will exhibit post-error behavioral adjustments. The PERI effect has speed and accuracy impacts: the difference in reaction times between compatible and incompatible cases will be lower in post-error trials than post-correct trials, due to an increase in response speed of post-error incompatible trials. Similarly, accuracy (in terms of error rate) is hypothesized to improve for the post-error incompatible case compared to post-correct incompatible trials.

2. Determine if the early to mid-latency somatosensory ERPs that are time-locked to the flanker/distractor stimulus, particularly the P100 component, are suppressed more in post-error trials compared to post-correct trials.

Hypothesis: The P100 of distractor stimuli will decrease in amplitude in the average of trials immediately following errors compared to the average of trials following correct trials. The earlier ERPs such as P50 and N70 that reflect SI processing will not be modulated significantly.

3. If post-error distractor P100 modulation is observed, explore correlations with degree of PERI, as well as rERN amplitude of the preceding error trial.

Hypothesis: A) Individuals with smaller post-error distractor P100 amplitudes will tend to exhibit faster reaction times and better accuracy in post-error incompatible trials.

B) Individuals with larger rERN amplitudes will tend to have smaller post-error distractor P100 amplitudes.

Chapter 3: *Modulation of somatosensory cortex underlying error compensation in a tactile speeded-response task*

Abstract: It is known that the ACC detects occurrence of errors, and either directly or through another source of cognitive control, modulates the motor and sensory areas to achieve compensatory behavioural changes (temporary adjustments in response speed, accuracy, and sensitivity to interference). Recruitment of the prefrontal area for cognitive control of post-error slowing has been demonstrated in fMRI experiments to some extent, while DLPFC enabled enhancement of selective attention against distracting stimuli has been theorized by the conflict monitoring model of error processing, but lacking in empirical evidence. Hence, the purpose of this study was to specifically implicate the DLPFC in post-error modulation of sensory processing, and the associated phenomenon of post-error reduction of interference. In a somatosensory version of the flanker task, vibrotactile stimuli were delivered to the fingertips for amplitude discrimination (between two levels). To enable isolation of the ERPs, the distractor (flanker) stimulus always preceded the target. The congruence ratio was 70%. Early somatosensory ERPs of the distractor stimulus were extracted and compared between post-error trials and post-correct trials to look for error related modulations. (The analysis focus is on distractor ERPs rather than target ERPs because the former is indicative of filtering/suppression of task-irrelevant inputs.) It was hypothesized that the custom flanker task will generate rERNs and produce PES, PIA, and PERI effects; the early ERPs will be modulated in post-error vs. post-correct trials; and individuals with larger rERN would exhibit more ERP modulations and greater PERI. The findings of the current study were that post error commission, the P50 component was suppressed and the P100 component was enhanced. These modulations did not occur in one specific error case, which was reported difficult for confident sensing of the stimuli

(even though the rERN of this case was equally as strong as other cases). Individuals with larger rERNs exhibited greater PERI effect. While other PEBA did not show subject-wise correlations with electrophysiological measurements, the individual absolute performance (rather than the change in performance, which defines PEBA) did exhibit a relationship to P100 amplitudes, and specifically occurring post error commission.

3.1 Introduction

The conflict monitoring theory of error processing (Yeung et al., 2004) gives a comprehensive model of the error processing system focusing on the response-locked ERN signal, including how it is generated, its purpose in recruiting cognitive control from pre-frontal areas, and the effect of such control to both better filter irrelevant sensory inputs and reduce priming of impulsive motor responses. In comparison, the reinforcement learning theory (Holroyd et al., 2005) reconciles feedback-ERN and impact of expectation on favourableness of on-going events, but lacks detailed explanation of post-error behavioural adjustments and particularly does not describe adjustments to the attention units handling input sensory information. Hence this study focused on investigating evidence for the conflict monitoring theory (although its most distinctive aspect – mechanism of error detection – is not relevant to this thesis).

As the conflict model suggests, error detection occurs in the ACC and pMFC areas; this signal is passed to the DLPFC to improve strategy toward future trials. There is a gap in empirical evidence for the DLPFC's role in modulating sensory processing and the associated PERI effect; particularly noteworthy is that existing data favour the scenario where ACC/pMFC is directly exerting control over sensory encoding regions (Danielmeier et al., 2011).

It is however, likely/possible that the DLPFC does influence sensory processing in response to errors. Firstly its recruitment is already demonstrated for the PES aspect of post-error adjustments. Secondly, the PERI effect – the temporary reduction in impact of distracting stimuli – reflects an increase in selective attention to task-relevant sensory input, and certain forms of selective attention are linked to DLPFC control. In particular, the aspect of spatial attention on somatosensory stimuli that is reflected by P100 ERP modulation is demonstrated to be exerted by the DLPFC (Bolton & Staines, 2011).

By designing an experiment (a modified flanker task) that utilizes asynchronous vibrotactile stimuli, it would be possible to monitor ERPs of attended and unattended (distractor) somatosensory input and look for modulations in the trials following error commission. Since DLPFC controls selective attention at the P100 stage by down-regulating task-irrelevant signal processing (Bolton & Staines, 2011), this study will focus on distractor stimuli ERPs. Hence if post-error suppression of distractor P100 can be demonstrated, the DLPFC will be implicated in the error processing mechanism for sensory processing adjustments. If such ERP amplitude modulation is further correlated with behavioural measures of PERI, then DLPFC becomes linked to the PERI phenomena described in error literature. Lastly if the rERN amplitude correlates with ERP modulations, then the recruitment of DLPFC by error detection stages in ACC and pMFC would be further verified for this particular context.

3.2 Materials and Methods

3.2.1 Subjects

Twelve neurologically normal young participants (aged 20 to 40 years) were recruited for this study. Participants were cognitively healthy and without history of neurological decrements.

Right-handed participants of any sex were sought. While the age and handedness of participants are not expected to affect the research objectives, it is possible that the reaction-time of older participants may differ systematically from younger participants, as well since responding is via repetitive and speeded clicking of a mouse in the right hand, left-handed participants may fatigue and exhibit error significantly sooner. Since error occurrence and processing is rather sensitive to timing related parameters, a relatively homogenous group of participants was more likely to all fall within the required error rate range without customization of protocol on a per-subject basis. Participants all verified their neurological health and history and gave their informed consent to participate in the study; the experimental procedures were approved by the Office of Research Ethics at the University of Waterloo.

3.2.2 Experimental procedure

The speeded-response flanker-task paradigm was utilized and several parameters judiciously tuned to suit the tactile domain, in order to create the essential conditions of an rERN and PEBA investigation: the vibrotactile stimuli amplitudes set to be easily discernible (unambiguous stimuli), the duration of stimulus set to be sufficiently long for adequate sensory processing (enable realization of error commission), and the appropriate time constraints applied to force responding before complete sensory information processing (induce the commonly sought 15-25% error rate).

3.3.2.1 Behavioural Task

Subjects received vibrotactile stimulation on the index and little fingers of the left hand, and push on one of two buttons with two fingers of the right hand. The input device is a simple computer mouse, selected for the ease of activation of the buttons, and obvious clicking

sensation to eliminate ambiguity on whether a response has registered. The layout is shown in Figure 1.

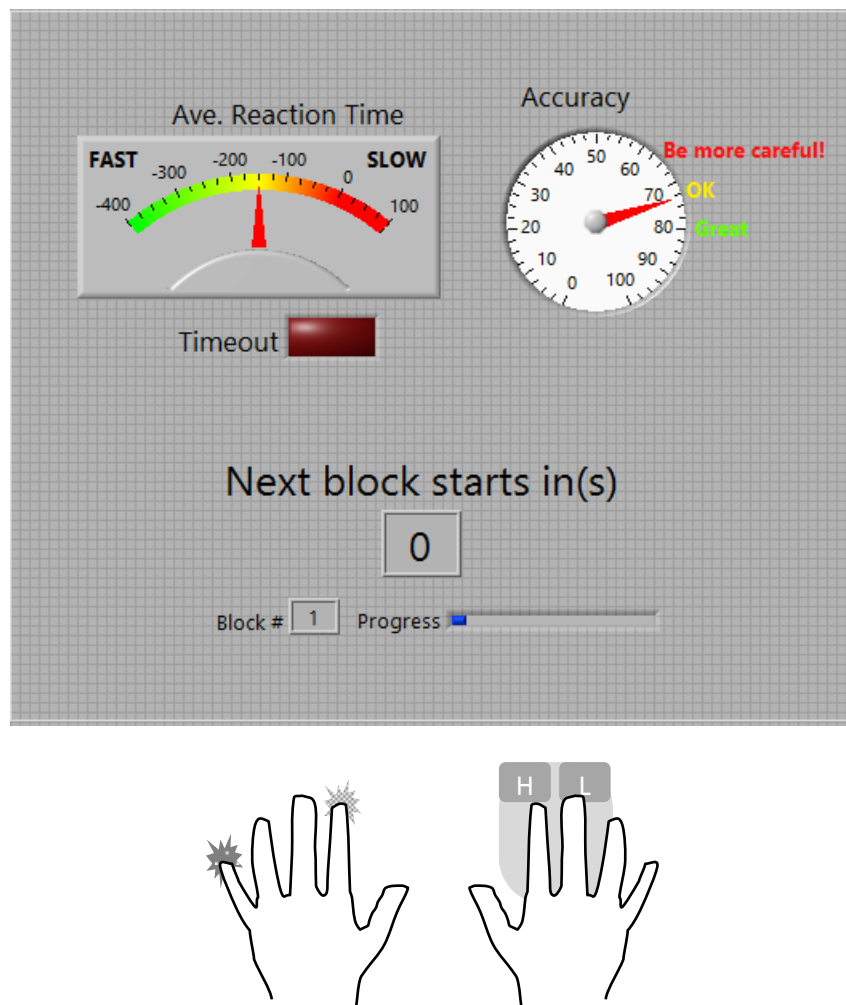


Figure 1: Physical layout of experiment interface.

The stimulation on both fingers were either high or low amplitude. Subjects were instructed to detect the amplitude at the little finger regardless of stimulation at the index finger, and respond as quickly and accurately as possible by pressing the appropriate button. A response was required every trial. Subjects were instructed to fixate on an on-screen feedback panel, which includes a timeout indicator that turns “on” if a trial had timed out, and that timeout is to

be avoided. The speed and accuracy gauges showed the on-going performance averages (cumulative) for the current block, where the accuracy gauge is dampened by the addition of a slow sinusoid to avoid giving instantaneous feedback and eliciting the feedback-ERN.

Subjects began the study by performing a short practice block, where an additional indicator is visible on screen to show whether each trial response was correct or in error. This was to familiarize subjects with the demands of the task (as timeouts occur very quickly) and learn the very simple stimuli-response mapping.

The study was broken up into eighteen blocks (60 trials per block) of approximately 2.5 minutes in duration to alleviate fatiguing, and give feedback/encouragement. Subjects that were particularly favouring accuracy or speed were reminded to try and keep both gauges balanced (in the yellow to green zone) throughout the trials. The optimal accuracy range was 75% to 85%.

3.2.2.2 Stimuli

The vibrotactile stimulation on index and little fingers were always onset asynchronously, with distractor (index finger) stimuli always onsetting first. The average time offset between target and distractor was 200 ms, within a randomized range of ± 50 ms. This delay gave at least 150 ms time for un-obscured ERPs to be recorded for the distractor stimuli. Each target stimulus persisted for 500 ms, while the distractor persisted to end synchronously with the target (preventing subjects from ever perceiving the target stimuli without interference).

After onset of target stimulus, 600 ms was given for subjects to make a response before timeout indicator is turned on. (If a response was made in time, the indicator will not turn on.) An 1800 ms response-stimulus interval was utilized, which served as a short break between trials. Hence even though subjects are very rushed to give a response upon stimulus perception, the

trial-to-trial timing was designed to be a comfortable pace (to allow adequate error processing to occur).

The vibrotactile stimulation was delivered by a piezo-bender oscillating at 25 Hz from a square wave signal. The “high” stimulus was four times greater in amplitude than the “low” stimulus. There was equal probability of “high” vs. “low” target stimuli; this prevented response bias effects. Out of all trials, 70% of trials were compatible, and 30% were incompatible. The smaller percentage of incompatible cases helped induce greater interference effect.

The experimental hardware was controlled by a custom LabVIEW (version 8.5, National Instruments, Austin, Texas) program, which generated stimulus waveforms, and captured responses to determine appropriate feedback on-screen indicators in real time. White noise was played during experiment blocks to mask out hardware vibration noises.

3.2.3 Data acquisition

EEG was collected during the experiment blocks (but not the practice block). The main electrodes of interest were, based on international 10-20 system for electrode placement: Fz, Fcz, Cz, for rERN detection; and C3, C4, Cp3, P3, Cp4, P4, for somatosensory ERP detection. Electrodes were referenced to linked mastoids, and their contact with the scalp was manipulated to reduce impedance to less than 5k Ω . EEG input was amplified and digitized at 500 Hz sampling rate and DC-100 Hz filtering (SynAmps, Neuroscan 4.3, Compumedics, USA). Every stimulus onset and subject response was captured by the LabVIEW program and inserted as identifying event codes into the EEG data stream.

3.2.4 Data analysis

EEG raw data collected from NeuroScan was processed into measurable form using EEGLAB (automated with custom scripting). The steps were as follows:

- 1) Initial preparation: high pass filter at 1 Hz, delete duplicate response events
- 2) Label blocks by detecting breaks in event data, to prevent error/post-error relationships from spanning across blocks
- 3) Epoch data time-locking to distractor events with intervals of 1 s pre-stimulus and 1.5 s post stimulus. Only strong distractor events were included, as ERPs were difficult to discern on the weak stimulus.
- 4) Recode response event of error trials, using different codes to represent different error cases (e.g. to enable categorizing random errors, flanker errors, etc.).
- 5) Recode response event of post-correct trials and post-error trials, using unique codes for each type of post-error trial. Up to two (correct) trials following each error was considered “post-error”. An unbroken chain of (correct) trials following four consecutive correct trials was considered “post-correct”.
- 6) Repeat the above step with error trials included in the labelling. (This set is only used for calculating trial accuracy.)
- 7) Inspect EEG traces of each individual and apply each of the following processing algorithms only if necessary.
 - Blink correction (via Independent Component Analysis in EEGLAB).
 - Artifact rejection by extreme value (for subjects with fewer blinks).
 - Artifact rejection by probability.
 - 25 Hz notch filter (ERPLAB), for occasions where the stimulus vibration frequency contaminates the EEG signal (3 subjects).
 - 10 Hz notch filter (ERPLAB) if the EEG exhibited strong alpha (2 subjects).

- 30 Hz low pass filter, when high frequency noise is problematic on the large size electrode cap (2 subjects).
- (Note: no dataset required more than one of the above frequency filters.)

8) Select epoch by event type, e.g. to isolate error trials for rERN, or to compare post-correct vs. a specific type of post-error trials).

9) Epoch on response event (for rERN) or stimulus event (for ERPs) at intervals of 200 ms and 600 ms, pre and post stimulus, respectively.

10) Apply baselining for a 100 ms pre-stimulus interval.

Quantities of interest were subsequently extracted. ERP components were quantified manually for each subject: first a grand average of all trials for the high-distractor case was generated (approximate $n = 350$, giving rise to the most clean/readable EEG signal), and the P50 and P100 latencies identified by inspection (only if clearly discernable positive peaks approximately 50 ms and 100 ms post stimulus onset were present); then, EEG datasets of interest (post-correct and various post-error conditions) were generated, and the P50 and P100 peaks identified as the highest peak within a plus/minus 15 ms time window around the template ERP latencies for the individual. Amplitude (peak to peak) of an ERP was quantified as the voltage level at the apex of the component minus the immediately preceding peak of the opposite polarity. Amplitude of the rERN was quantified as the voltage level of the most negative peak, within 50 ms to 150 ms latency range from response onset, for each individual. Reaction times were measured via automated scripting as the time delay between target stimuli onset and response onset. Accuracy was measured via automated scripting by counting the quantity of corrects and errors in the trials designated as post-correct and various types of post-error.

Analyses conducted for the specific hypotheses are as follows:

1. A) Paired T-test of average reaction time and error rate between compatible and incompatible cases was performed to detect interference effect.

B) Presence of rERN was verified by inspection, with reference to literature.

C) One-tailed paired T-test of reaction time between post-correct and post-error trials was performed to detect PES. Likewise, one tailed paired T-test of accuracy between post-correct and post-error trials was performed to detect PIA. The interference (performance difference between compatible and incompatible cases) was calculated and then compared between post-correct and post-error cases using paired T-tests (separately for reaction time and accuracy) to detect PERI.

All of the above were repeated, where sufficient data was available, for each error case individually to look for any specific category of errors that elicited different levels of post-error adjustment.

2. Comparisons of peak to peak amplitudes and peak latencies of distractor time-locked P50 and P100 were performed between post-correct and post-error trials. Modulation of each component's parameters was tested using a paired T-test. The grand averages of ERP waveforms were regenerated for each error case, to inspect for any specific category of errors that elicited different levels of post-error ERP modulation. The N70 and N140 components were not measured due to the N70's proximity to the P50 and P100, and the observation that N140 in a number of subjects occurred close to or later than 150 ms, which is confounded by ERP activity of the target stimulus (following the distractor stimulus by 150-250 ms).

3. A). Subject-wise correlation was tested between distractor P100 amplitude vs. reaction time and accuracy in post-error trials. One-tailed probability (only valid for the hypothesized direction) was determined using Pearson's r and sample size.

B). Subject-wise correlation was tested between post-error distractor P100 amplitude and rERN amplitude of the preceding error trial. One-tailed probability was determined using Pearson's r and sample size.

3.3 Results

The analyses in part A through C pertain to “obvious-errors”, excluding the “ambiguous-error” case (explanation see Results part D & Section 3.4). p -values are two-tailed unless otherwise specified. Subject-wise graphs are colour-coded consistently, i.e. same colour for the same participant, throughout the thesis.

A) Post-error somatosensory cortical modulation

There was significant reduction of the P50 amplitude (peak to peak, $t_{11} = -4.05$, $p = 0.0019$) and enhancement of the P100 amplitude (peak to peak, $t_{11} = 3.57$, $p = 0.0044$) in the post-error trials compared to the post-correct trials (Figure 2).

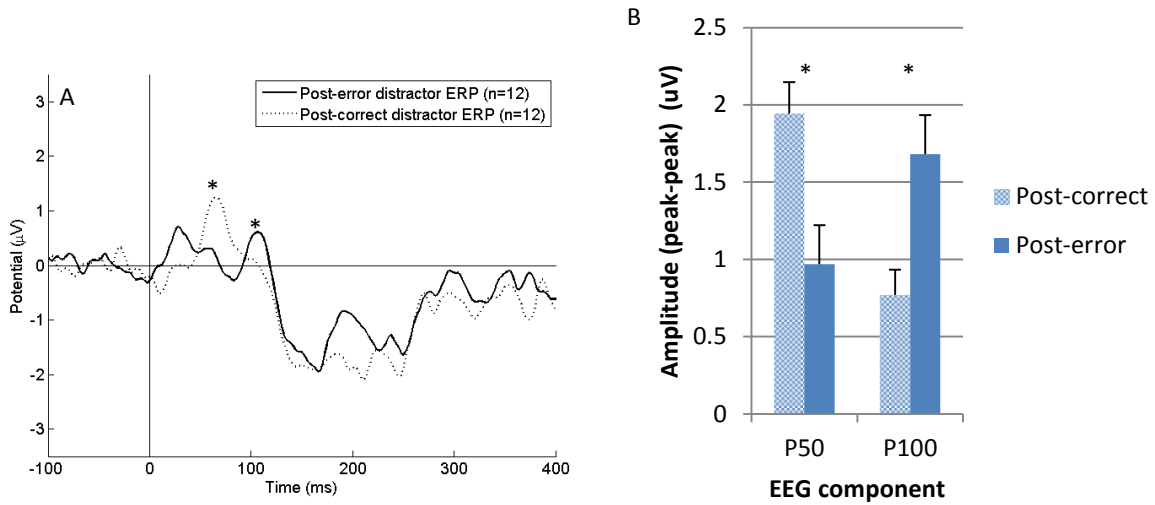


Figure 2: (A) Grand average of distractor time-locked ERPs for post-correct vs. post-error trials at CP4. (B) Mean of peak to peak amplitudes of individual data, for the P50 and P100 components depicted in A, showing significant post-error modulations. (* = $p < 0.05$)

B) Error-related signal and behavioural effects

By subtracting response-locked EEG traces on correct trials from error trials, a significant negative peak, the rERN, emerged approximately 100 ms post response (Figure 3).

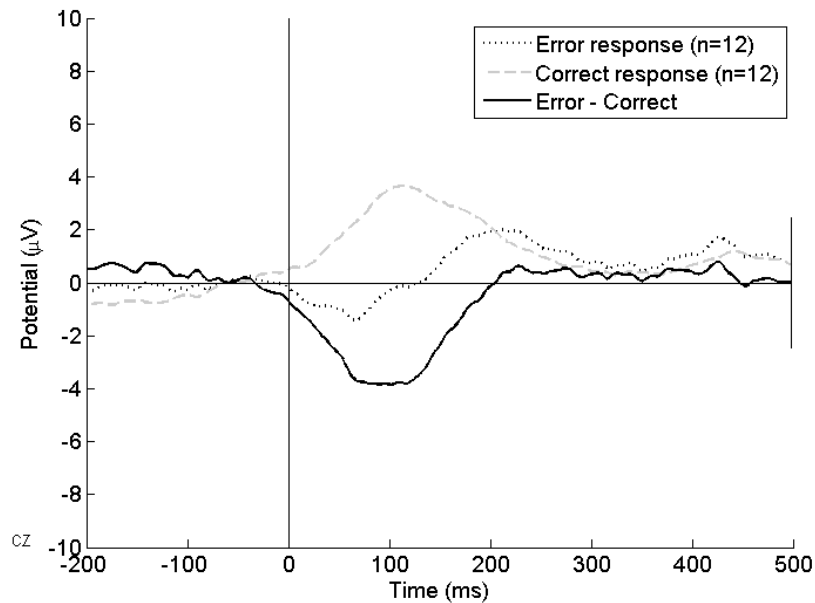


Figure 3: Grand average of the response-locked ERN at Cz, including all error types.

The global interference effect in compatible vs. incompatible cases were significant, both in reaction time and accuracy ($t_{11} = -9.75$, $p = 9.6E-7$; $t_{11} = -8.76$, $p = 2.7E-6$; respectively).

The typical post-error behavioural adjustments were tested. As illustrated in Figure 4, there was detectable PES ($t_{11} = 1.99$, 1-tailed $p = 0.036$), PIA ($t_{11} = -2.17$, 1-tailed $p=0.026$), but no significant PERI was found.

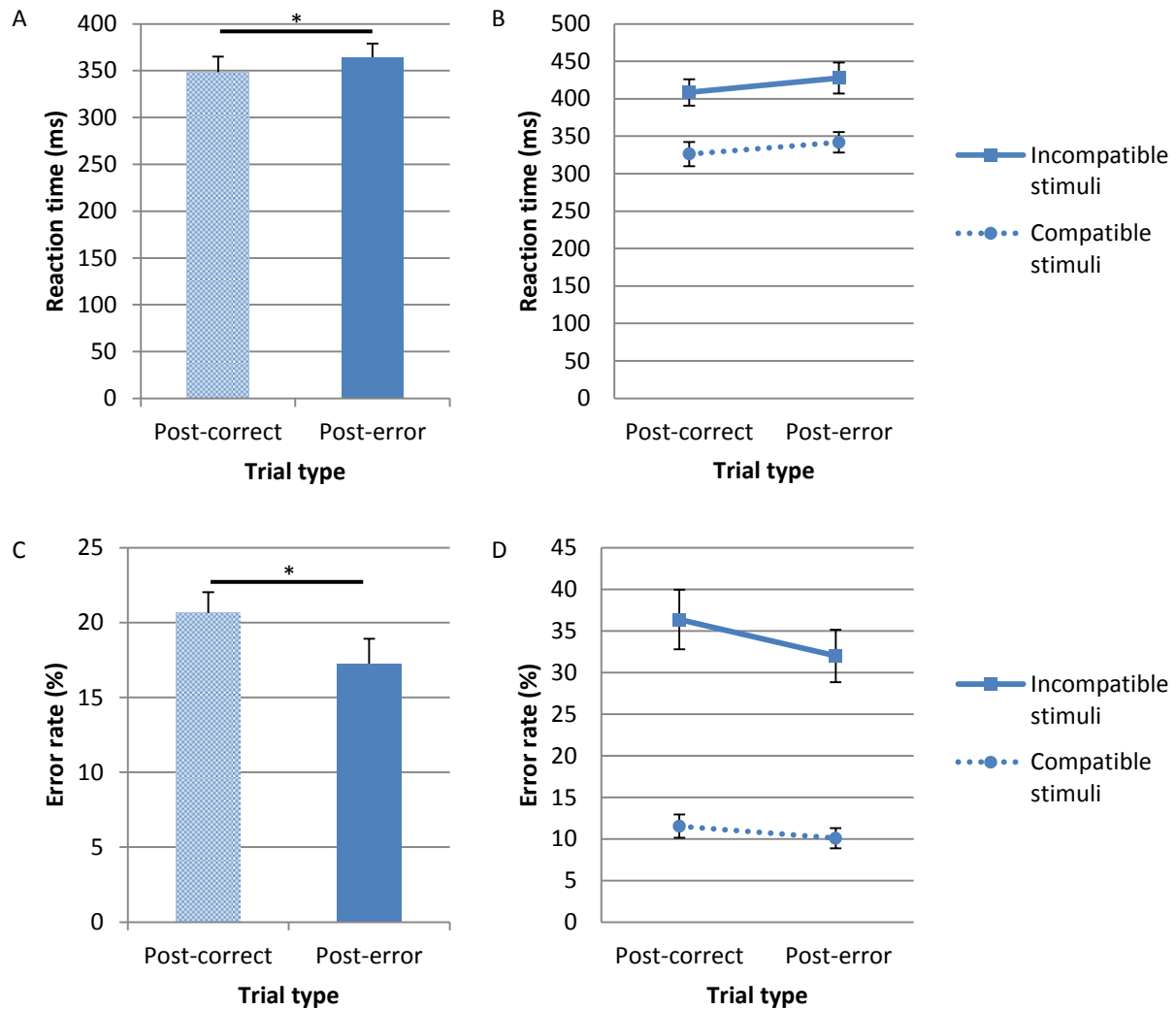


Figure 4: Analysis for presence of characteristic post-error behavioural adjustments. (A) Post-error slowing. (B) Plot of post-error reaction time adjustment in compatible vs. incompatible cases (no significant reaction-time-PERI). (C) Post-error improvement in accuracy. (D) Plot of post-error accuracy adjustment in compatible vs. incompatible cases (no significant accuracy-PERI). If PERI effects were present, the points for compatible and incompatible performance in the post-error column in B & D would significantly approach each other.

C) Subject-wise correlation between rERN, P100, and performance

There was a trend of correlation between the rERN amplitude and the post-error P100 amplitude ($r = 0.509$, 1-tailed $p = 0.045$; Figure 5). No correlation existed between the rERN and the amount of modulation on the P100, or the post-correct amplitude.

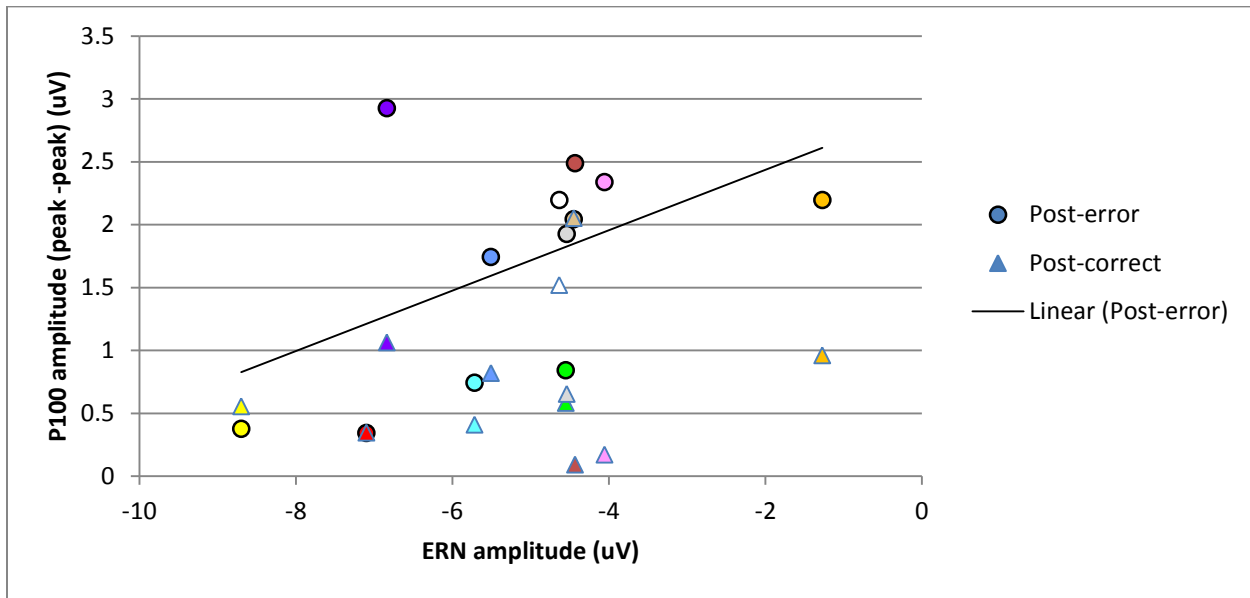


Figure 5: After error commission, individuals that generated larger rERNs tended to exhibit smaller P100 components; while before error commission (post-correct) the P100 did not cluster with a trend.

There was significant correlation between both the absolute post-error accuracy and reaction time with respect to the post-error P100 amplitude ($r = 0.770$, 1-tailed $p = 0.0017$; $r = 0.603$, 1-tailed $p = 0.019$; respectively; illustrated in Figure 6). There was no correlation between post-correct performance and post-correct P100 amplitude.

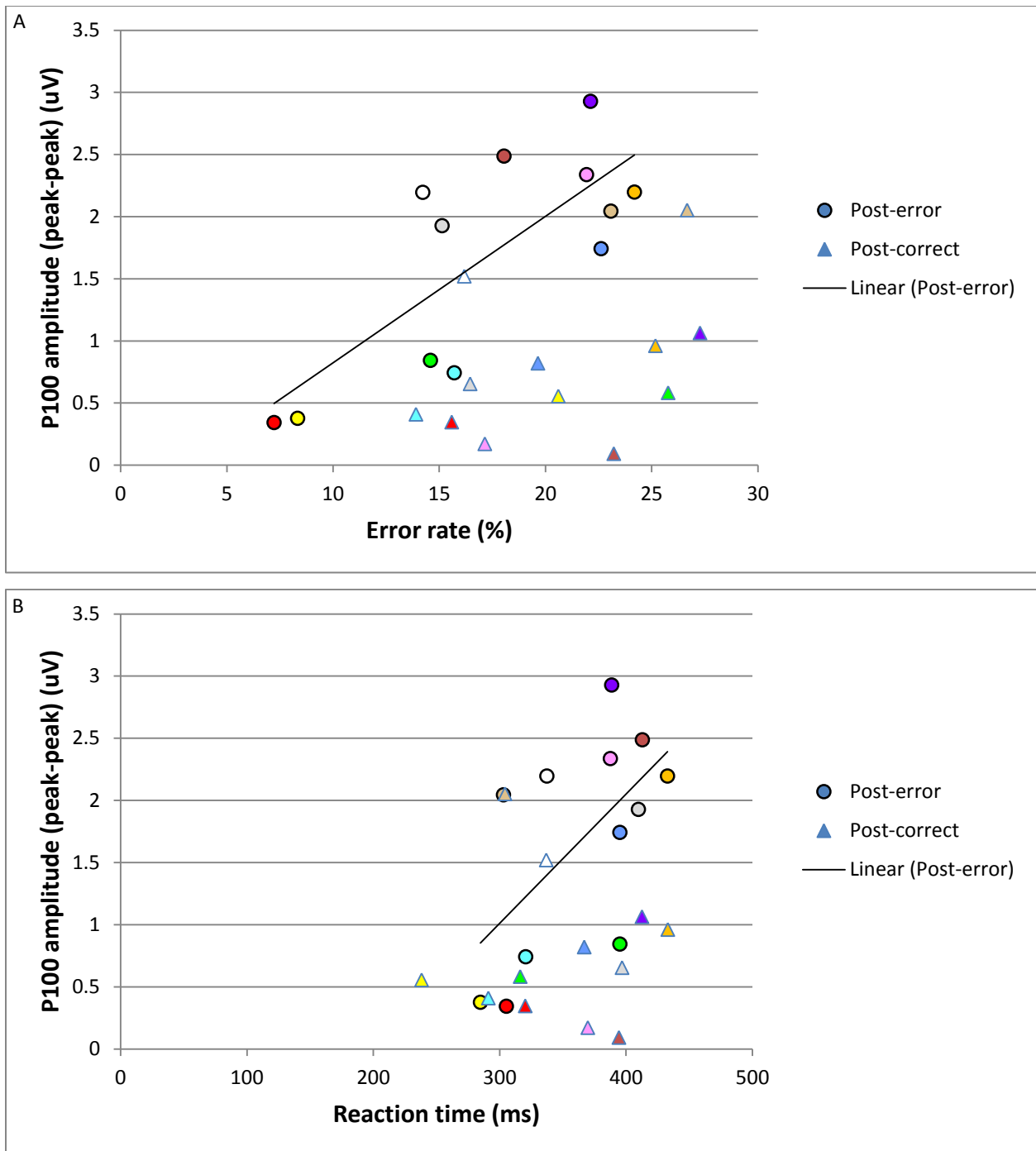


Figure 6: After error commission, individuals with smallest P100 amplitudes demonstrated the best accuracy (A) and reaction time (B). Before error commission (post-correct), performance and the P100 component were uncorrelated.

When the same correlation tests were performed between performance and amount of P100 modulation (amplitude difference between post-error and post-correct levels), it presented a

significant correlation to both post-correct ($r = 0.800$, $p = 0.0018$) and post-error ($r = 0.754$, $p = 0.0047$) reaction time (Figure 7), but not to accuracy. (Note that post-correct and post-error reaction times were strongly related within each individual).

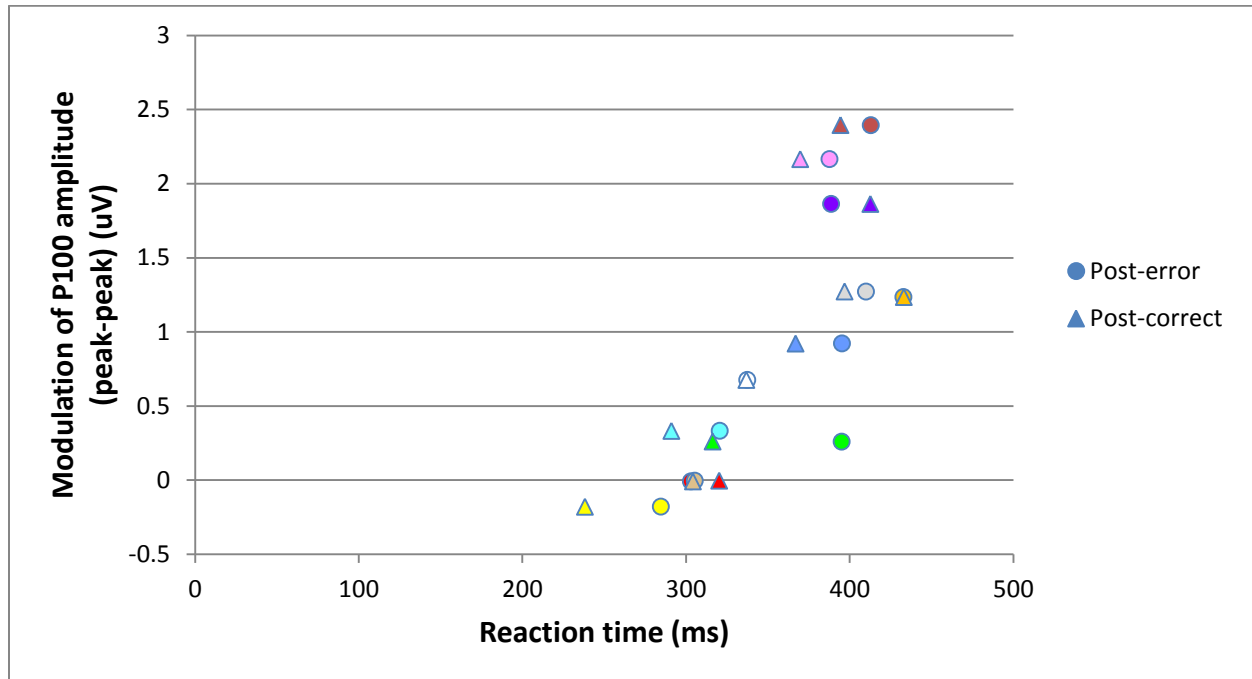


Figure 7: Regardless of whether trials are pre or post error, individuals that showed greater amount of post-error increase in P100 amplitude performed slower in the task.

Among various additional post hoc testing for correlations between electrophysiological markers and behavioural changes (adjusting for multiple comparisons), there was one significant relationship detected between the rERN amplitude and accuracy-PERI ($r = 0.779$, $p = 0.0028$; Figure 8). A noteworthy point is that the overall accuracy-PERI did not reach significance in this study ($t_{11} = -0.703$, $p = 0.25$), indicating that this effect may be subject to individual strategy, as suggested by King et al. (2010).

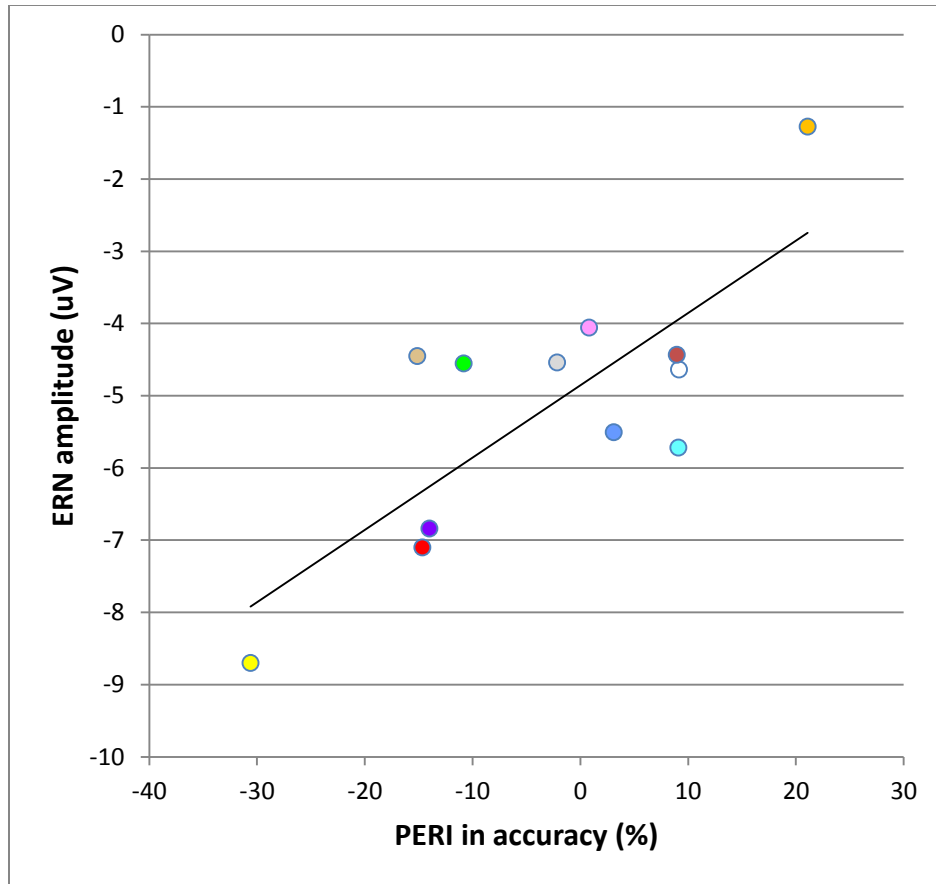


Figure 8. Individuals with larger rERNs displayed stronger reduction of interference in post-error trials (the reduced accuracy disparity between compatible and incompatible cases).

D) Impact of stimuli cases

There are four distinct combinations of stimuli, abbreviated LL, HH, LH, and HL. The two letters denote the level of distractor and target vibrotactile stimulation, respectively; L = low amplitude, H = high amplitude. These conditions generated various levels of accuracy and reaction time (Figure 9).

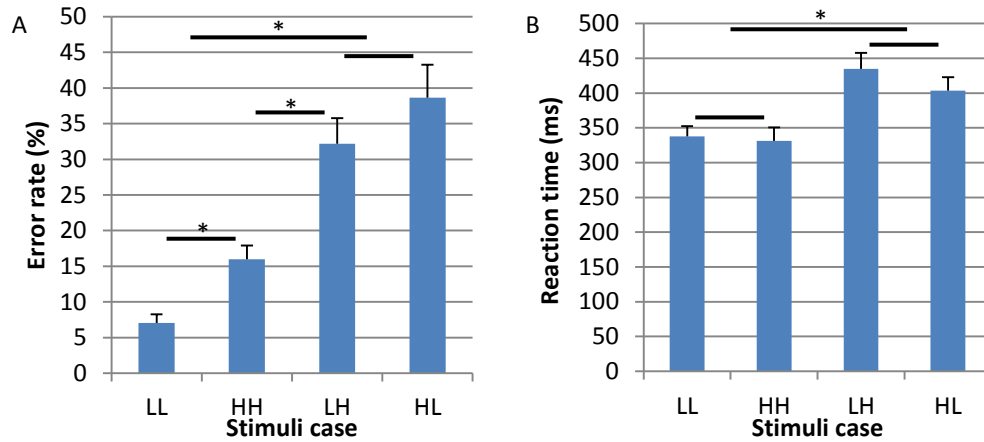


Figure 9: Mean error rate (A) and reaction time of correct trials (B) are shown for every stimuli case. Differences in performance were tested between compatible (LL & HH) vs. incompatible categories (LH & HL) ($t_{11} = -8.76$, $p = 2.7E-6$ in error rate, $t_{11} = -9.75$, $p = 9.6E-7$ in reaction time), and between specific cases for error rate: LL vs. HH ($t_{11} = -4.08$, $p = 0.0018$), HH vs. LH ($t_{11} = -4.99$, $p = 0.0004$), and LH vs. HL ($t_{11} = -1.00$, $p = 0.34$).

Inspection of ERP traces on the four cases revealed that the HL error case alone did not readily exhibit post-error modulation (Figure 10).

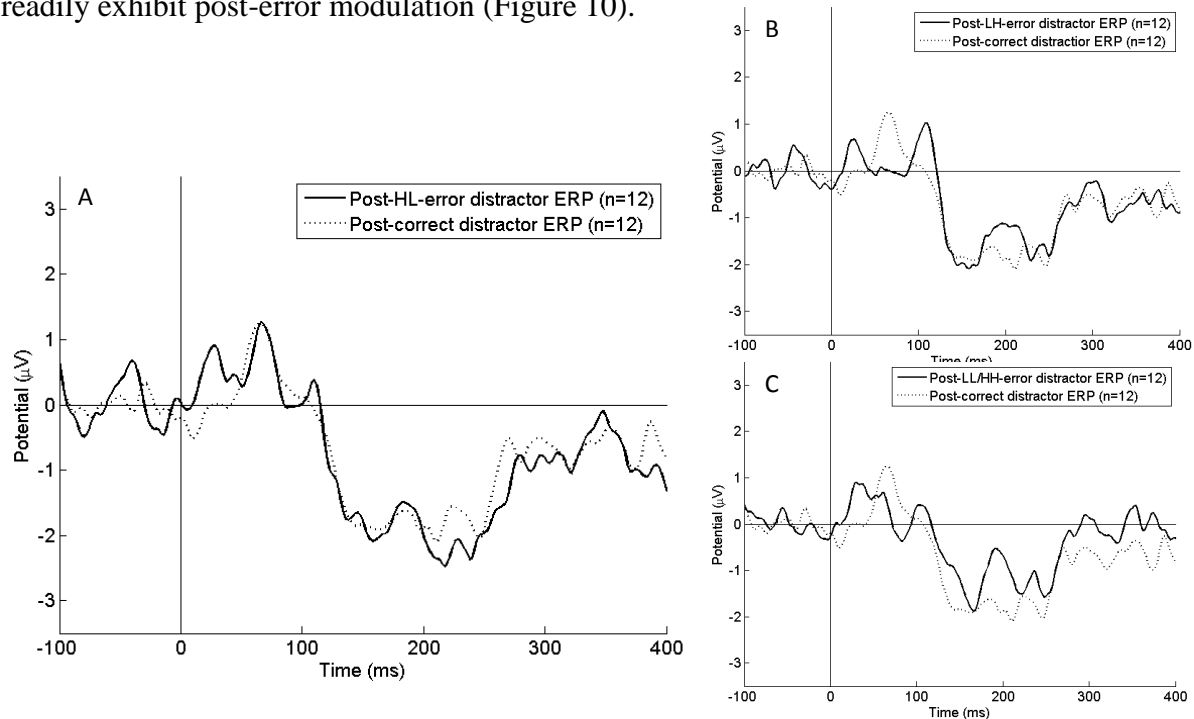


Figure 10: (A) Grand average of distractor time-locked ERPs for post-correct vs. post-error trials for only the ambiguous-error case (other types of post-error trials were excluded from the trace) at CP4. The P50 and P100 components were much less altered (if at all) after this type of error, compared to obvious-incompatible-errors (B), and compatible-errors (C).

Figure 11 shows that the HL case rERN did not differ significantly from the other three cases ($t_{18} = 1.20, p = 0.24$; $t_{18} = 1.07, p = 0.30$; for amplitude and latency, respectively. Only 8 subjects produced clean enough rERN signals to be measured for this specific condition.)

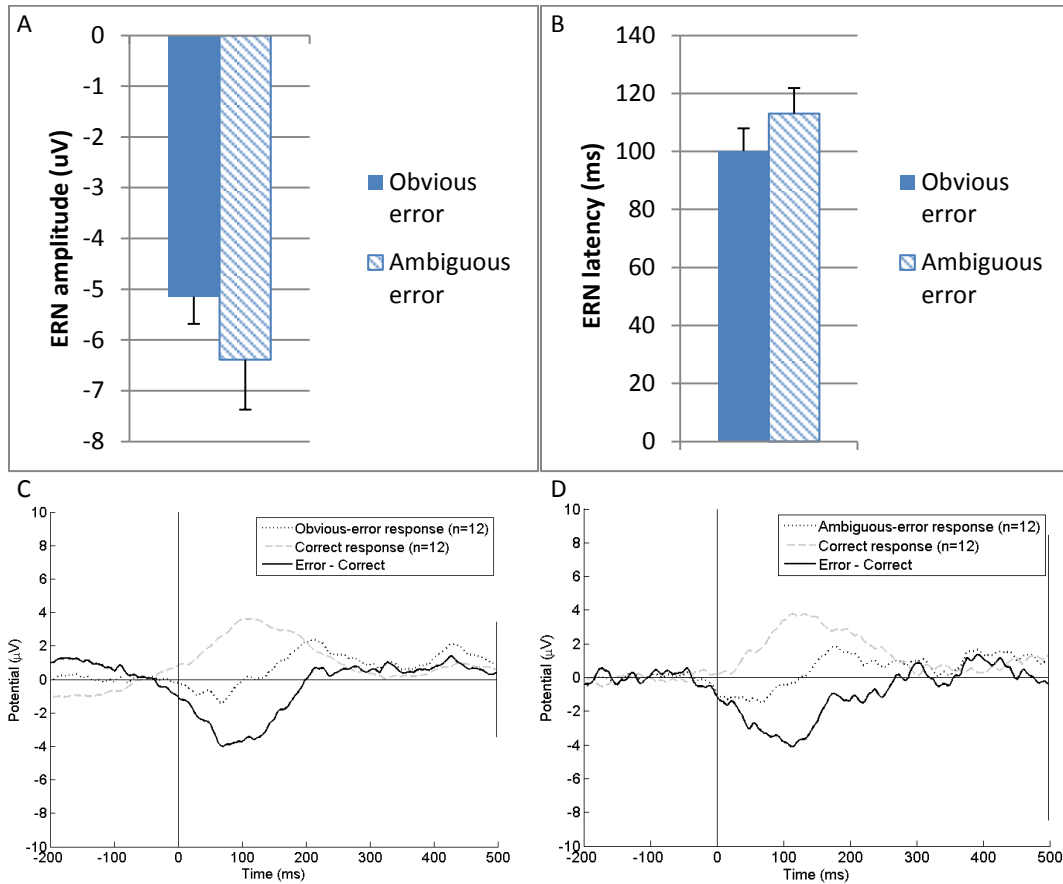


Figure 11: Comparison of the response-locked ERN signal of obvious (C) and ambiguous errors (D). The mean ($n = 8$) of component amplitude (A) and latency (B) were not significantly different.

Separating the HL case in behavioural data, the PERI in error rate is significantly different between the post-HL-error case and combined rate of LL, HH, and LH cases (Figure 12). (However, neither reaches statistical significance when tested against post-correct accuracy).

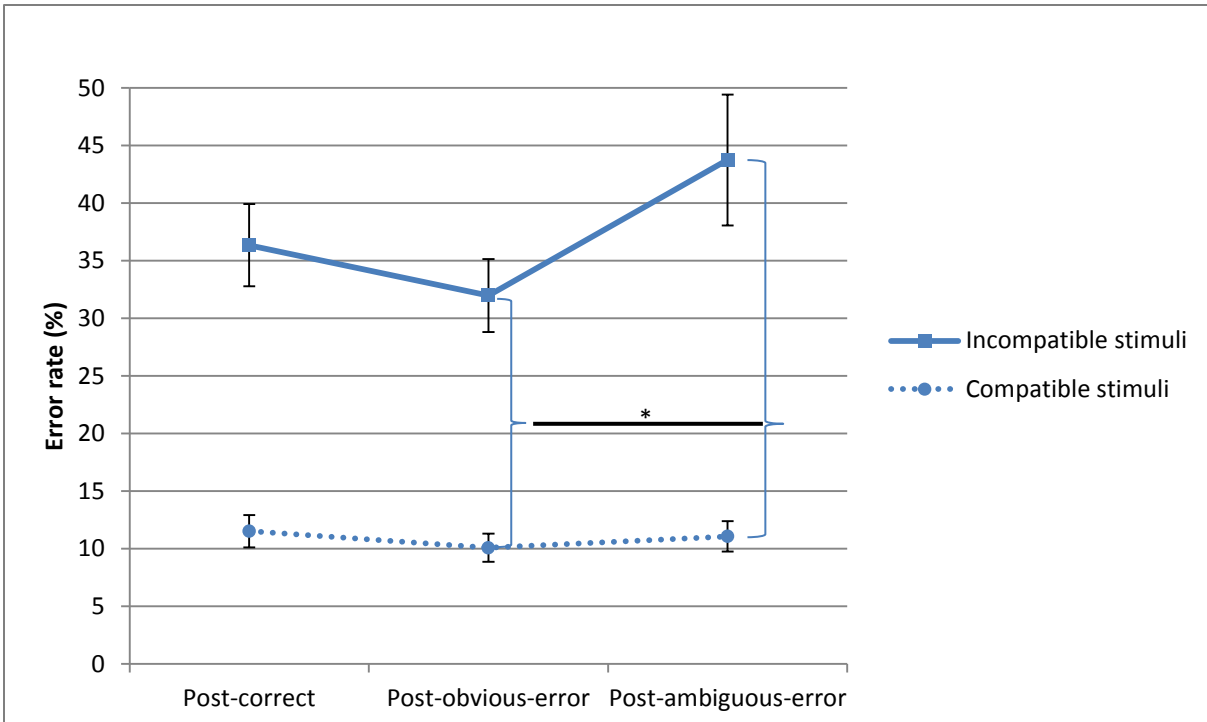


Figure 12: The type of error, obvious vs. ambiguous, lead to significantly different accuracy disparity between compatible and incompatible cases in subsequent trials ($t_{11} = -2.60$, $p = 0.025$). It appears that obvious errors tended to maintain/heighten interference management, while ambiguous errors hindered it.

3.4 Discussion

In this experiment, we aimed to find evidence of DLPFC involvement in post-error compensation. Specifically, DLPFC is expected to suppress task irrelevant sensory input processing, which would be reflected by modulation of early somatosensory ERPs. Additionally, we aimed to link the selective spatial attention modulations to behavioural changes if possible.

The main findings were:

- Certain categories of errors elicited clear modulation in distractor P50 (reduction) and P100 (enhancement), in a few subsequent trials. Subsequent interference management was maintained.

- One category of error did not induce selective attention change even though a consistent rERN indicated adequate error detection. Subsequent interference management was poor.
- The rERN amplitude marginally correlated with post-error distractor P100 amplitude: individuals with the largest rERN exhibited the smallest P100.
- Post-error distractor P100 amplitude correlated with post-error performance: individuals with the smallest P100 performed better both in accuracy and reaction time in post-error trials; this correlation did not exist in post-correct trials.
- Individuals with the largest rERN exhibited the most post-error reduction of interference. (Note group level accuracy-PERI did not reach significance).
- Individuals with the least degree of distractor P100 modulation between pre-error and post-error states had the quickest reaction times, but were equally accurate, than those with large modulations.

On the effectiveness of protocol, both the rERN signal and the post-error behavioural data align with existing literature on response-ERN targeted studies (Gehring et al., 2012). PES tends to be a prevalent post-error adjustment, while PIA (subject to response-stimulus interval (Dudschig & Jentsch, 2009)) and PERI effects (subject to response failure mode (Maier et al., 2011)) are not consistently observed in the literature. In this experiment, both PES and PIA were found while PERI effect was not significant. Overall the combination of the rERN signal, PES, and PIA, demonstrates that this protocol activates the ERN-related error processing system, and by comparing post-error and post-correct trials, EEG differences in the stimulus-locked ERPs can be interpreted as the cortical modulations that result from error processing.

The ERP data singles out the HL error case, which elicits no distractor ERP modulations on post-error trials. Upon consideration of subject experience, this case may be substantially more ambiguous than the LL, HH, and LH conditions: when both distractor and target stimuli are weak, responding “high” is clearly an error; likewise when both stimuli are strong, responding “low” is clearly incorrect; lastly when the distractor is weak, a strong target is easy to perceive and easy to recognize erring on. The HL case however, due to the strong and early onset distractor stimulus, perception/judging of the low amplitude target is comparatively more difficult (some participants reported they occasionally do not detect the target). Hence, these two categories will be referred to as “obvious errors” and “ambiguous errors” for intuitive purposes.

It is worth noting that ambiguous errors maintained the same amplitude and latency rERN as obvious errors, as well they did not differ significantly from LH (the other incompatible stimulus case) in reaction time and accuracy. This seems to indicate the difference in cognitive control is a function of conscious interpretation of the error circumstances, rather than due to error detection or performance attributes. This effect demonstrates that the rERN amplitude cannot predict the level of subsequent cognitive control, i.e. interpretation of errors can prevent the DLPFC from exerting error handling measures.

There is evidence that PERI effect is achieved by boosting selective attention (King et al., 2010; Maier et al., 2011), thus the post-correct and post-error interference levels were examined, with separate categories for: compatible errors (LL & HH), obvious incompatible errors (LH), and ambiguous incompatible errors (HL). By inspection of the plot in Figure 13, compatible errors and obvious incompatible errors appear similar, and do not significantly impact the interference level, while ambiguous errors exacerbate the interference effect. More specifically in the plot of individual PERI data (Figure 14), while some participants improve and others

worsen in interference control post error, almost all were extra error-prone to incompatible stimuli post ambiguous errors, perhaps due to disorientation and becoming prone to triggering by the early onset distractor stimulus.

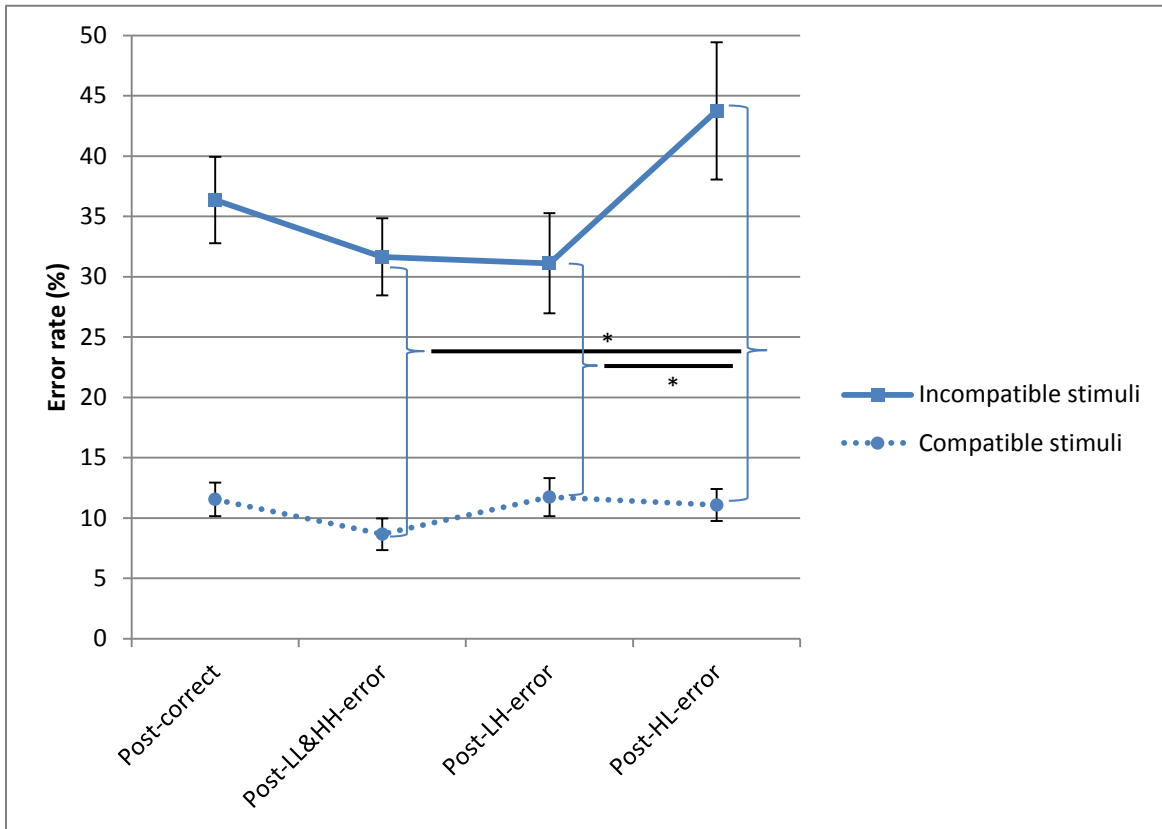


Figure 13: Elaborating on content in Figure 12 by breaking down obvious errors into compatible errors and incompatible low-distractor errors: both had similar effect on post-error interference management (maintaining / slightly improving on the post-correct state), and both differed significantly from the ambiguous error case ($t_{11} = -2.23$, $p = 0.048$; and $t_{11} = -3.01$, $p = 0.012$; respectively).

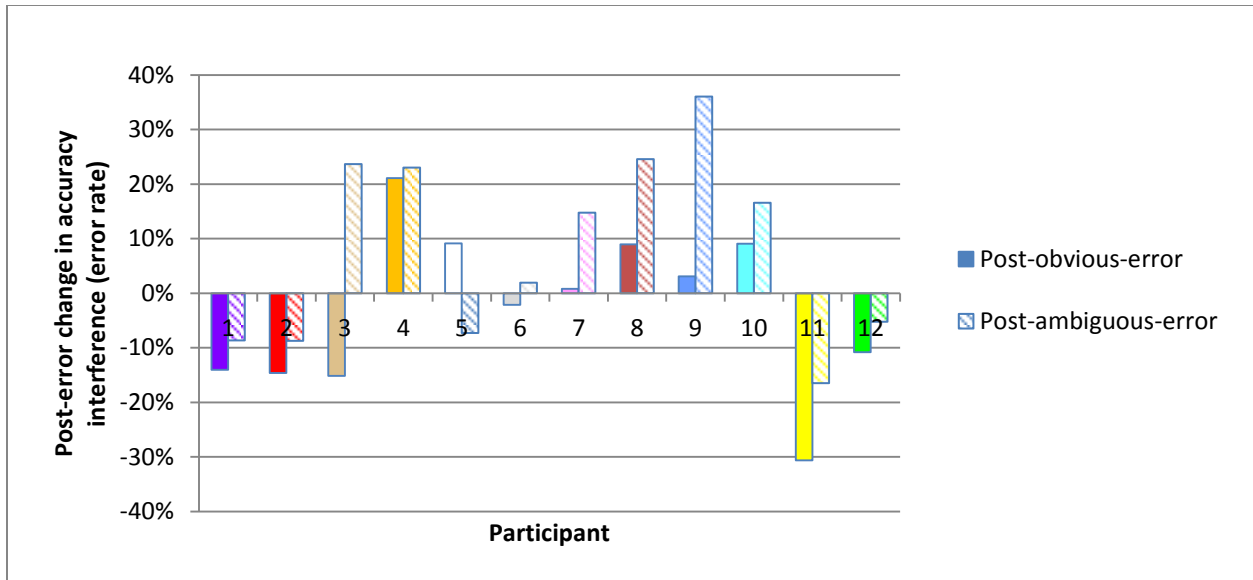


Figure 14: In almost all subjects, obvious-errors lead to better reduction in interference than ambiguous-errors (solid bars are more negative than patterned bars). This is regardless of whether the subject demonstrated PERI in general (i.e. whether the bars are positive or negative).

Taken together, both cognitive control and interference management are affected by interpretation of error circumstances: post obvious-errors, distractor P50 and P100 modulations are applied, and resistance to interference is maintained/enhanced; while post ambiguous-errors the distractor stimuli processing is not modulated, and resistance to interference is degraded. These findings corroborate the findings of King et al. (2010), that sensory encoding regulation and behavioural interference control are in some way linked. These results modify the findings of Maier et al. (2011), where PERI was conditional to flanker errors (incompatible stimuli). It is clear from the current study that errors occurring under conditions with high distraction do not always improve interference management in subsequent trials.

The distractor ERP modulations found in this study were only significant in peak-to-peak measures but not absolute amplitudes, however the small p-values indicate the difference is quite distinct. It is possible that activity preceding the P50 and P100 were also modulated and confounded the absolute amplitude values.

The group level direction of P100 modulation opposed the hypotheses of this thesis, as did the occurrence of P50 change. The vibrotactile discrimination task of Bolton & Staines (2011), from which this study borrowed relevant elements of protocol, had demonstrated a P100 amplitude increase with enhanced spatial selective attention to vibrotactile stimuli, but no effect of attention on the P50 component. Hence, the P100 of distractors was hypothesized to be somewhat detectable in post-correct trials (as subjects may rely on the distractor for cuing / reaction time benefits), and become suppressed in post-error trials (as subjects cease to attend to the distractor due to its tendency to mislead), and the P50 to not be significantly altered post error. Yet, in this protocol, the distractor P100 became enhanced post-error, and the distractor P50 exhibited a large suppression. However, as these components are regulated by the DLPFC, while the direction of modulation did not match the hypotheses, the data effectively supports the main purpose of investigation, which is to find evidence that error detection in the ACC recruits the DLPFC for post-error adjustments in selective attention. Additionally, taking into account the higher difficulty of discriminating amplitude on the little finger during simultaneous index finger stimulation (possibly comparing between the digits), and time-sensitive motor task, the current task required more sensory processing effort and vigilant motor planning. In such contexts, the attentional modulations has been shown to occur as early as the P50 stage (Staines et al., 2014).

The opposite directions in which distractor P50 and P100 were modified is interesting. From general comments of participants, the distractor stimulus was also utilized (in addition to serving as a cue to the target) as an amplitude reference for comparison against vibration levels on the little finger (since the index finger was described by participants to be more sensitive). It may be that the two components differentially reflect reliance on the distractor as a cue and as an amplitude reference. If, post-error, accuracy becomes a higher priority than reaction time, the

cuing role should become diminished and comparison role heightened. One hypothesis would be that P50 suppression curbs cuing effect, and P100 enhancement boosts sensory comparison.

Subject-wise analyses showed a correlating trend (Figure 5) between rERN amplitude and post-obvious-error distractor P100 amplitude. The correlation and direction are as hypothesized (Section 2, part 3B), where individuals with larger rERN generated smaller post-error distractor P100. As this relationship is not present for the post-correct P100, it is not due to general subject traits, but more likely that error-related processing is setting the subsequent levels of sensory processing. Interestingly, the rERN and the amount of P100 modulation did not significantly correlate, which could indicate that this neural mechanism operates with absolute levels rather than relative levels.

Subject-wise correlations showed that in general, individuals with smaller post-error distractor P100 are more accurate (Figure 6A) and quicker to respond (Figure 6B) in post-error trials, with particularly large impact to the incompatible case (Figure 15). This relationship is as hypothesized (Section 2, part 3A), and corroborates the general understanding that it is undesirable to leave distracting sensory inputs unfiltered, and the more a person can focus selective attention away from task-irrelevant stimuli, the better performance will be on incompatible trials.

Taken together, one possible explanation for the various phenomena at play is that upon error detection, the DLPFC is recruited to rapidly readjust sensory processing and motor planning to some conservative strategy (possibly to limit cuing effects of the distractor and facilitate stimulus comparison between digits, reflected by group level suppression of P50 and boosting of P100), but the greater the response conflict detected by the ACC during error

commission, the greater it will signal the DLPFC to filter task-irrelevant sensory input, resulting in again a beneficial limiting at the P100 processing stage.

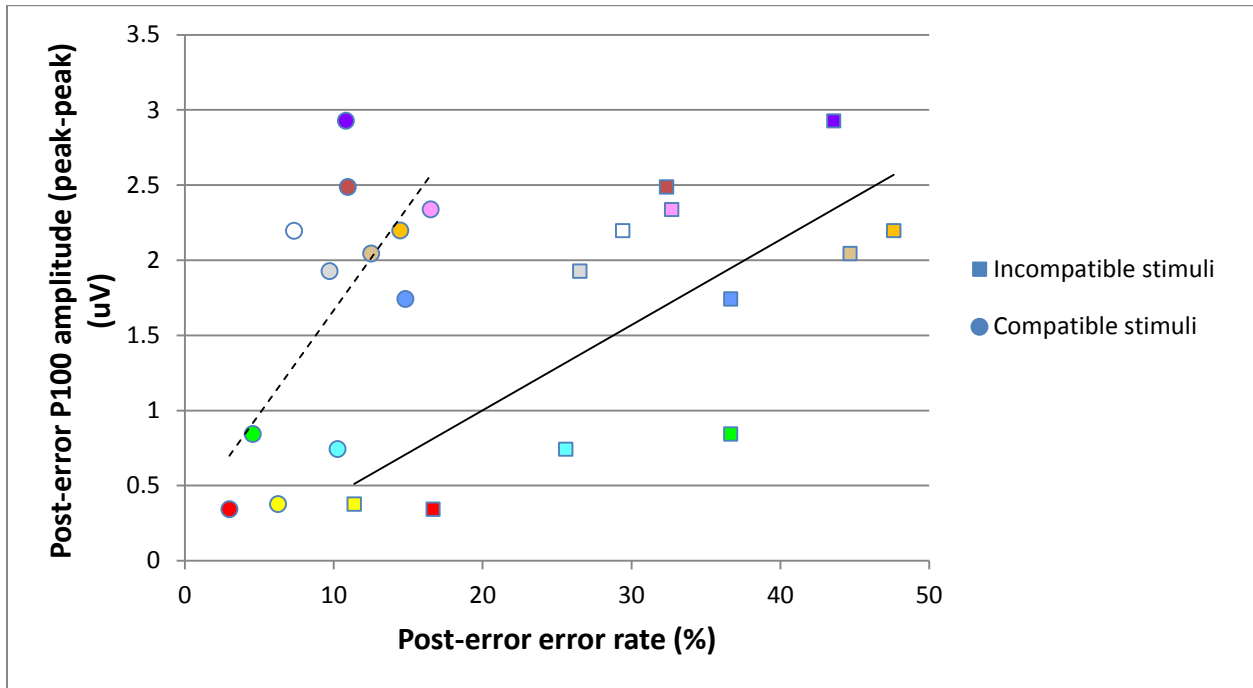


Figure 15: Elaborating on Figure 6A, post-error data is separated by compatible and incompatible stimuli. Smaller P100 was observed in individuals with better post-error accuracy, particularly affecting the incompatible trials.

It was interesting that the correlation between the distractor P100 and performance does not exist in the post-correct trials. One possible explanation is that in the post-correct state, amplitudes of the distractor P100 are at the minimal level possible for each subject, rather than a calibrated level reflective of individual strategy.

The correlation found between reaction time and amount of distractor P100 modulation (regardless of post-correct vs. post-error scenarios), can be interpreted to indicate that individuals expending more effort on adjusting selective attention are slower on average. Comparatively there is a lack of significant correlation between amount of modulation and accuracy. This seems

to imply that greater dynamics in cognitive control, in this task, is not a successful strategy to maximize both speed and accuracy.

Literature has shown (Danielmeier et al., 2011; Pastötter et al., 2010) that there can be direct correlations between post-error behavioural adjustments and ACC activation without related DLPFC activity. Consistent with this finding, in the current study, when only the typical PEBA are considered (i.e. difference between post-error and post-correct performance levels), the only significant relationship is between accuracy-PERI and the rERN amplitude (ACC based). However, as discussed earlier, if post-error behaviour data is examined directly, relationships between the DLPFC guided components and performance emerge.

Chapter 4: General Discussions

4.1 Limitations and Future Directions

It would be beneficial to collect more data on each participant, so as to produce cleaner EEG averages and investigate potential modulations on the N70 component. As well, more trials would enable grouping of trials by properties such as reaction time and subsequently investigating differences in electrophysiological signals. It was undesirable that the four stimuli cases were perceived to be all different levels of difficulty. Ideally in a flanker task, the difficulty level should only be governed by the compatible vs. incompatible criterion. It would be very beneficial to collect on more participants. It was shown (King et al, 2010) that slowing and reduction of interference are two distinct and unrelated forms of post-error adjustment. Hence, these behavioural effects would be conceivably stronger if participants in the current study could be partitioned into the two subgroups (“speeders” and “slowers”) and analysed for error detection and cortical modulation differences. Lastly it was observed that the vibrotactile stimulus signal (25 Hz) itself occasionally leaked into the EEG data (likely through parasitic coupling in the electrical setup, which is difficult to completely eliminate), it may be sufficient to adjust the stimulus vibration frequency such that it is farther from the target ERP component frequencies (20 Hz).

4.2 Conclusions

Using vibrotactile stimuli to the finger tips, the cognitive control aspects of rERN-related post-error adjustments were investigated at high temporal resolution by analysing modulations of early somatosensory event-related potentials. Depending on conscious interpretation of the cause of errors, the DLPFC may enhance SI and SII filtering of task irrelevant stimuli (as reflected by

P50 and P100 components). In subject-wise analyses certain post-error behavioural adjustments were correlated with the rERN, while absolute performance became correlated with P100 amplitude after error commission. These findings will help substantiate and fill in neurocorrelates to theories of error processing, specifically ones such as the conflict model that posit DLPFC involvement in error compensation.

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