ELECTROPHYSIOLOGICAL CORRELATES OF PERFORMANCE MONITORING AND ERROR DETECTION IN RESPONSE TO AUGMENTED FEEDBACK

by

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ABSTRACT

The ability to monitor performance and detect errors is essential for intelligent behaviour. Motor behaviourists have long been interested in how information about the performance of motor skills is used to facilitate learning. Recently, cognitive neuroscientists have also been interested in studying performance monitoring, particularly after the discovery of an event-related potential (ERP) component linked to error processing. This ERP component, aptly termed the error-related negativity (ERN), is observed in response to physical errors and also upon presentation of augmented feedback indicating performance errors or monetary losses. The neural generator of the ERN is thought to be located in the anterior cingulate cortex (ACC), a structure situated in the medial frontal wall of the human frontal lobe. ERN studies along with functional imaging experiments have suggested that ACC acts as part of an error detection system.

In this thesis I challenge the notion that ACC activity, as measured by feedback ERN (f-ERN), is in fact related to errors. Experiment 1 measured participants' expectation of feedback by asking them to estimate their performance on each trial of an anticipation-timing task. The results show that f-ERN is elicited by feedback indicating both correct performance and errors, so long as expected feedback does not match the actual feedback. Experiment 2 replicated the results of Experiment 1 without asking participants to estimate their performance. This was accomplished by presenting false correct feedback in situations in which participants made errors. Taken together, the results of Experiments 1 and 2 suggest that ACC might not be selectively activated by errors, and that f-ERN might not be elicited exclusively by feedback indicating performance errors and monetary losses. I propose that f-ERN is the outcome of a more general system that searches the environment for violations of expectancy.

DEDICATION

To my uncle Antonio Cezar Pereira (1962-2004), for being a great teacher

and for inspiring my curiosity and desire to understand the world better

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I extend my gratitude to my senior supervisor Dr. David Goodman for giving me the opportunity to explore new avenues of research, for challenging me and giving me support. Thank you also to the other members of my supervisory committee: Dr. John McDonald, for opening up the doors to the lab, allowing me to conduct the experiments for this thesis, and providing me with important insight, and Dr. John Dickinson, for always being available and providing insightful comments.

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I cannot go without thanking God and my family for providing me the opportunity to achieve what my goals and to continue dreaming. I feel blessed to have had the opportunities that I have had and for that, I sincerely thank you.

Finally, I would like to thank Roberta for the patience, love and support. You make my life easier and happier. You are the reason why at the end of each day I smile.

QUOTE

"The unexamined life is not worth living"

Socrates (469 BC – 399 BC)

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ACRONYMS

ACC: Anterior cingulate cortex

ANOVA: Analysis of variance

CE: Constant error

CI: Confidence interval

EEG: Electroencephalography

EMG: Electromyography

ERN: Error-related negativity

ERP: Event-related potential

f-ERN: Feedback-locked error-related negativity

LED: Light emitting diode

MFN: Medial frontal negativity

r-ERN: Response-locked error-related negativity

RMSE: Root mean square error

RT: Reaction Time

VE: Variable error

1 Introduction and Review of Literature

"The first step towards amendment is the recognition of error"

Seneca (5 BC - 65 AD)

1.1 Introduction

The recognition that detecting errors is essential for intelligent behaviour and learning is self-evident. Without the ability to identify and utilize information about errors, it would be impossible to develop simple adaptive behaviour, let alone achieve high-levels of motor performance such as that found in elite athletes, top-level musicians and skilled surgeons. Indeed, motor learning is thought to depend on the availability and utilization of information about performance (Magill, 2004). For decades, numerous behavioural studies have been conducted to investigate how errors are processed during motor skill learning (Bilodeau, Bilodeau, & Schumsky, 1959; Rabbitt, 1966a, 1966b, 2002; Rabbitt & Phillips, 1967; Trowbridge & Cason, 1932). Only recently, however, advances in functional brain imaging have allowed researchers to begin understanding how processing of information about the result of actions—more specifically errors—is done in the human brain. Understanding the neural mechanisms underlying error processing is vital for an enhanced comprehension of how error-based learning occurs, of how substance abuse may affect the ability to process errors (Holroyd & Yeung, 2003; Ridderinkhof et al., 2002), and of pathological dysfunctions, such as Attention Deficit Hyperactivity Disorder [ADHD] (Liotti, Pliszka, Perez, Kothmann, & Woldorff, 2005;

Wiersema, van der Meere, & Roeyers, 2005), Schizophrenia (Bates, Kiehl, Laurens, &
Liddle, 2002; Gehring, Himle, & Nisenson, 2000; Hajcak & Simons, 2002; Johannes et
al., 2001; Laurens, Ngan, Bates, Kiehl, & Liddle, 2003; Nieuwenhuis, Nielen, Mol,
Hajcak, & Veltman, 2005), Obsessive Compulsive Disorder [OCD] (Gehring et al., 2000;
Hajcak & Simons, 2002; Johannes et al., 2001; Nieuwenhuis et al., 2005), and Major
Depressive Disorder (Ruchsow et al., 2005; Ruchsow et al., 2004), all associated with
troubled ability to monitor performance and to identify errors.

1.2   Thesis Outline

In this introductory chapter, I define the two main sources of information about
performance (i.e., intrinsic and augmented feedback), discuss how two influential
theories of motor learning view the use of information about performance in the process
of motor learning, and review the literature on the neural basis of performance
monitoring. Increased emphasis is put on a review of the error-related negativity (ERN),
a component of the event-related brain potentials (ERPs) observed upon the perception of
errors. In Chapters 2 and 3, I challenge the notion that the anterior cingulate cortex
(ACC), a structure located in the medial frontal surface of the frontal lobe in the human
brain, is part of a dedicated error detection mechanism, and also that ERN represents the
activity of such a mechanism. This evidence comes from two experiments looking at the
ERN elicited by augmented feedback. I conclude the thesis by summarizing the findings
and suggesting a revision of the current models that attempt to explain ERN.

1.3   Definition of intrinsic and augmented feedback

When performing a motor skill, learners have two potential sources of

information about their performance. Information can be available intrinsically, through

the learners' processing of sensory stimuli related to the motor response, which could

consist of proprioceptive feedback from the limbs involved in the movement and also

visual, auditory and tactile feedback about the performance and outcome of the action.

Information can also be available extrinsically, via an augmented source such as an

observer that may provide the learner with extra information about the *result* of an action

(knowledge of results or KR) and/or the characteristics of the *performance* of this action

[knowledge of performance or KP] (Winstein, 1991). Learning is thought to depend on

the availability of information about performance and is not thought to occur in the

absence of it (Magill, 2004). The usefulness of augmented feedback is thus highly

dependent on the availability and usability of intrinsic feedback. Augmented information

is essential for learning in the absence of intrinsic information about performance

(Adams, 1971; Bilodeau et al., 1959; Trowbridge & Cason, 1932), but may be redundant

in the presence of abundant information from intrinsic sources (Magill, Chamberlin, &

Hall, 1991).

1.4   Adams (1968; 1971) and Schmidt's (1975) motor learning theories

The study of how information is used to drive motor learning and performance

has been at the heart of motor behaviour research, with the work of Adams (1968; 1971)

and Schmidt (1975) being particularly influential. Adams, through his closed-loop theory

of motor learning, suggested that an internal representation is used to detect errors. This

representation, termed the *perceptual trace,* is strengthened by each repetition of a correct

3

response and is used as a reference of correctness. Adams further suggested that another centrally stored representation, which he called the *memory trace,* is used to initiate the movement. In Adams' view, coordinated actions are thus the result of an initial impulse generated by the memory trace and online corrections achieved by comparing feedback coming from the limbs and trunk to the perceptual trace. An interesting prediction of Adams' theory was that errors committed during repetition of skills are harmful to learning. This is because the perceptual trace, as he conceptualized it, was thought to be an average representation of all repetitions of an action and would thus be improved by each repetition of a correct response but would be impoverished by erroneous responses.

Schmidt (1975), on the other hand, suggested that error and variability are vital for learning. According to Schmidt's *Schema Theory,* the representation of correctness, which he termed *recognition schema,* is not degraded by errors but is rather strengthened by them. This is possible because the schema was thought to be composed of general rules linking different actions to their respective outcome. In this way, errors provide enhanced causal relations between variations in task parameters such as force and angle, and the outcome generated by those variations. A focal prediction of this theory was therefore that the absence of information about the outcome of actions greatly impedes learning. Thus, schema theory suggested that augmented feedback plays a major role in learning, a notion that has received substantial empirical support (see Magill, 2004, pp 268-304; Schmidt & Lee, 1999, pp. 323-354 for reviews on the interplay between intrinsic and augmented feedback).

1.5 Neural basis of action monitoring and error detection

Following Adams' and Schmidt's work in the 1970's, numerous behavioural studies were conducted looking at and how information about performance and error is processed during the acquisition of motor skills. It was not until the early 1990's, however, that the study of action monitoring and error detection began to flourish among cognitive neuroscientists. The increase of experiments looking at the neural basis of action monitoring was greatly influenced by advances in techniques that measure brain function non-invasively, and happened in parallel to the behavioural studies, with little inter-disciplinary collaboration.

The study of event-related brain potentials (ERPs) has been particularly helpful in the attempt to understand the neural mechanisms underlying error processing. Shortly after humans commit an error, a negative component of the scalp recorded ERPs (for reviews on ERPs, see Coles & Rugg, 1995; and Picton, Lins, & Scherg, 1995) is elicited. This component was first studied in the early 1990's concomitantly but independently by two different groups. Gehring, Coles, Meyer, & Donchin (1995; 1990) termed the component the Error Related Negativity (ERN) and Falkenstein, Hohnsbein, Hoormann, & Blanke (1990; 1991) termed it Error Negativity (Ne)[1].

The ERN is represented by a negative deflection seen in the averaged ERP signal, starting at around 30 ms after the onset of electromyographic (EMG) activity related to the erroneous response, which has led to suggestions that this component is associated with an efference copy (Bernstein, Scheffers, & Coles, 1995; Coles, Scheffers, & Holroyd, 2001; Rodriguez-Fornells, Kurzbuch, & Munte, 2002). The peak of the negativity occurs at around 100-150 ms following EMG activity onset and around 50-100

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[1] For the purpose of conventionality, the ERN/Ne component will hereafter be referred to as ERN

ms after response onset[2] (Stemmer, Vihla, & Salmelin, 2004). The ERN scalp

representation is maximal fronto-centrally (Allain, Hasbroucq, Burle, Grapperon, &

Vidal, 2004; Ruchsow, Grothe, Spitzer, & Kiefer, 2002; Suchan, Zoppelt, & Daum,

2003), although it has also been reported to be maximal at central locations (Badgaiyan &

Posner, 1998). Equivalent dipole modelling of the scalp-recorded ERN has pointed to a

single neural generator located in anterior cingulate cortex (ACC) as responsible for the

ERN (Bush, Luu, & Posner, 2000; Carter et al., 1998; Elton, Band, & Falkenstein, 2000;

Holroyd, Dien, & Coles, 1998; Pailing, Segalowitz, Dywan, & Davies, 2002; Vidal,

Hasbroucq, Grapperon, & Bonnet, 2000). This is consistent with evidence from error

processing studies using magnetoencephalography (MEG) (Miltner et al., 2003) and

functional magnetic resonance imaging (fMRI) (Carter et al., 1998; Holroyd,

Nieuwenhuis, Yeung, & Cohen, 2003; Holroyd, Nieuwenhuis, Yeung et al., 2004; Kiehl,

Liddle, & Hopfinger, 2000). However, some studies have also suggested that the

supplementary motor area (SMA) (Dehaene, Posner, & Tucker, 1994; Luu, Tucker,

Derryberry, Reed, & Poulsen, 2003; Miltner, Braun, & Coles, 1997) or even a more

distributed network of brain regions including parietal and occipital areas (Stemmer et al.,

2004) might be involved in the generation of the ERN.

The ERN mechanism has been shown to be quite generic as evidence points to a

modality independency of the component at the input and output levels (Falkenstein et

al., 1991; Holroyd et al., 1998). Falkenstein et al (1991) showed that ERN is unaffected

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[2] The difference between the latency to EMG activity onset and response onset is due to the motor reaction time, which is represented by the delay between the detection of EMG activity and the generation of movement triggered by this activity. Motor reaction time is the interval between the time when the muscle(s) involved in movement generation receive input from the central nervous system and the time that those muscles generate torque. This delay is thought to represent physiological processes related to the activation of the motor units (for a complete view on all of the components of reaction time please refer to Schmidt & Lee, 1999, pp. 27-29).

by changes in the modality in which the stimuli are presented, and Holroyd et al. showed that the ERN is also independent of the effectors used to respond (i.e., hands or feet). Evidence also suggests that ERN is not restricted to the erroneous response, but it is also elicited during the observation of errors (Miltner, Brauer, Hecht, Trippe, & Coles, 2004; van Schie, Mars, Coles, & Bekkering, 2004). It seems as though the ERN is sensitive to intention and willed behaviour, as Stemmer, Witzke, and Schonle (2001) showed that intentional error did not elicit the ERN. Affective behaviour (Bush et al., 2000; Vidal et al., 2000) as well as motivation (Rodriguez-Fornells et al., 2002; Swick & Turken, 2002) may influence the amplitude of the ERN, possibly through reward based learning (Pailing et al., 2002).

A similar negative component to the response-locked ERN is observed upon the presentation of feedback indicating errors in performance as well as after feedback indicating whether participants are being financially rewarded or punished (Holroyd, Nieuwenhuis, Mars, & Coles, 2004). This ERP component has been observed in response to feedback indicating errors that include magnitude, such as Reaction Time (RT) (Luu et al., 2003) and time estimation (Mars, De Bruijn, Hulstijn, Miltner, & Coles, 2004), as well as correct/incorrect type feedback (Miltner et al., 1997; Ruchsow et al., 2002).

The feedback negativity, or feedback ERN (f-ERN), peaks around 200-350 ms after feedback onset and is more posterior than the response ERN with maximal amplitudes reported at central (Cz electrode) rather than fronto-central (Fz or FCz electrodes) recording sites (Badgaiyan & Posner, 1998; Holroyd, Larsen, & Cohen, 2004; Holroyd et al., 2003; Luu et al., 2003; Mars et al., 2004; Miltner et al., 1997; Ruchsow et al., 2002). Despite those differences, source localization from electroencephalography

7

[EEG] (Luu et al., 2003; Miltner et al., 1997) as well as fMRI data related to negative

feedback processing (Bush et al., 2002; Holroyd, Nieuwenhuis, Yeung et al., 2004;

Ullsperger & von Cramon, 2003) also points to ACC as the neural generator of the

feedback ERN, suggesting that both feedback-locked and response-locked components

are a product of the same general error detection system (Holroyd & Coles, 2002; Miltner

et al., 1997).

The functional significance of the ERN is still a matter of debate (see Botvinick,

Cohen, & Carter, 2004; Gehring & Fencsik, 2001; and Rushworth, Walton, Kennerley, &

Bannerman, 2004 for recent reviews). On one side it has been suggested that the ERN

reflects a dedicated error detection mechanism (Bernstein et al., 1995; Coles, Scheffers,

& Fournier, 1995; Falkenstein, Hohnsbein, & Hoormann, 1995; Falkenstein et al., 1991).

On the other side, several authors (Botvinick, Braver, Barch, Carter, & Cohen, 2001;

Carter et al., 1998; van Veen & Carter, 2002b) have argued against the ERN being

directly related to an error processing mechanism. Despite numerous studies investigating

the response-locked and feedback-locked versions of the ERN, relatively little has been

done to try to elucidate the mechanism behind this component. Two main theories have

been put forth trying to explain how the ERN is elicited. The conflict monitoring theory

(Botvinick et al., 2001; Botvinick et al., 2004; Carter et al., 1998; Yeung, Cohen, &

Botvinick, 2004) suggests that ERN is elicited as the result of conflict and response

competition—which would be indirectly related to error—but not with error *per se*. This

theory states that situations involving conflict in response production generally lead to

errors and thus give the false impression that errors are the essential component needed to

elicit the ERN. Initial disagreement with the conflict monitoring theory came from the

conception that, according to the theory, it would be expected that correct trials involving more conflict would elicit larger post-response negativities than would correct responses involving less conflict. The evidence available, however, suggested that this was not the case. Correct responses involving conflict did not appear to elicit larger post-response negativities than correct responses that did not involve conflict (Scheffers & Coles, 2000; Ullsperger & von Cramon, 2001). Nevertheless, Yeung, Cohen, and Botvinick (2004) recently proposed a computational model, supported by empirical data, that accounts for the lack of an ERN in correct trials by suggesting that conflict occurs prior to the response in those types of trials. Notwithstanding, Yeung et al's model, as well as other conflict detection explanations for the ERN, fail to explain ERNs elicited to tasks that do not involve response conflict (Ruchsow et al., 2002) and also cannot adequately account for feedback ERN (Miltner et al., 1997) and ERN elicited by the observation of errors (Miltner et al., 2004; van Schie et al., 2004).

Holroyd and Coles (2002) have suggested a different account of the ERN based on dopamine-induced modulation of the ERN. The reinforcement learning theory, as it was termed, suggests that the basal ganglia evaluate ongoing events and generate predictions of success or failure. In the case of success, the basal ganglia induce phasic increases in activity in dopaminergic neurons in the midbrain and in case of failure, phasic decreases in this activity are induced (Schultz, 2002). Dopamine signals then act on the ACC such that phasic decreases in dopamine activity are linked to large ERNs and phasic increases in dopamine activity to small ERNs. As a corollary, this theory predicts that larger errors would entail larger ERNs (Nieuwenhuis, Holroyd, Mol, & Coles, 2004). However, evidence from recent studies with feedback ERN has been at the very best

mixed in regards to this hypothesis. Mars, De Bruijn, Hulstijn, Miltner and Coles (2004) using a time-estimation task, did not find any differences in the size of the ERN in response to feedback of different direction (i.e., over- or under-estimation) and magnitude (i.e., large or small estimation errors). In fact, it appears that the increased information contained in the feedback might have diminished the impact of the valence dimension of the feedback (Nieuwenhuis, Holroyd et al., 2004), as the ERN in this condition had smaller amplitude than in a condition in which feedback only discriminated whether the response was correct or incorrect [this also signalled whether participants were being financially rewarded or punished] (Mars et al., 2004). Contrarily, Holroyd, Larsen, and Cohen (2004) found that the magnitude of the ERN varied monotonically with three different levels of feedback (i.e., worst, middle and best) in a guessing task. These authors further suggested that feedback ERN is context dependent. According to them, the amplitude of the negativity is modulated by the magnitude of the reward relative to the context in which the reward is presented. For instance, in situations in which feedback consists exclusively of losses, large losses (the worst outcome) will have the same effect as small wins (also the worst outcome) in situations containing only wins. Yeung and Sanfey (2004), also using a guessing task, suggested that f-ERN is not sensitive to the magnitude of the reward received, and only to the valence of the feedback (i.e., win or loss). Moreover, the authors found that the P300, an ERP component sensitive to infrequent task-relevant events, was shown to vary according to reward magnitude (i.e., large and small) but not to the valence of the reward (Yeung & Sanfey, 2004). The results of Yeung and Sanfey, however, are compatible with Holroyd, Larsen et al's (2004) view that f-ERN is context dependent. f-ERN amplitude was of equal amplitude when

comparing large losses to large wins and small losses to small wins. This suggests that

the amplitude of the f-ERN is not modulated by the absolute magnitude of the error or of

the reward, but rather that it is determined by the degree of deviation from the expected

to the actual outcome (or feedback about the outcome) of a task (Holroyd & Coles,

2002). However, this proposition has also received mixed evidence from recent studies.

Holroyd et al. (2003) found that larger f-ERNs were elicited by unexpected negative

feedback than expected negative feedback in a guessing task. Conversely, Hajcak,

Holroyd, Moser, and Simons (2005), also using a guessing task, found no differences

between unexpected and expected negative feedback. One common factor between those

studies (i.e., Hajcak et al., 2005; Holroyd, Larsen et al., 2004; Holroyd et al., 2003;

Yeung & Sanfey, 2004) is the fact that they all used guessing tasks that did not allow

participants to generate an estimation of their performance based on their response.

Feedback—positive or negative—was presented randomly according to a predetermined

frequency independent of the participants' response. Manipulations of expectancy were

made by changing the frequency of presentation of feedback. The authors then assumed

that participants' expectancy would change accordingly. For instance, Holroyd et al.

(2003) had two different conditions in which participants received negative feedback on

25% or 75% of the trials. Similarly, Hajcak et al. (2005) had three different conditions in

which negative feedback was presented on either 25%, 50% or 75% of the trials. The

authors reasoned that participants would create expectations based on the probability that

each type of feedback was presented. However, it is possible that participants'

expectation changes on a trial by trial basis and this information is lost due to the

averaging procedures needed for ERP analysis (Picton et al., 1995).

1.6 Purpose and hypotheses

In the experiments presented in Chapters 2 and 3 of this thesis I was interested in investigating the hypothesis that ERN is modulated by a deviation between the expected and actual outcome in a perceptual-motor task. Unlike the guessing and gambling tasks used in the experiments mentioned above, perceptual-motor tasks provide participants with intrinsic sources of feedback. Consequently, instead of creating an expectation of the content of the augmented feedback based on the probability of negative (or positive) feedback presentation, participants can estimate their performance on a trial-by-trial basis by comparing sensory information coming from sources intrinsic to the response to what they presume a correct response would be like. When practising motor skills, besides executing the task, learners plan, anticipate the outcome, and then evaluate the action. Based on the final evaluation, it is possible to reinforce or update the internal model of the response, and also the stored representation of correctness. Thus, the evaluation of the outcome might at the same time lead to suppression of a motor program used to generate an incorrect response and reinforcement of the internal representation used to evaluate the outcome or vice-versa. In tasks that provide intrinsic feedback, it is therefore possible to evaluate if the f-ERN is a product of information indicating an error in execution, an error in estimation of the outcome, or both.

The interplay between intrinsic and augmented feedback also allows testing of another prediction of the reinforcement-learning theory (Holroyd & Coles, 2002). According to this theory, the ERN is elicited to the earliest source of information about an error. As a consequence, when participants identify an error through intrinsic feedback, an ERN should not be expected following augmented feedback that is

redundant. Given this, I chose to use an anticipation timing task that would allow participants to generate an estimation of the result of their response but would not provide participants with sufficient information to accurately predict the outcome of the task on every trial.

In a manner similar to what has been proposed to response ERN through the conflict monitoring theory, I hypothesized that feedback ERN is not elicited by the activity of a dedicated error detection system. Rather, I suggest the possibility that f-ERN is part of a more general system that monitors deviations from expectancy (Luu & Pederson, 2004; Pritchard, Shappell, & Brandt, 1991).

2 EXPERIMENT 1: Performance Monitoring in Anterior Cingulate is Not Error Dependent[3]

2.1 Introduction

As outlined in Chapter 1 of this thesis, two primary theories have been put forth in an attempt to explain what gives rise to the ERN. According to the reinforcement-learning theory, the ERN is elicited when events are evaluated to be *worse* than expected (Holroyd & Coles, 2002). This theory proposes that the ERN is the end result of a sequence of neurophysiological changes in the basal ganglia, midbrain, and ACC: When performance is evaluated to be worse than expected, the basal ganglia induce a phasic decrease in the activity of dopaminergic neurons in the midbrain, which leads to increased activity in the ACC and a larger scalp-recorded ERN. According to an alternative conflict-monitoring theory, the r-ERN is elicited by response competition rather than error detection *per se* (Botvinick et al., 2001; Botvinick et al., 2004; Carter et al., 1998; Yeung et al., 2004). This theory, however, does not explain f-ERN (Botvinick et al., 2004; Yeung et al., 2004).

Although these theories provide reasonable accounts of the ERN, neither can account for one observation: A similar (albeit smaller) medial frontal negativity (MFN) is elicited by feedback about correct responses or monetary rewards (de Bruijn, Hulstijn, Meulenbroek, & Van Galen, 2003; Hajcak et al., 2005; Holroyd, Larsen et al., 2004; Mars et al., 2004; Muller, Moller, Rodriguez-Fornells, & Munte, 2005; Sato et al., 2005;

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[3] This chapter is a modified version of a manuscript prepared for publication and co-authored by Drs. John J. McDonald and David Goodman.

Yeung & Sanfey, 2004). This MFN has been given relatively little attention, but it may have important implications for the understanding of the performance-monitoring functions of the ACC. In particular, it may indicate that positive[4] feedback also elicits f-ERN. This would indicate that f-ERN is not associated with errors and that ACC is not selectively activated by errors or evaluations of poor performance.

Here I investigated the hypothesis that ACC acts not solely as part of an error-processing system that is triggered by negative feedback but as part of a broader system that detects deviations from expectancy. This explanation posits that f-ERN is an outcome of a monitoring process that compares the participants' expected performance to the performance indicated by the feedback signal. Specifically, f-ERN is hypothesized to arise when a mismatch is detected between the estimated performance and the reported performance. According to this explanation, f-ERN could be elicited by positive as well as negative feedback, so long as the reported performance deviates from the estimated performance. Although the fact that f-ERN is generally observed exclusively in response to negative feedback is seemingly inconsistent with our expectancy-deviation hypothesis, social psychologists have demonstrated that humans are biased when making judgments when uncertain (Tversky & Kahneman, 1974) and are overly optimistic when estimating their performance (D. T. Miller & Ross, 1975). According to the expectancy-deviation hypothesis, such a bias would make it difficult to observe f-ERN to positive feedback conditions since participants would seldom expect negative events and thus would rarely experience a mismatch between an expected error and a reported correct response.

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[4] For the purposes of this thesis, I define negative feedback as feedback indicating performance errors and/or monetary losses and positive feedback as feedback indicating correct behaviour and/or monetary wins.

The goal of the current study was to determine whether positive as well as negative feedback could elicit f-ERN when participants' expectations on each trial were known. To measure expectations, I asked participants to estimate their own performance on each trial after making their response and before receiving feedback. The rationale used here was that participants would come to expect augmented feedback that was consistent with how they thought they had performed. The inclusion of the performance estimates thus enabled me to compute f-ERN separately for trials on which the expected performance and the reported performance matched or mismatched.

2.2 Methods

2.2.1 Participants

Fourteen healthy members of the university community (7 males, 7 females, mean age = 22.1 years, range = 19-28 years) volunteered to participate in the study (three received course credit for their participation). Participants were all right-handed, experiment-naïve and had normal or corrected-to-normal vision. Participants signed informed consent according to procedures approved by the university ethics committee prior to their participation and received $15 upon completion of the experimental session. Due to excessive noise in the EEG signal, data from one participant were excluded from f-ERN analysis. Data from this participant were nevertheless included in all behavioural analyses. Data from the last two blocks of the testing session of another participant were lost due to a system malfunction. This participant's data were excluded from CE, VE and RMSE analyses, but were included in all other analyses.

2.2.2 Apparatus and task

The apparatus used for this experiment consisted of 24 Light Emitting Diodes (LEDs) mounted side-to-side on a box 3 cm apart from each other. Participants sat in front of a desk in a dark room and had a computer monitor, the LED box, a mouse and an estimation panel in front of them (Figure 2.1). The task started with the sequential lighting of the LEDs, giving the illusion of a moving stimulus. The LED box was positioned such that the LED row was in the horizontal plane and the lights appeared to move right-to-left or left-to-right depending on the trial. Participants were instructed to press the right mouse button with their left hand in coincidence with the moving stimulus

reaching the end of the LED sequence. To serve as a reference of the target location, the last LED in sequence was always on. To increase difficulty of the task and estimation of performance, I occluded the latter half of the stimulus trajectory and asked participants to use the information from the earlier half to anticipate when the stimulus would reach the target. There were four different speeds for the moving stimulus. The time between the onset of the first LED in the sequence and the target time (onset of the last LED in the sequence) was either 480 ms, 600 ms, 720 ms or 840 ms. On each block of trials a random combination of two speeds was used. The direction of the moving stimulus was randomly assigned to each block to control for any potential stimulus laterality effects, as well as to make the task more difficult. Direction remained constant throughout the trials of the block.

After responding to the moving stimulus, participants were prompted to estimate their performance. A question mark that was displayed on the computer screen cued participants to press one of five buttons on an estimation panel with their right hand. The buttons represented: "I am very confident that I was early", "I think I was early", "I think I was right on target", "I think I was late" and "I am very confident that I was late". After the estimation, participants received feedback about their performance signalling that they had responded early ("-"), late ("+") or right on target ("0") [see figure 2.2 for a schematic representation of all events happening during each trial]. Feedback was determined based on the following procedure: Error was computed online as the time difference between the response and the time the moving stimulus reached the target such that early responses were represented by negative errors and late responses by positive errors. Trials were considered on target if the error fell within a 250 ms time band centred

on the target (i.e., from -125 ms to 125 ms post-target). Responses were considered early if the error was less than the negative edge of the time band and late if error was greater than the positive edge of the time band. This time band changed throughout the experiment based on participant's performance. After every incorrect trial, the size of the time band was increased by a factor of 1.10 and after each correct response the size of the time band was decreased by a factor of 0.85. However, there was a limit on how much the time band could decrease as it was never less than 120 ms (-60 to 60 ms).

Before recording commenced, participants were instructed on how to perform the task and were told that their estimation of performance was only being used as an index of how they thought they were doing. It was stressed that their primary task was responding to the moving stimuli, and that they would be evaluated on this task. They were further instructed that every time they responded on target they would win a bonus of 4 cents and every time they responded early or late they would lose 4 cents—this procedure was only used as a motivational tool, as participants would unknowingly receive the same amount at the end of the testing session. The experimental session consisted of 850 trials divided into 17 blocks of 50, and lasted approximately 90 minutes. Participants had self-controlled rest breaks halfway through each block and a mandatory 5 second break followed by a self-controlled period at the end of each block. To avoid contamination by electro-oculographic (EOG) activity, I asked participants to blink as little as possible and not to move their eyes by fixating their vision on a marked central location on the computer screen during the trials.

2.2.3   Electrophysiological recording and measures

Electroencephalographic (EEG) activity was recorded using tin electrodes attached to an elastic-fabric cap (Electro-Cap International, Inc), arranged according to the 10-10 international system (American-Electroencephalographic-Society, 1994), from midline channels FPz, Fz, FCz, Cz, Pz and Oz. Electrodes were also placed on the external canthi of both eyes and on the left mastoid. All scalp electrodes were referenced to an electrode placed on the right mastoid. Electrode impedances were kept below 10 kΩ for all scalp electrodes and below 5 kΩ for the electrodes placed on mastoids and on the external canthi of both eyes. EEG signals were amplified by a gain of 20,000 and a band pass of 0.1-80 Hz, digitized at 500 Hz and stored on a microcomputer for offline averaging. Automated artefact rejection was done offline to discard trials contaminated by eye movements and blinks or when amplifier blocking occurred. I extracted 800 ms epochs (0 to 800 ms) time-locked to feedback presentation (baseline: -200 ms to feedback onset). These epochs were digitally low-pass filtered at 12 Hz (Ford, Whitfield, & Mathalon, 2004; Gehring & Willoughby, 2004; Holroyd et al., 2003; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004), averaged for each participant and re-referenced to the average of both mastoids.

I measured f-ERN amplitude base-to-peak on the averaged waveforms at electrodes Fz, FCz and Cz, where f-ERN is reported to be maximal (Holroyd, Larsen et al., 2004; Holroyd et al., 2003; Luu et al., 2003; Mars et al., 2004; Miltner et al., 1997), according to the following procedures: First I identified the most positive peak 160-270 ms following feedback presentation. I then found the most negative peak that followed this positivity in a window extending to 350 ms after feedback onset, and the most positive peak following the negativity up to 500 ms from feedback presentation. Peaks

were defined as samples[5] that were more positive/negative than the preceding and following samples and of the average of the five preceding and following samples. f-ERN amplitude was quantified as the voltage difference between the negative-going peak and the average of the preceding and following positive-going peaks (Yeung & Sanfey, 2004). If no negative-going peaks were found in the time window defined above or if the negative-going peak found was less than 0.5 μV more negative than either the preceding or following positive-going peaks, the ERP component was defined as a positivity and f-ERN amplitude was considered 0 μV. Along with the computer algorithm used for this procedure, I visually inspected each individual averaged waveform to ensure that the algorithm had picked a valid peak (Picton et al., 1995).

2.2.4 Behavioural recording and measures

I calculated constant error (CE) as a measure of response bias, variable error (VE) as a measure of consistency and root mean square error (RMSE) as a measure of accuracy. RMSE is thought to represent the best overall measure of performance accuracy (Henry, 1975) and is defined as:

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum\left(x_i - t_i\right)^2}$$

Where n is the number of trials, x_i is the time that the response on trial i occurred and t_i is the target time on trial i. These measures were accurate to 2 ms given the system's sample rate of 500 Hz. I excluded trials that had absolute errors greater than 400 ms from the CE, VE and RMSE analyses. The mean number of trials excluded per participant was

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[5] Samples are data points corresponding to a voltage value. Given the sampling rate of 500 Hz, the time interval between each sample was 2 ms.

7.5 (*standard deviation* = 6.7), representing less than 1% of the total trials. I further

calculated the percentage of trials participants responded on target, early and late, as well

as the percentage of trials that participants estimated to be on target, early and late, and

the percentage of trials in each condition that were accurately estimated. For the purpose

of the calculations above, I collapsed 'I am very confident that I was early/late' with 'I

think I was early/late' estimations, such that I only used three levels of estimation (i.e,

early, on target and late).

2.2.5 Statistical Analysis

I used repeated measures analyses of variance (ANOVAs) for all statistical

comparisons involving more than two conditions and paired-samples t-tests for all

statistical comparisons involving two conditions. All behavioural analyses involved

single factor ANOVAs or t-tests. f-ERN amplitude was analyzed on the three electrodes

in which f-ERN is most commonly reported to be maximal (Holroyd, Larsen et al., 2004;

Holroyd et al., 2003; Luu et al., 2003; Mars et al., 2004; Miltner et al., 1997) through a 3

(electrode: Fz, FCz and Cz) by 2 (mismatch: present and absent) by 2 (feedback: correct

or error) factorial ANOVA with repeated measures on all factors. Whenever a violation

of the assumption of sphericity was detected, I used the Greenhouse-Geisser correction of

degrees of freedom, and to break down any significant main effects I performed pairwise

comparisons with Bonferroni adjustments for multiple comparisons. Confidence levels

were set at .95 for all statistical tests.

2.3 Results

2.3.1 Behavioural results

Participants demonstrated no clear bias towards responding early or late as shown by measures of constant error (CE) (M = -3.8 ms, 95% confidence interval [CI] = -15.5 ms, 8.0 ms), and no significant changes in CE were observed over blocks ($F_{16, 192}$ < 1)[see Table 2.1 for means and standard errors of individual participants]. Participants had a mean variable error (VE) of 85.3 ms, a mean root mean square error (RMSE) of 87.8 ms and showed learning effects, improving their consistency and accuracy significantly over blocks (VE: $F_{16, 192}$ = 7.24, p < .001, ε = .37; RMSE: $F_{16, 192}$ = 7.87, p < .001, ε = .27, see Figure 2.3 for a graphical representation of the CE, VE and RMSE results). Post-hoc trend analyses showed significant linear and quadratic trends for both VE ($F_{1, 12}$ = 22.60, p < .001; and $F_{1, 12}$ = 14.42, p < .005 respectively) and RMSE ($F_{1, 12}$ = 22.05, p < .001; and $F_{1, 12}$ = 12.00, p < .01 respectively)

I used paired t-tests to compare the percentage of trials that participants responded early and late, and the percentage of trials that participants estimated to be early and late, and found no differences (p > .2). Given this, I collapsed the two conditions into a single 'error condition'. The results presented here and on Figure 2.4 reflect comparisons using the collapsed error condition.

As expected, participants were overly optimistic about their performance (Figure 2.4). Not only did they judge their responses to be on target more often than off target (t_{13} = 6.43, p < .001), they judged their responses to be on-target more often than was actually the case (t_{13} = 6.03, p < .001) and to be off-target less often than was actually the

case ($t_{13} = 6.03$, $p < .001$). A corollary of the above findings is that participants correctly estimated on-target trials more often than off-target trials ($t_{13} = 8.03$, $p < .001$).

2.3.2 Electrophysiological results

To investigate the neurophysiological correlates of performance monitoring, I first examined the ERP waveforms to positive and negative feedback, collapsed over the expected performances (on- and off-target). Consistent with prior work, I found an ERN 200-350 ms after the onset of negative feedback and a much smaller MFN 200-350 ms after the onset of positive feedback[6] (Figure 2.5A). To test the predictions stemming from the expectancy-deviation hypothesis, I next sought to determine whether such negative-going ERP deflections were present when participants received unexpected positive or negative feedback about their performance. Similar to what was done for the behavioural results, I collapsed the early and late trials to create a general 'error condition' (see Figure 2.6 for a graphical representation of all conditions). The ANOVA used to analyze the amplitude of the negative-going deflections showed a significant electrode main effect ($F_{2, 24} = 7.92$, p $< .01$, $\varepsilon = .65$), indicating that f-ERN amplitude was smaller at Cz than at Fz and FCz ($p < .05$ for both comparisons) and not reliably different at Fz and FCz ($p > .3$). As predicted, there were no significant differences between f-ERNs elicited to correct ($M = 3.6$ μV) and error ($M = 3.5$ μV) feedback ($F_{1, 12} < 0.1$) when collapsed over whether there was a match or a mismatch between the expected and actual outcome. As hypothesized, on the other hand, a significant mismatch main effect ($F_{1, 12} = 29.18$, $p <$

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[6] The relative frequency of early and late feedback was much smaller than correct feedback. Because of this, it was expected that larger P300 waves would be elicited to error signals shifting f-ERN down [i.e., the f-ERN is observed on top of a larger positive-going deflection] (Yeung & Sanfey, 2004), which was indeed the case. Consequently, the waveforms were compared in light of the presence or absence of a negative-going peak within the time window in which f-ERN is known to be elicited (200-350 ms) rather than by creating difference waves.

.001) shows that trials in which participants expectation did not match actual feedback (M = 5.2 μV) elicited significantly larger f-ERNs than trials without this mismatch (M = 2.0 μV). Negative feedback elicited a f-ERN when the participants expected to be on-target but not when they expected to be off-target (Figure 2.5B). Such a result follows from the expectancy-deviation hypothesis, which predicts a f-ERN to be observed only when feedback fails to match expected performance, and with the reinforcement-learning theory (Holroyd & Coles, 2002), which would predict a f-ERN to be observed only when events are worse than expected. The ERPs elicited by positive feedback, however, are consistent with only the expectancy-deviation hypothesis. Specifically, positive feedback elicited a f-ERN (or MFN) when participants expected to be off-target; the positive feedback elicited no f-ERN when participants expected to be on-target (Fig. 2.5B) [see Table 2.2 for means and standard errors of individual participants].

2.4 Discussion

The results of this study demonstrate that, as hypothesized, f-ERNs were elicited by feedback indicating both errors and *correct* performance if there was a mismatch between the expected and the actual outcome. Conversely, f-ERN was practically non-existent when expectancy matched the actual outcome. This pattern of results indicates that the f-ERN is not specifically related to errors and it suggests that the ACC does not act exclusively as part of a specialized error-related system. I found evidence that f-ERN is elicited in response to mismatches between expected and actual outcome irrespective of the valence of the feedback. The f-ERN may represent the activity of a more general monitoring system that is also responsible for the MFN observed in response to positive feedback and possibly to other MFNs associated with expectancy-deviation (Luu & Pederson, 2004; Pritchard et al., 1991). For instance, the sequence-deviant N2 observed in serial reaction-time tasks is elicited by a violation of a learned contingency. Whenever a stimulus fails to conform with the learned sequence a large MFN is elicited (Eimer, Goschke, Schlaghecken, & Sturmer, 1996). Oddball N200 (Holroyd, 2004) and the NoGo N2 in the GoNoGo paradigm (Bokura, Yamaguchi, & Kobayashi, 2001) are observed upon presentation of task-relevant infrequent stimuli (Pritchard et al., 1991). The "Aha!" N380 is elicited when an unforeseen solution to a problem is presented (Mai, Luo, Wu, & Luo, 2004). Similar to the f-ERN, these MFNs are tied to mismatches between expected and actual stimuli signalling increased need of cognitive control, and are thought to represent the activity of an ACC generator. f-ERN appears functionally similar to the other MFNs in that they are all elicited by unexpected stimuli, but different in that the expectancy for f-ERN is modulated by predictions of success or failure as

opposed to learned contingencies in the case of the sequence deviant N2, the frequency of events in the case of oddball N200 and the NoGo N2, and the failure to identify a suitable solution to a problem in the case of the "Aha!" N380. It is nevertheless possible that these components represent the same underlying mechanism responsive to violations in expectancy. I suggest the reason why error feedback is found to elicit larger negativities than correct feedback lies in the fact that humans tend to expect to be correct (or to receive financial reward) more often than not (D. T. Miller & Ross, 1975). The behavioural results of this experiment are in accordance with this notion (Figure 2.4). Given that event-related procedures rely on averaging a large number of trials to improve signal to noise ratio (Picton et al., 1995), differences in the percentage of trials presenting mismatches between expected and actual feedback in each condition might account for the difference in f-ERN amplitude. For instance, in this study when averaging simply based on the type of feedback presented (Figure 2.5A), trials with mismatches between expected and actual feedback carried over three times as much weight in the final averaged ERP of error trials than of correct trials (66.4% and 22.1% of total trials in each condition respectively, see Figure 2.4 for details). This results in the legitimate observation that larger negativities are elicited to error feedback (Figure 2.5A), but in the false interpretation that f-ERN and ACC are selectively sensitive to error information.

An alternative explanation for the present results is that participants may have perceived an error to have occurred whenever the feedback did not match their own evaluation of performance. Although I cannot rule out this possibility, this alternative is unlikely for two reasons. First, the experimental procedures were designed with *a priori* knowledge of this potential confound. Instructions strongly emphasized the estimation

task was merely for the purposes of monitoring the participants' perception of accuracy and that the only task on which they were evaluated was responding to the moving stimulus. Furthermore, participants were told that they would receive financial bonuses based on how well they performed (and consequently on the type of feedback presented to them). It was accentuated they would earn money whenever they received feedback indicating correct responses and lose money whenever they received feedback indicating they responded early or late. Second, and perhaps more importantly, a large body of evidence from previous studies supports our interpretation. I discuss them next.

One major prediction of my proposition is that an equivalent negativity to the f-ERN should be elicited to correct feedback, only on smaller scale. Despite receiving little attention, correct feedback negativities have been observed often (de Bruijn et al., 2003; Hajcak et al., 2005; Holroyd, Larsen et al., 2004; Mars et al., 2004; Muller et al., 2005; Sato et al., 2005; Yeung & Sanfey, 2004). Moreover, increasing the relative frequency of negative feedback should enlarge this correct feedback negativity by changing the expectation of participants. Empirical evidence from Hajcak *et al.* is supportive of this (Hajcak et al., 2005). Another prediction of the mismatch account of the f-ERN is that negativities would not be elicited, or would at least be largely reduced, in situations where participants have reliable information about the error prior to the presentation of feedback. de Bruijn and colleagues (2004) presented feedback to participants indicating their performance on a Flankers task. In this paradigm, participants have to discriminate the central letter (H/S) in a letter string (HHHHH, HHSHH, SSSSS, SSHSS) by pressing different buttons. Given that errors in this task do not go unnoticed, augmented feedback is redundant and according to the expectancy-deviation interpretation of f-ERN, should

not activate ACC. Consistent with this notion, the authors found no differences between correct and error feedback ERPs, and importantly no ERN-like activity. Holroyd and Coles (2002) found similar results with modelling and experimental data. In their study, however, they manipulated how much participants (or the model) could predict the outcome of a probabilistic learning task by using intrinsic task-related information. They found that f-ERNs were gradually reduced in the presence of more predictive information, leading them to suggest that ERN reflects a prediction error and that "...feedback stimuli that disconfirm these predictions should elicit relatively large ERNs, whereas feedback stimuli that confirm these predictions should elicit relatively small ERNs". They further suggested that "the ERN is produced when the system first detects that the consequences of an action are worse than expected". Our evidence is in agreement with the notion that ERN reflects a prediction error and is thus produced in response to the first evidence of this mismatch. However, our data are inconsistent with the notion that f-ERN is elicited when events are *worse* than expected, suggesting that it is elicited when events are simply *different* than expected.

A recent study (Muller et al., 2005) supports this. Müller and colleagues presented a red "X" following incorrect responses and a blue "X" following correct responses on 80 % of trials of an association learning task. On the remaining 20 % of trials, 'equivocal' ("??") feedback was presented and participants were told that in those cases the computer was unable to determine whether the response was correct or erroneous. Participants could not estimate when they would receive this form of feedback as it was presented randomly, therefore generating mismatches between expected and actual feedback. Despite not providing any information about performance, the equivocal feedback

elicited a MFN that was 3 times the amplitude of the one elicited to error feedback. Our data also account for the observation that tasks that give participants a chance to generate predictions based on intrinsic task-related information (de Bruijn et al., 2003; Mars et al., 2004) (and thus allow learning by comparing estimated and actual feedback) have been linked to smaller f-ERNs than guessing and gambling tasks (de Bruijn et al., 2004), in which participants are not able to estimate the outcome and are likely biased towards expecting rewards (Gilovich, 1983).

Although not directly related to errors, the expectancy-deviation account I propose to explain ACC activity observed in response to errors can nevertheless be seen as a simple mechanism for error detection, learning and adaptive behaviour. ACC might act as part of a system that drives learning by identifying errors in the internal representation used in comparison with intrinsic task-related information to generate predictions of success and failure. This would signal an increased need for cognitive control (Brown & Braver, 2005; Kerns et al., 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ridderinkhof & van den Wildenberg, 2005) to allow an update in the internal model of 'what to do' and 'what not to do' as well as improve the use of external information to judge performance. This expectancy-deviation account of the f-ERN is consistent with an explanation of the ERN based on phasic dopaminergic activity induced by basal ganglia (Holroyd & Coles, 2002). Although traditionally linked to rewards, a recent alternative theory suggests that dopaminergic-neurone activity might not be reward-related but rather functionally linked to the process of switching attention to unexpected, behaviourally-relevant stimuli (Redgrave, Prescott, & Gurney, 1999). This is supported by empirical evidence from single cell studies showing that dopamine neurons

are activated by salient stimuli signalling the need for behavioural change regardless of the valence of the simuli [i.e., rewarding or aversive] (Horvitz, 2000), and also from functional imaging studies showing that both striatum and ACC are activated by unexpected non-rewarding stimuli (Davidson et al., 2004; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004).

In this study I demonstrated that f-ERN is not directly related to errors, similarly to what had been proposed previously for r-ERN (Botvinick et al., 2001; Botvinick et al., 2004; Carter et al., 1998; Yeung et al., 2004). Alternatively, I suggest an expectancy-deviation explanation of the f-ERN, which could also account for other ERP components attributed to ACC activity (Bokura et al., 2001; Eimer et al., 1996; Holroyd, 2004; Mai et al., 2004) as well. The explanation for an increased MFN elicited by errors might lie in the social phenomenon that humans tend to be overoptimistic when judging their own performance (D. T. Miller & Ross, 1975). Taken together, this evidence appears to show that ERN might not be error-related after all. I suggest it is time for a re-evaluation of the idea that ACC is part of an error processing system, a notion that has been largely influenced by a label developed in the early days of the study of the (perhaps wrongfully termed) error-related negativity.

Table 2.1: Mean constant error (CE) in milliseconds for each block of trials of each individual participant

Paticipant	Block																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
P2	-8	-10	-58	-49	-35	-57	-51	-36	-53	6	-1	-27	-35	18	-24	6	-20
P3	-69	-123	-18	-43	42	94	116	36	30	50	66	61	65	23	55	40	59
P4	-38	8	-36	41	-75	-14	-21	56	-38	-1	20	10	3	-35	-21	26	-15
P5	-82	-95	-37	-22	-59	-31	-36	-18	-11	-48	-17	-77	-27	-36	-6	-37	-15
P6	72	-1	-24	-26	21	-15	11	19	35	-11	30	11	19	-19	-15	12	3
P7	-17	-22	18	54	21	19	2	4	-18	-6	10	-2	17	12	-14	-13	2
P8	20	-14	-33	-17	5	1	-27	-21	27	-1	-12	21	-5	1	-5	-17	-56
P9	22	44	12	63	-7	38	7	8	18	-15	-16	9	-25	-26	0	11	-9
P10	52	34	-36	-5	32	-22	-30	-31	-51	-35	-41	-69	-41	2	7	3	-20
P11	34	4	-24	-36	-4	-32	-12	-36	-3	-45	9	-27	-36	-12	-29	-28	-34
P12	178	183	75	16	38	18	59	50	35	2	23	-40	30	5	35	-8	9
P13	-14	-14	-68	-15	-35	-42	-19	-46	-4	-20	-34	35	-20	-11	18	-8	3
P14	26	-3	-15	3	-45	-14	-13	-8	-8	-11	-5	-14	-17	-1	-7	-5	9
Mean	14	-1	-19	-3	-8	-4	-1	-2	-3	-10	2	-8	-6	-6	0	-1	-6
Standard Error	18	19	10	10	10	11	12	9	8	7	8	11	8	5	6	6	7

Note: Negative values indicate early responses and positive values indicate late responses. The two last rows represent the total mean and standard error for all participants. Data from Block 17 of P1 were lost due to a system malfunction. This participant's data were excluded from CE analysis and are not shown in this table.

Table 2.2: Mean medial frontal negativity amplitude (in microvolts) for individual participants

Participant	Electrode											
	Fz				FCz				Cz			
	Estimated/Actual Feedback Pair				Estimated/Actual Feedback Pair				Estimated/Actual Feedback Pair			
	C/C	E/E	C/E	E/C	C/C	E/E	C/E	E/C	C/C	E/E	C/E	E/C
P1	-1.10	0	-3.58	0	0	-0.79	-3.77	0	0	0	-3.94	0
P2	0	0	0	-2.17	0	-0.56	0	-2.45	0	0	0	-1.93
P3	0	-2.26	-4.62	-4.48	0	-2.30	-5.13	-5.38	-2.81	-2.38	-5.72	-5.19
P4	-5.13	-3.83	-5.61	-7.00	-5.98	-4.54	-6.63	-7.10	-5.53	-4.50	-6.79	-7.12
P5	0	-4.85	-6.65	-13.55	0	-4.20	-5.01	-10.75	0	-2.53	-3.39	-8.78
P6	0	-5.29	-6.95	-4.94	0	-4.90	-6.39	-4.08	0	0	0	-3.21
P7	-2.49	-1.29	-6.71	-11.51	-2.08	0	-7.10	-10.68	-0.85	0	-4.97	-7.41
P8	-7.51	-5.94	-11.60	-17.42	-6.44	-5.34	-9.87	-15.49	-3.99	-4.82	-7.80	-12.52
P9	-5.10	-5.15	-7.21	-8.75	0	-5.09	-5.63	-7.49	0	-5.18	-4.90	-6.25
P10	-1.58	-1.70	-1.43	-1.24	-1.57	-1.33	-1.42	-1.17	0	0	-1.22	-1.38
P11	-1.99	0	-5.03	-5.48	0	0	-5.88	-5.27	0	0	0	0
P12	-2.84	-4.88	-5.36	-6.74	-2.13	-3.57	-3.42	-5.64	-2.03	-3.45	-3.19	-4.70
P13	0	0	-5.36	0	0	0	-5.95	-2.81	-0.85	0	-6.75	0
Mean	-2.13	-2.71	-5.39	-6.40	-1.40	-2.51	-5.09	-6.02	-1.23	-1.76	-3.74	-4.50
Standard Error	0.68	0.65	0.79	1.47	0.64	0.60	0.70	1.20	0.51	0.59	0.76	1.08

Note: Amplitudes are separated by the electrodes of interest and according to the estimated/actual feedback pair. The bottom two rows represent the total Mean and Standard Error. C/C = Correct/Correct, E/E = Error/Error, C/E = Correct/Error, E/C = Error/Correct.
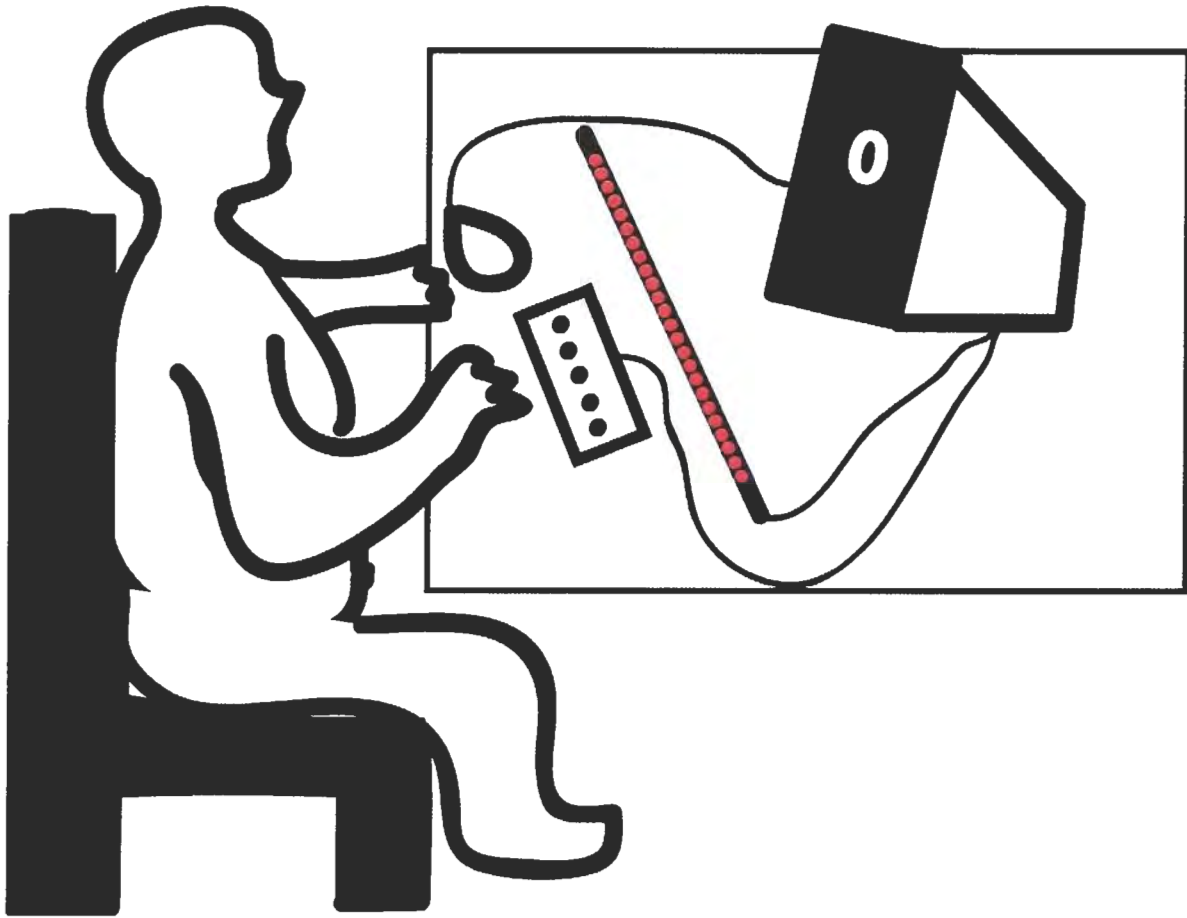
Figure 2.1: Schematic view of the apparatus and experimental setup
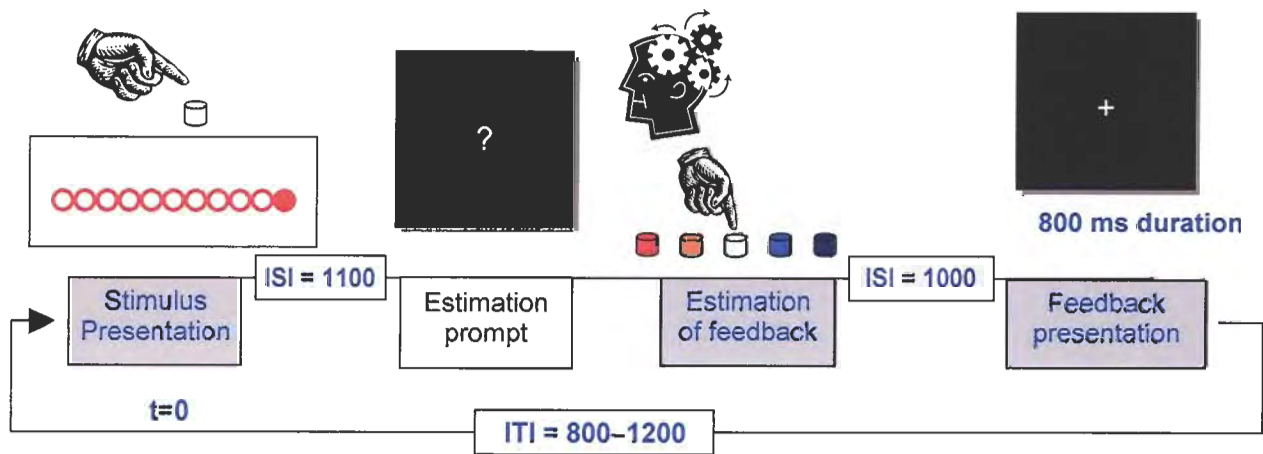
Figure 2.2: Events during a typical trial

Stimulus presentation starts at time (t) zero, with response ideally occurring in coincidence with the moving stimulus reaching the target location. This is followed by a prompt of participants' estimation of the feedback on a five-option scale. The time between the estimation prompt and the estimation is variable as it depends on how much time the participant takes to choose and press the appropriate button. Following estimation, feedback is presented (duration of feedback presentation is 800 ms). Inter-stimulus intervals (ISI) are set at 1000 ms and inter-trial interval (ITI) is set at 800-1200 ms.
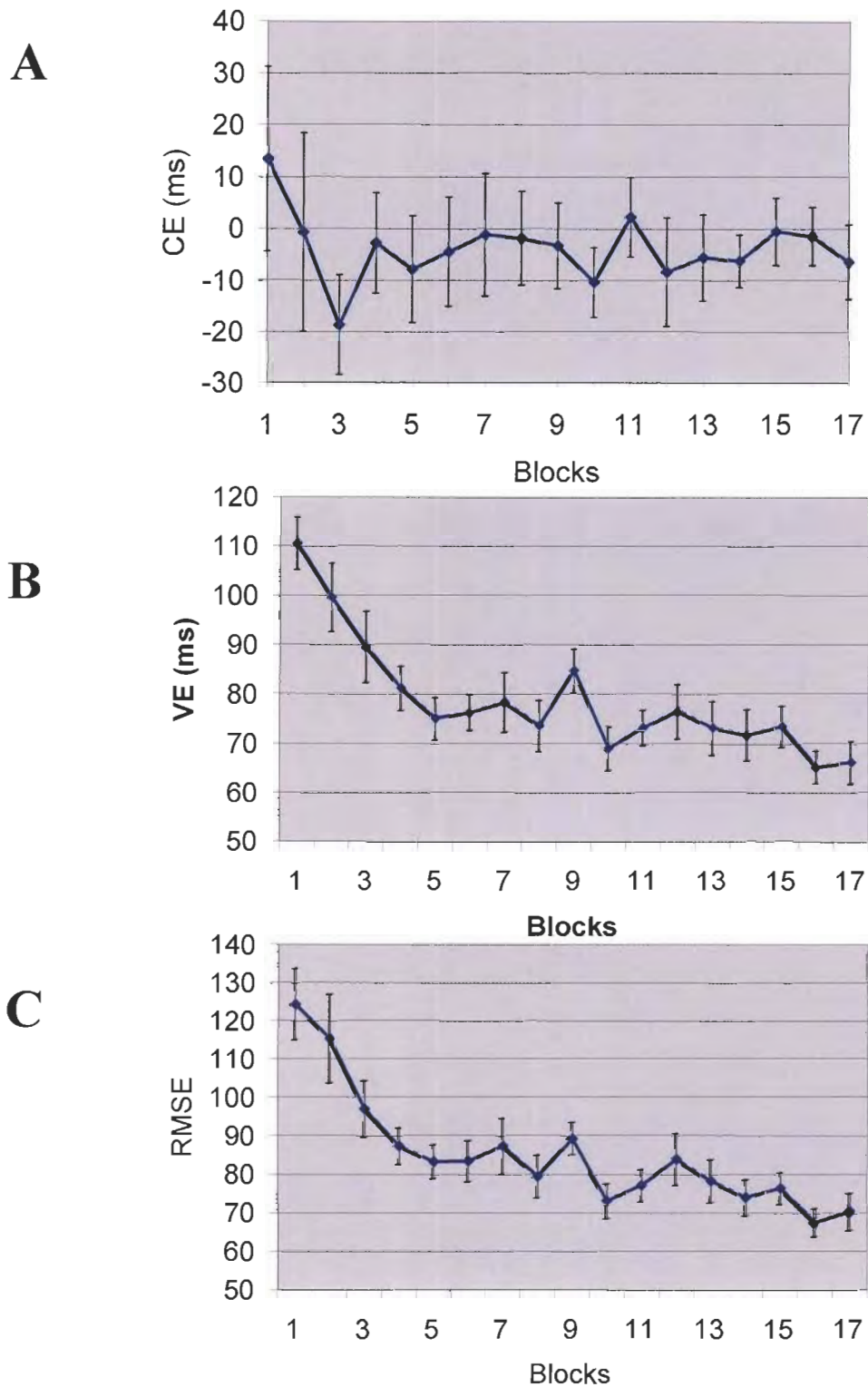
Figure 2.3: Response Bias, Consistency and Accuracy

(A) Constant Error (CE), **(B)** Variable error (VE), and **(C)** Root Mean Square Error (RMSE) Results are presented in milliseconds for each of the 17 blocks of trials. Bars denote standard error of the mean.
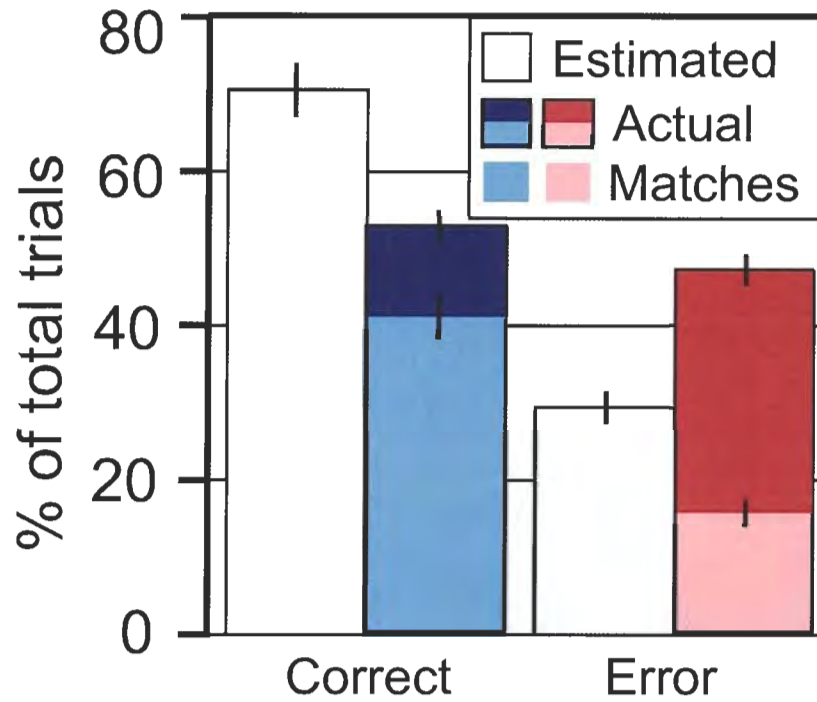
Figure 2.4: Estimated and Actual Performance

Percentage of total trials in which participants estimated their response to be correct or erroneous and actual percentage of trials that were correct or erroneous.

Columns denoting actual outcome are divided into trials with matches between estimated and actual outcome (light colours: 77.9 % of correct and 33.6 % of errors) and trials with mismatches between estimated and actual outcome (dark colours). Bars denote standard error of the mean.
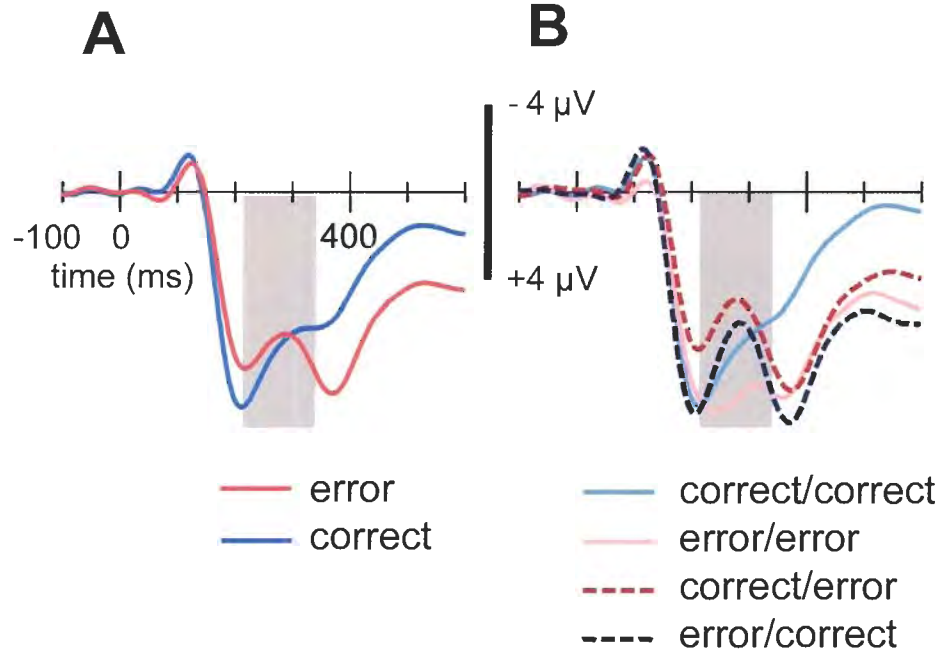
Figure 2.5: Grand-average ERP waveforms

Grand-average (n = 13) ERP waveforms recorded from electrode Fz, time-locked to feedback presentation (time 0) and separated by **(A)** type of feedback presented, and **(B)** estimated/actual feedback pairs. On **(B)**, dark coloured dashed lines represent conditions with mismatches between estimated and actual feedback and light coloured solid lines represent conditions with matches between the two. The grey shaded area represents the range in which the peak of the f-ERN and the correct MFN were found. f-ERN is the negative-going deflection observed within the shaded area. Negative is plotted up by convention.

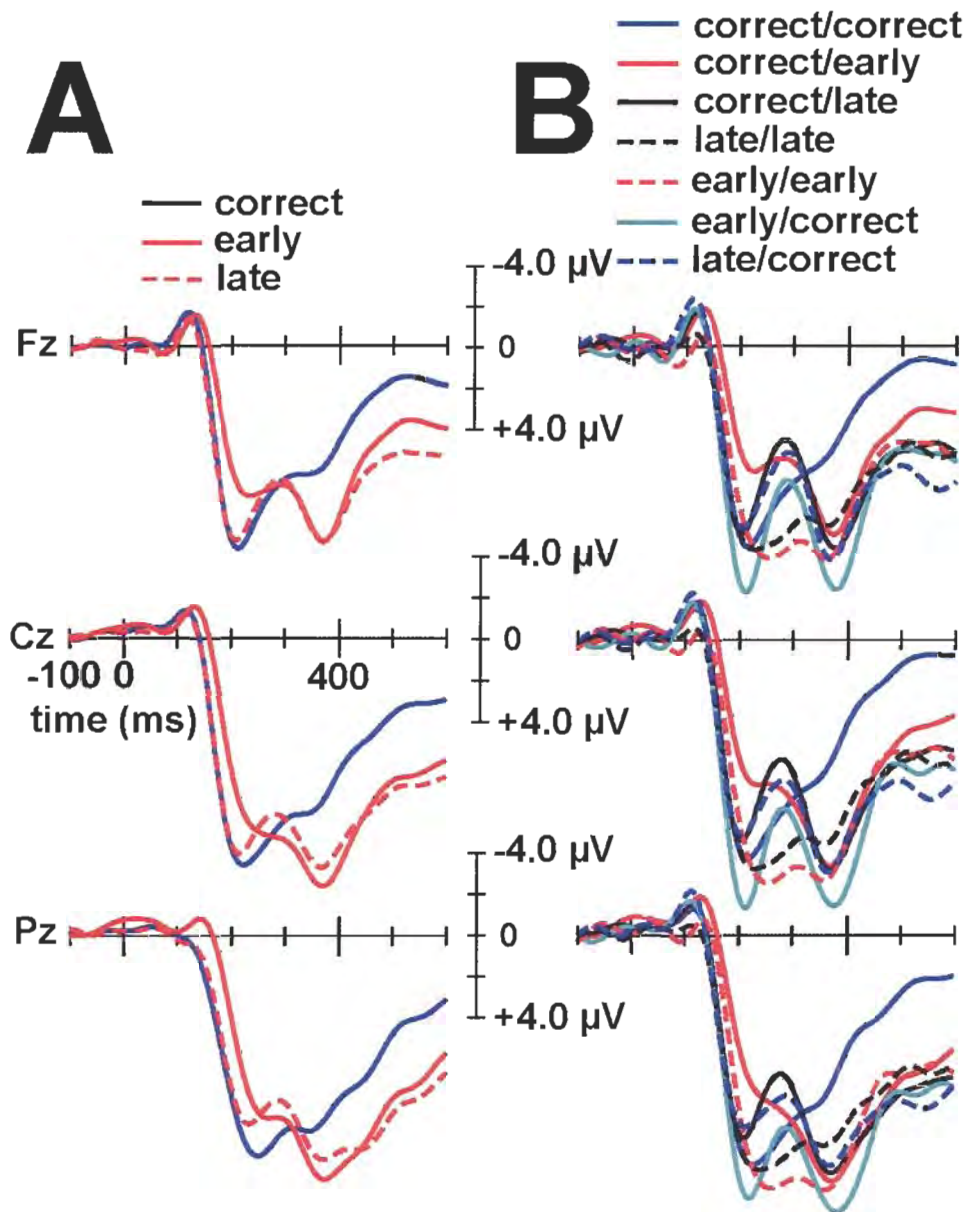**Figure 2.6: Grand-average ERP waveforms for all conditions**

Grand-average (n = 13) ERP waveforms recorded from frontal (Fz), central (Cz) and posterior (Pz) electrodes along the scalp midline, time-locked to feedback presentation (time 0) and separated by **(A)** type of feedback presented, and **(B)** estimated/actual feedback pairs. Negative is plotted up by convention.

3 EXPERIMENT 2: False correct feedback elicits feedback ERN

3.1 Introduction

In Chapter 2, I suggested that f-ERN is not error-specific and proposed an alternative expectancy-deviation explanation of the f-ERN. However, Experiment 1 had a potential confound in the fact that participants were instructed to estimate their performance prior to receiving feedback. This could have influenced participants' perception of the goal of the task. Although measures were taken to prevent this from happening, it is possible that participants considered an error in estimation, and not an error in the primary task, to ultimately constitute an error in the task. To address this possibility and eliminate this potential confound, I conducted a second experiment in which participants would not have to estimate their performance as part of the task. Not having a direct measure of expectancy, however, makes it somewhat tenuous to test the expectancy-deviation hypothesis, as it is impossible to separate trials based on participants' perception of whether they responded correctly or erroneously. Notwithstanding, in tasks that provide enough intrinsic task-related feedback, it is reasonable to assume that participants will use this information to generate fairly accurate estimations of success and error. In this case, it is possible to generate mismatches between expected and actual augmented feedback by presenting false feedback. Indeed, this approach has been successful in previous experiments (de Bruijn et al., 2004; Nieuwenhuis et al., 2002). de Bruijn et al. (2004) used a flankers task (Eriksen & Eriksen, 1974) in their study. In this task participants have to discriminate the central letter (H or

S) in a letter string (HHHHH, SSSSS, HHSHH, SSHSS) by pressing the appropriate button. Because this task gives unambiguous cues about whether the response is correct or wrong, de Bruijn and colleagues presented the letter strings for only 50 ms. By doing this, they intended to increase the ambiguity of the stimuli so participants would be at least slightly hesitant in their judgement of whether they responded correctly or incorrectly. Following their response, participants received feedback according to their performance. However, on a small percentage of trials on which participants responded correctly, they were presented with false feedback indicating an error. Although the authors interpreted the results as showing an increased P300 and no f-ERN elicited to the false feedback, an alternative interpretation of their results is that the f-ERN is simply masked by the larger P300. If the waveforms are compared not by subtraction, but rather in light of the presence or absence of a negative-going deflection around the latency in which f-ERN is known to occur (i.e., 200-350 ms), then false feedback appears to show a large f-ERN.

Nieuwenhuis and colleagues (2002) used a stimulus-response mapping task, which participants had to learn by trial and error. There were three different mapping conditions: in the 100% mapping condition, a particular stimulus was associated with either a right or left mouse button response so that every time participants responded with the correct button they would receive feedback indicating a monetary win and every time they responded with the incorrect button they would receive feedback indicating a monetary loss; in the 50% mapping condition, feedback was presented randomly, irrespective of the button pressed; and in the 80% mapping condition, participants were presented with feedback that was inconsistent with the dominant mapping on 20% of the

trials. The inconsistent feedback in the stimulus-response mapping task is comparable to the false feedback in de Bruijn et al's study. The f-ERN elicited by the inconsistent error feedback in the 80% mapping condition had the largest amplitude among the conditions analyzed by Nieuwenhuis and colleagues and the largest averaged f-ERN reported in the literature (Nieuwenhuis, Holroyd et al., 2004). Unfortunately, the authors did not report the results related to inconsistent correct feedback, seemingly because these types of trials were very infrequent.

Both Nieuwenhuis et al (2002) and de Bruijn et al (2004) suggested an explanation of their results based on Holroyd and Coles' (2002) reinforcement-learning theory. According to this theory, ERNs are elicited in response to an error in reward prediction that occurs when events are *worse than expected.* The results of Nieuwenhuis et al and de Bruijn et al are consistent with this theory. However, the authors did not address the possibility that the f-ERN elicited to false error feedback might not occur selectively in response to situations in which events are worse than expected, but rather more generally by situations involving deviations from expectancy, in which case *false correct feedback* would be expected to generate similar results. Although the use of false feedback has proven to be a useful tool in the study of the f-ERN, to the best of my knowledge there are no studies that have used false *correct* feedback in the study of this component. The objective of Experiment 2 was thus to test the hypothesis that false correct feedback would elicit f-ERN. This hypothesis was generated based on the expectancy-deviation account of the f-ERN proposed in Chapter 2 and is incompatible with the reinforcement-learning theory proposition that the ERN is elicited when events

are worse than expected, as well as with the notion that f-ERN is elicited exclusively by feedback signalling errors.

3.2   Methods

3.2.1   Participants

Thirteen healthy members of the university community volunteered to participate in the study. Participants provided informed consent according to procedures approved by the university ethics committee prior to their participation and received $15 upon completion of the experimental session. Due to unusually poor performance, data from one participant were excluded from all analyses. This participant's behavioural performance (as measured by root mean square error) deviated by more than 8 standard deviations from the mean of the other participants. The remaining twelve participants (8 males, 4 females, mean age =25.1 years, range 20-35 years) were all right-handed, experiment-naïve and had normal or corrected-to-normal vision. Due to a system malfunction, data from block 1 of one participant were lost. This participant was excluded from all behavioural analyses. Due to excessive noise in the electrophysiological recordings, data from another participant were excluded from all electrophysiological analyses.

3.2.2   Apparatus

The apparatus used for this experiment was the same as in Experiment 1, with the exception that the estimation panel was not used in this experiment (Figure 3.1).

3.2.3   Task and Procedures

The experimental session consisted of 900 trials of the task described below, divided into 15 blocks of 60 trials, and lasted approximately 90 minutes. Participants had

self-controlled rest breaks upon completion of every 15 trials, and a mandatory 5 second break followed by a self-controlled period at the end of each block. During trials participants were asked to blink as little as possible and were instructed not to move their eyes by fixating their vision on a marked central location on the computer screen.

Participants sat in front of a desk in a dark room and had a computer monitor, the LED box, and a mouse in front of them. The task started with the sequential lighting of the LEDs, giving the illusion of a moving stimulus. The LED box was positioned such that the LED row was in the horizontal plane and the lights appeared to move right-to-left or left-to-right depending on the trial. Participants were instructed to press the right mouse button with their left hand in coincidence with the moving stimulus reaching the end of the LED sequence. To serve as a reference of the target location, the last LED in the sequence was always on. Unlike Experiment 1, I did not occlude the latter half of the LEDs and provided full vision of the moving stimulus up to the target. The reason for this modification was that I wanted to enable participants to generate accurate estimations of whether they responded on- or off-target. There were four different speeds for the moving stimulus. The time between the onset of the first LED in the sequence and the target time (onset of the last LED in the sequence) was either 432 ms, 600 ms, 768 ms or 936 ms. On each block of trials a random combination of two speeds was used. The direction of the moving stimulus was randomly assigned to each block and remained constant throughout the trials of the block.

After 2100 ms from the targeted response time, I presented feedback in the form of "-", "+" and "0", representing early, late and correct responses respectively. Feedback stimuli stayed on the screen for 800 ms and were determined based on the following

procedure. Error was computed online as the time difference between the participant's response and the stimulus reaching the target such that early responses were represented by negative errors and late responses by positive errors (Figure 3.2). Trials were considered on target if the error fell within a 250 ms time band centred on the target (i.e., from -125 ms to 125 ms post-target). Responses were considered early if the error was less than the negative edge of the time band and late if error was greater than the positive edge of the time band. This time band changed throughout the experiment based on participant's performance. After every incorrect trial, the size of the time band was increased by a factor of 1.10 and after each correct response the size of the time band was decreased by a factor of 0.85. However, there was a limit on how much the time band could decrease as it was never less than 80 ms (-40 to 40 ms). This limit was smaller than in Experiment 1 because in Experiment 2 participants had full vision of the LEDs and thus the task was deemed easier than in Experiment 1. To enable participants to develop a good idea of what a correct, an early and a late trial would be, I presented participants with feedback according to their performance on every trial of the first 3 blocks. On the remaining 12 blocks, however, I introduced false feedback as the main experimental manipulation. In trials when participants were off-target by more than 1.8 times the band described above, there was a .5 probability that participants would receive a "0" as the feedback instead of "-" for early responses and "+" for late responses. To ensure that participants would receive false feedback in a sufficient amount of trials, if participants did not have at least 10 trials with an error greater than 1.8 times the band by the end of block 6, false feedback was at that point presented with a probability of .5 whenever the error was greater than 1.5 times the band. This adjustment was necessary for two of the

twelve participants. To make the analyses consistent across participants and to ensure that the error was substantive, false feedback in trials that had an error of less than 90 ms were excluded from all statistical analyses.

Before starting recording, participants were instructed on how to perform the task and were told that every time they responded correctly they would win a bonus of 5 cents and every time they responded early or late they would lose 5 cents. This procedure was only used as a motivational tool, as participants would unknowingly receive the same monetary amount at the end of the testing session.

3.2.4   Electrophysiological recording and measures

Electroencephalographic (EEG) activity was recorded using 64 tin electrodes, including 60 scalp electrodes attached to an elastic-fabric cap (Electro-Cap International, Inc): 4 nonstandard sites located inferior to the occipital row of electrodes and 56 from the 10-10 system (FPz, FP1, FP2, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FCz, FC1, FC2, FC3, FC4, FC5, FC6, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP1, CP2, CP3, CP4, CP5, CP6, Pz, P1, P2, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, Iz, and M1) (American Electroencephalographic Society, 1994). Horizontal electrooculographic (EOG) signals were recorded bipolarly at both external canthi. All electrodes from scalp sites were referenced to an electrode placed on the right mastoid (M2). Electrode impedances were kept below 10 kΩ for all scalp electrodes and below 5 kΩ for the electrodes placed on mastoids and on the external canthi of both eyes. EEG signals were amplified by a gain of 20,000 and a band pass of 0.1-80 Hz, digitized at 500 Hz and stored on a microcomputer for offline averaging. Automated artefact rejection was done offline to discard trials contaminated by eye movements and blinks, or when

amplifier blocking occurred. I extracted 800 ms epochs (0 to 800 ms) time-locked to feedback presentation (baseline: -200 ms to feedback onset). These epochs were digitally low-pass filtered at 37.5 Hz, averaged for each participant and re-referenced to the average of both mastoids.

I measured f-ERN amplitude base-to-peak on the average waveforms at electrodes Fz, FCz and Cz, where f-ERN is reported to be maximal (Holroyd, Larsen et al., 2004; Holroyd et al., 2003; Luu et al., 2003; Mars et al., 2004; Miltner et al., 1997), according to the following procedures. First I low-pass filtered the data in the channels of interest at 20 Hz[7] to get rid of high-frequency noise. I then identified the most positive peak 140-300 ms following feedback presentation. Next, I found the largest negative-going peak that followed this positivity in a window extending to 400 ms after feedback onset, and the largest positive-going peak following the negative-going peak up to 500 ms from feedback presentation. Peaks were defined as samples that were more positive/negative than the preceding and following samples and of the average of the five preceding and following samples. f-ERN amplitude was quantified as the voltage difference between the negative-going peak and the average of the preceding and following positive-going peaks (Yeung & Sanfey, 2004). If no negative-going peaks were found in the time window defined above or if the negative-going peak found was less than 0.5 μV more negative than either the preceding or following positive-going peaks, the ERP component was defined as a positivity and f-ERN amplitude was considered 0 μV. Along with the computer algorithm used for this procedure, I visually inspected each individual waveform to ensure that the algorithm had picked a valid peak (Picton et al., 1995)

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[7] The data was low-pass filtered at 20 Hz to measure the f-ERN. However, the waveforms presented in figure 3.4 represent grand averages of the data low-pass filtered at 37.5 Hz.

3.2.5 Behavioural recording and measures

I computed constant error (CE) as a measure of response bias, variable error (VE) as a measure of consistency and root mean square error (RMSE) as a measure of accuracy. These measures were accurate to 2 ms given the system's sample rate of 500 Hz. I excluded trials that had absolute errors greater than 600 ms from all behavioural analyses.

3.2.6 Statistical Analysis

I used repeated measures analyses of variance (ANOVAs) for all statistical comparisons. All behavioural analyses involved single factor ANOVAs, whereas the f-ERN analysis was done through a 3 (electrode: Fz, FCz and Cz) by 3 (feedback: correct, error and false correct) factorial ANOVA with repeated measures on both factors. Whenever a violation of the assumption of sphericity was detected, I used the Greenhouse-Geisser correction of degrees of freedom, and to break down any significant main effects I performed pairwise comparisons with Bonferroni adjustments for multiple comparisons.

3.3 Results

3.3.1 Behavioural results

Participants were slightly biased towards responding early as indicated by their mean CE (M = -9 ms, 95% confidence interval [CI] = -17 ms, 0 ms). Moreover, a significant block effect showed that CE changed across blocks ($F_{14, 140}$ = 3.59, p < 0.1, ε = .35). As can be seen in Figure 3.3A, participants were biased towards responding early in the first block, but changed this tendency reversing the bias towards responding late in block 3. It appears as though participants were inherently attracted towards responding early, however, as they slowly moved back towards an early-response bias (see Table 3.1 for individual participants' means and standard errors).

I found no significant differences across blocks in VE and RMSE (p >.15) (Figures 3.3B and 3.3C, respectively). The mean VE collapsed over blocks was 69 ms (95% CI = 61 ms, 78 ms) and the mean RMSE was 71 ms (95% CI = 64 ms, 79 ms). A cross-experiment comparison suggests that the modifications implemented in Experiment 2 successfully made the task easier ($VE_{Exp 1}$ = 85 ms $RMSE_{Exp 1}$ = 88 ms). It is possible that the lack of a significant reduction in VE and RMSE across blocks stems from the fact that the task was too easy and that participants thus reached an asymptote early during the testing session. However, it is also possible that participants were not as engaged in the task as participants in Experiment 1[8]. The estimation requirement in Experiment 1 could have worked as a motivational tool breaking the repetitiveness of the experimental

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[8] This is corroborated by the electrophysiological results. In Experiment 2 the f-ERNs were smaller than in Experiment 1 and had a longer latency to peak f-ERN. According to Pailing et al. (2002) these characteristics are reliable indicators of response control. Motivation is thought to increase the gain on the monitoring system, influencing the activity represented by the ERN (Rodriguez-Fornells et al., 2002; Swick & Turken, 2002).

session. During debriefing of Experiment 2, most participants reported being bored by the task.

3.3.1.1 Trial-by-trial error correction

I calculated CE and VE in trials immediately following the presentation of each type of feedback to investigate how feedback affected trial-by-trial error correction. The repeated measures ANOVA for VE was not significant, showing that the type of feedback that preceded the trials did not affect variability in performance. In contrast, the ANOVA for CE was significant ($F_{4, 40} = 19.28$, $p < .001$) showing differences between types of feedback. Newman-Keuls post-hoc procedures showed that false correct feedback presented following early responses led participants to respond with a significantly larger early-response bias than any other type of feedback ($p < .05$ for all comparisons), and false correct feedback presented following late responses led participants to respond with a significantly larger late-response bias than any other type of feedback ($p < .01$ for all comparisons). There were no significant differences in CE between any of the other conditions ($p > .3$ for all comparisons; see Table 3.2 for means and standard errors). These results show that on average, false feedback misled participants, inducing them to repeat the same type of error committed on the previous trial.

3.3.2 Electrophysiological results

The 3 electrode (Fz, FCz and Cz) by 3 feedback (false correct, error and correct) repeated measures ANOVA used to analyze f-ERN amplitude yielded a significant feedback main effect ($F_{2, 20} = 9.71$, $p < .005$) but no electrode main effect or electrode by

51

feedback interaction ($p > .1$ for both effects). As hypothesized, f-ERNs elicited by false correct feedback were significantly larger than f-ERNs elicited by correct feedback ($Ms =$ -2.44 μV and -1.11 μV respectively; $p < .01$), and no different than f-ERNs elicited by error feedback ($M = -1.75$ μV, $p > .1$) [refer to Table 3.3 for individual participants' f-ERN amplitudes]. The difference between the amplitude of f-ERNs elicited by error feedback and correct feedback was only marginally significant ($p = .052$). Due to large inter-participant latency to peak f-ERN variability, the grand-averaged ERP (Figure 3.4) is not graphically representative of the statistical results presented above. For illustrative purposes, Figure 3.5 shows the averaged ERP waveforms of two representative participants.

3.4   Discussion

In this experiment, I used false correct feedback to test the expectancy-deviation explanation of the f-ERN, as proposed in Chapter 2 of this thesis. Specifically, I tested the prediction that correct feedback presented falsely after large errors would elicit larger f-ERNs than correct feedback following correct responses. The results supported this hypothesis and the notion that f-ERN can be elicited by both error feedback and *correct* feedback, as long as there is a mismatch between expected and actual feedback. These results challenge an error-specific view of the f-ERN (Miltner et al., 1997) and the notion that events have to be worse than expected to engage the neural system underlying the f-ERN (Holroyd & Coles, 2002). In contrast, the findings support the proposition that f-ERN is the outcome of a more general system that detects expectancy-deviations.

Table 3.1: Mean constant error (CE) in milliseconds for each block of trials of each individual participant

Participant	Block														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
P2	-32	-33	1	-19	-41	-9	-5	-17	-22	1	-49	-25	-38	39	2
P3	17	41	93	48	13	6	1	-27	-8	1	-3	-5	-62	-20	-31
P4	-11	5	12	16	3	-18	-26	-4	8	-26	-8	-12	-30	-17	-12
P5	-38	3	2	5	-11	8	20	-15	-7	70	7	13	35	-18	14
P6	-25	-23	3	0	-14	-7	-13	-38	-19	-40	-56	-18	-45	-61	-53
P7	-3	12	-3	1	22	-25	20	-20	17	-56	2	-58	-40	-13	30
P8	-27	6	18	-21	13	3	-21	0	10	-1	-26	-29	-15	15	-15
P9	-13	7	25	45	54	4	48	-14	9	-25	-50	-13	-5	-28	-29
P10	-61	-33	-37	-8	-21	-18	-41	-20	-22	-24	-35	-44	-28	-48	-61
P11	-2	20	9	55	42	14	39	30	-21	21	-45	-12	-37	1	-29
P12	-66	-45	1	-22	-27	-10	-2	5	-5	-4	-32	-21	-35	-24	-36
Mean	-24	-4	11	9	3	-5	2	-11	-5	-8	-27	-20	-27	-16	-20
Standard Error	8	8	9	9	9	4	8	5	4	10	7	6	8	8	8

Note: Negative values indicate early responses and positive values indicate late responses. The two last rows represent the total mean and standard error for all participants. Data from Block 1 of P1 were lost due to a system malfunction. This participant's data were excluded from CE analysis and are not shown in this table.

54

Table 3.2: Mean constant error (CE) for trials that immediately followed each type of feedback.

Condition	Mean CE	Standard Error
False correct feedback following early response + 1	-26.8 ms[*]	+/- 4.7 ms
False correct feedback following late response + 1	15.7 ms[#]	+/- 6.1 ms
Correct feedback + 1	-6.7 ms	+/- 3.6 ms
Early feedback + 1	-6.2 ms	+/- 4.0 ms
Late feedback + 1	-14.4 ms	+/- 5.4 ms

Note: *significantly different than all other conditions at $p < .05$, [#]significantly different than all other conditions at $p < .0$

Table 3.3: Mean medial frontal negativity amplitude (in microvolts) for individual participants

Participant	Fz			FCz			Cz		
	False Correct	Feedback		False Correct	Feedback		False Correct	Feedback	
		Error	Correct		Error	Correct		Error	Correct
P1	-2.90	-2.33	-2.03	-2.93	-1.63	-2.05	-4.14	-1.63	-2.32
P2	-2.50	-2.45	-2.67	-2.60	-2.45	-2.74	-2.43	-2.51	-2.38
P3	-3.36	-2.73	-2.70	-3.52	-2.45	-2.54	-2.83	-2.15	-2.49
P4	-1.55	-3.09	0	-2.42	-3.47	0	-3.85	0	0
P5	-5.15	-1.50	0	-3.82	-0.99	0	-3.46	-0.98	0
P6	-2.36	-2.49	-1.55	-2.38	-2.14	-1.35	-1.95	-2.67	-1.06
P7	-1.27	-0.66	0	-1.41	-1.15	0	-1.10	-0.77	0
P8	0	0	0	-1.95	0	0	-1.30	0	0
P9	-2.44	-2.22	0	0	-1.37	-1.86	0	-1.23	-1.45
P10	-3.12	-1.46	-0.88	-3.46	-1.56	-1.06	0	-0.93	0
P12	-3.96	-2.54	-1.87	-3.05	-2.85	-1.78	-3.38	-3.27	-1.80
Mean	-2.60	-1.95	-1.06	-2.50	-1.82	-1.21	-2.22	-1.47	-1.04
Standard Error	0.42	0.28	0.34	0.33	0.29	0.32	0.44	0.33	0.33

Note: Amplitudes are separated by the electrodes of interest (Fz, FCz and Cz) and according to the type of feedback presented. The bottom two rows represent the total Mean and Standard Error for all participants.
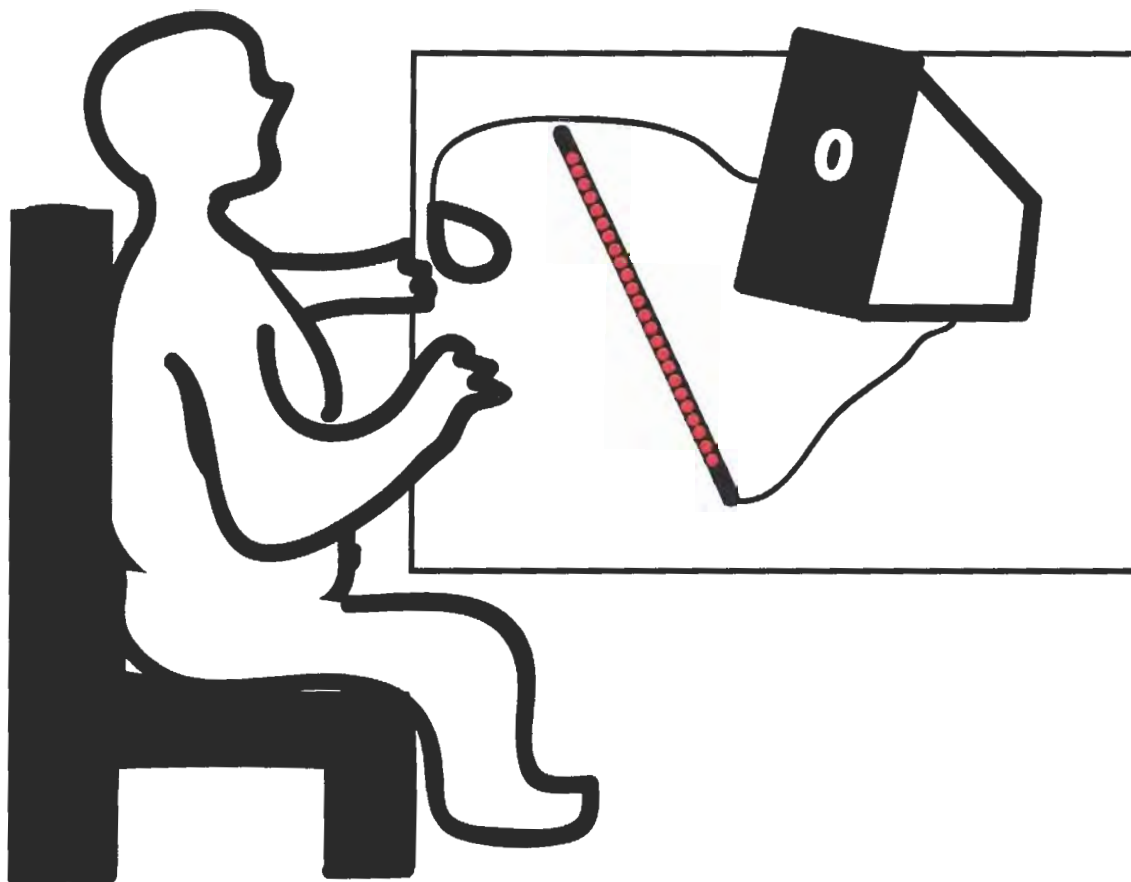
56

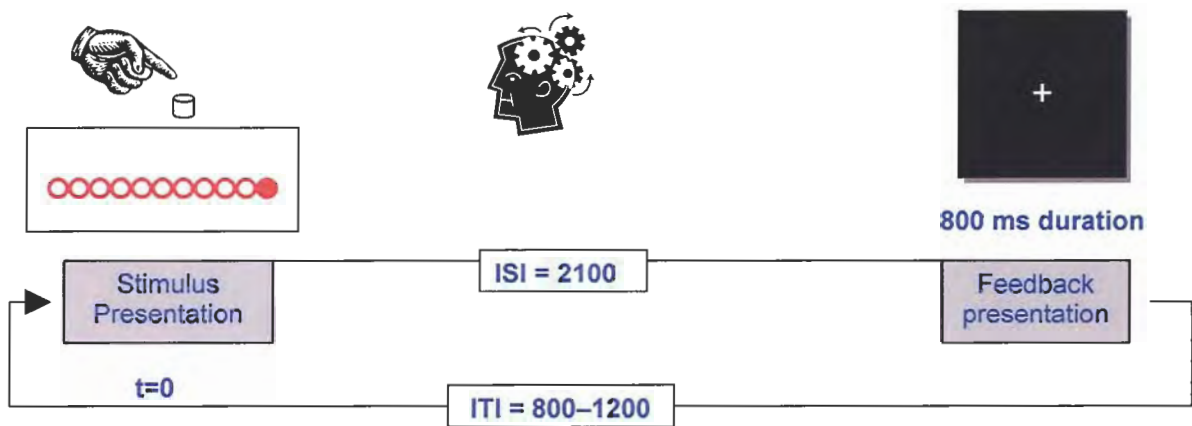Figure 3.1: Schematic view of the apparatus and experimental setup

Figure 3.2: Events during a typical trial

Stimulus presentation starts at time (t) zero, with response ideally occurring in coincidence with stimulus end. After a 2100 ms inter-stimulus interval (ISI) feedback is presented (duration of feedback presentation is 800 ms). Inter-trial interval (ITI) is set at 800-1200 ms.
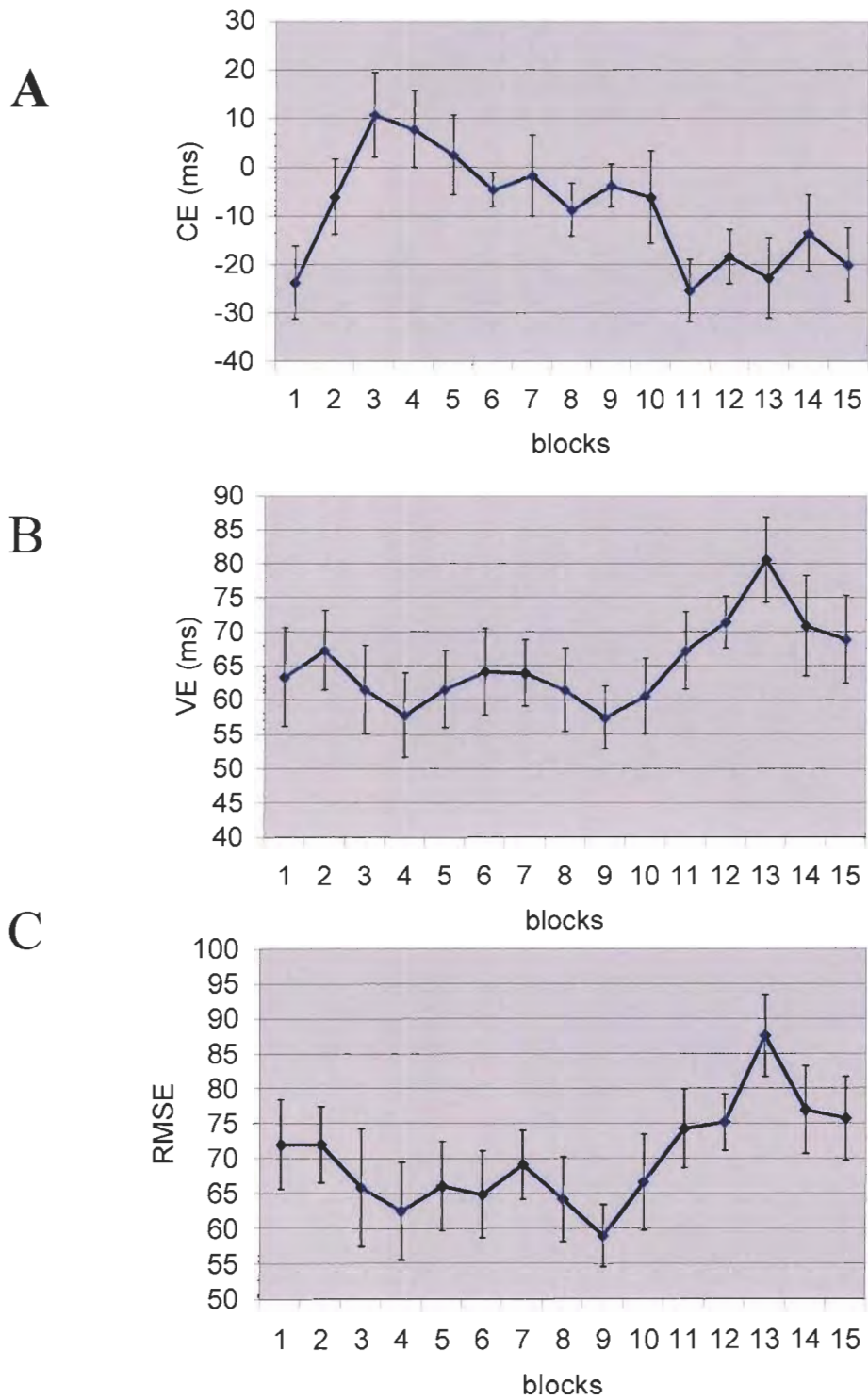
Figure 3.3: Response Bias, Consistency and Accuracy

(A) Constant error (CE), **(B)** Variable error (VE), and **(C)** Root mean square error (RMSE) across the 15 blocks of trials. Bars denote standard error of the mean.
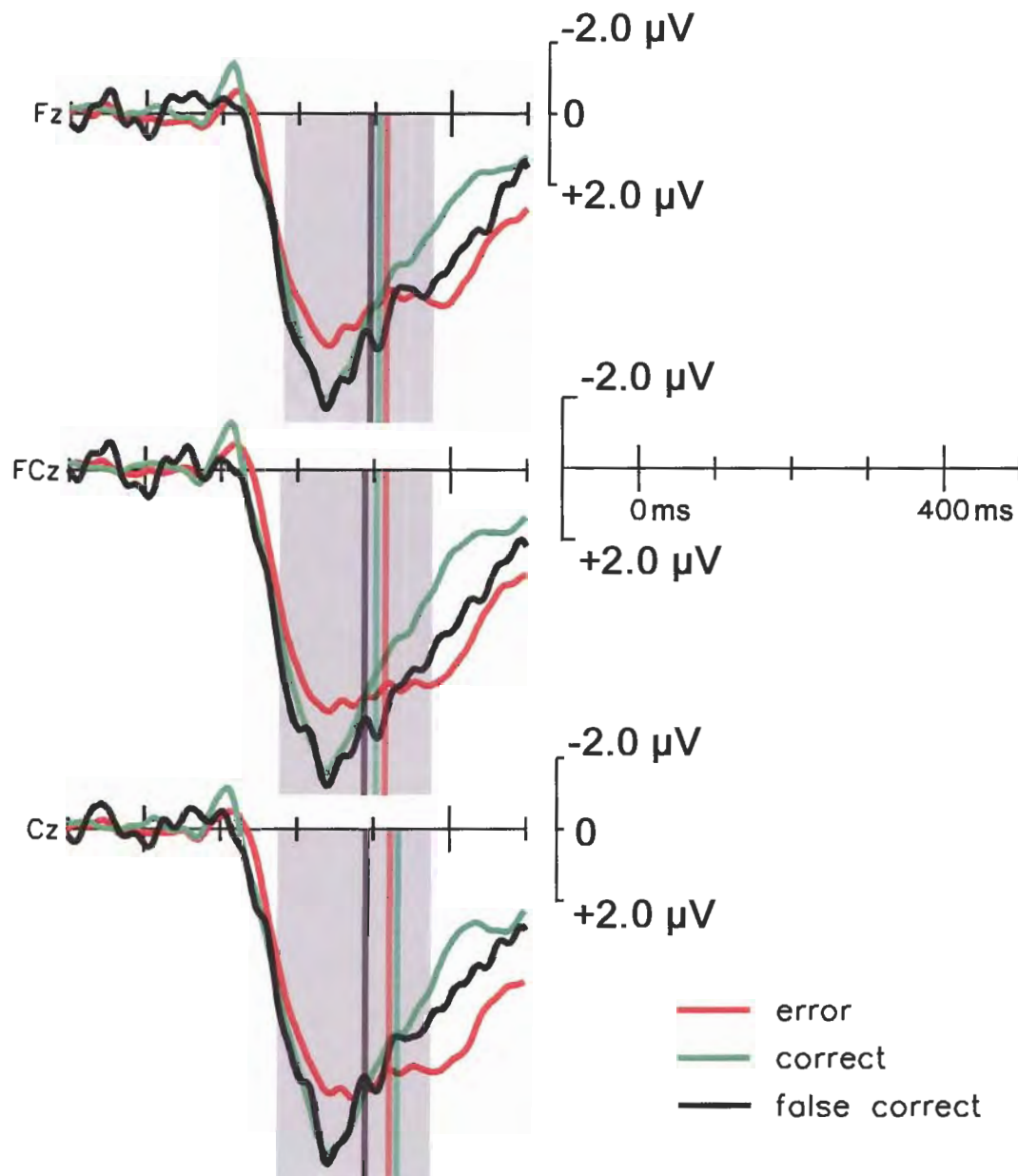
Figure 3.4: Grand-average ERP waveforms

Grand-average ERP waveforms (n = 11) from frontal (Fz), fronto-central (FCz) and
Central (Cz) electrodes along the scalp midline. The range of latencies in which the f-
ERN peaked is shaded in grey. Vertical bars represent the mean latency to peak f-ERN
for each type of feedback. Time zero represents the onset of the feedback stimulus.

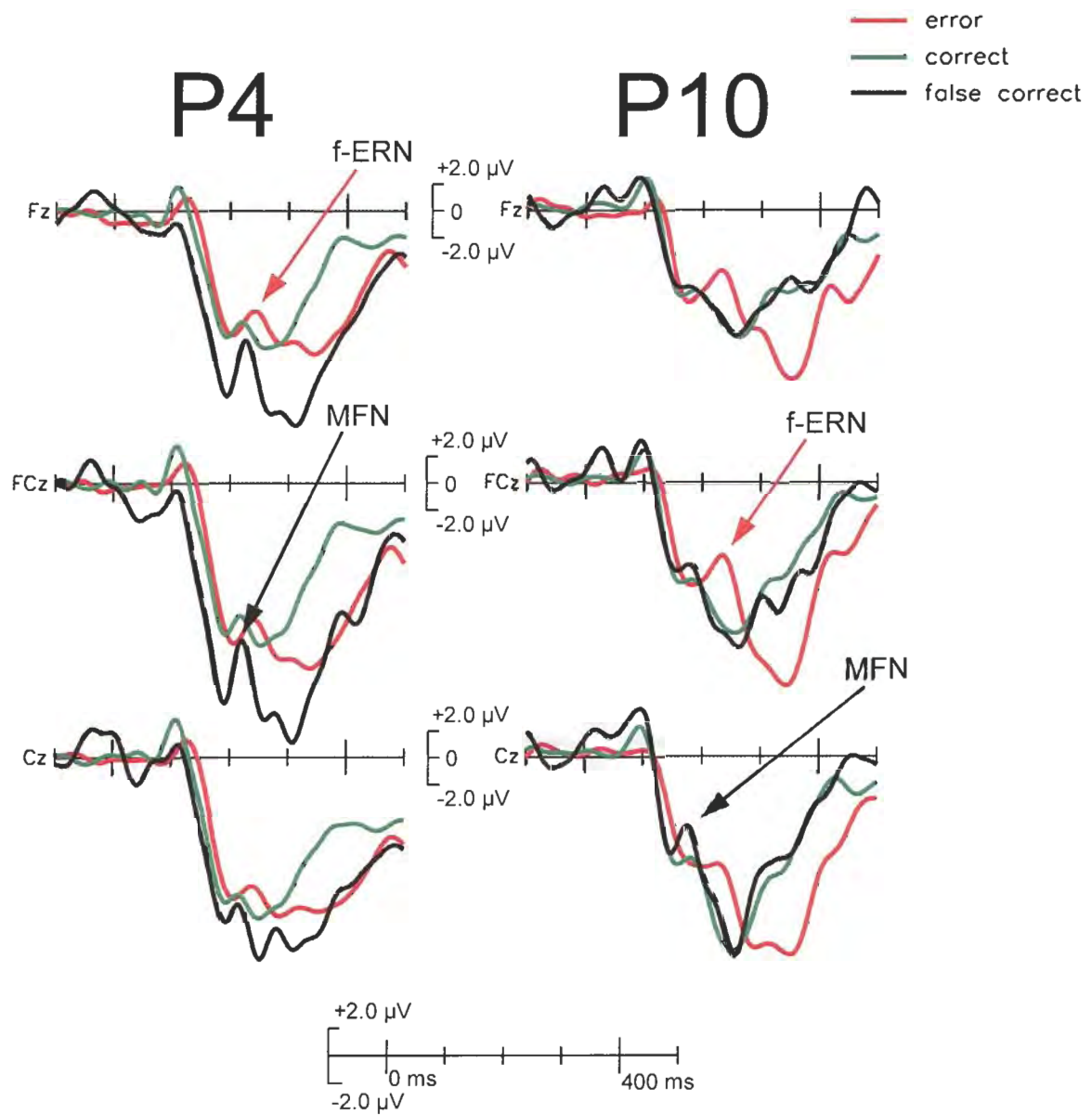**Figure 3.5: Representative individual participant ERP waveforms**
Averaged waveforms from frontal (Fz), fronto-central (FCz) and central (Cz) electrode sites for each feedback condition for participants **P4** and **P10**. Arrows point to the negative-going deflections identified as the feedback ERN (**f-ERN**) elicited by error feedback, and the medial frontal negativity (**MFN**) elicited by false correct feedback.

4 GENERAL DISCUSSION AND CONCLUSION

4.1 General Discussion

Understanding how information about errors and performance influences the process of skill learning has been a popular topic of research for kinesiologists, psychologists, and rehabilitation scientists, among a large group of researchers and professionals that deal with skill learning. A more fundamental question, however, is how the human central nervous system monitors performance and detects errors. The popularization of this topic among scientists has been largely influenced by the recent advances in techniques that permit non-invasive measures of brain function. Despite the numerous studies investigating this issue, the neural mechanisms involved in performance monitoring and their specific contributions are still unclear. There appears to be a general consensus surrounding the proposition that the anterior cingulate cortex (ACC), a structure located in the medial surface of the frontal lobe, is involved in monitoring the environment (Luu, Flaisch, & Tucker, 2000; Ridderinkhof et al., 2004; Schall, Stuphorn, & Brown, 2002). The specific function of ACC in performance monitoring, however, is a matter of debate. The view that ACC has a specific error processing function has recently gained significant ground with the discovery of the ERN. Nevertheless, the acceptance of this proposition is not unanimous. A group of influential researchers led by Carter and Cohen, has strongly advocated for an alternative view that suggests the ACC is involved in resolving conflict and response competition rather than processing errors *per se* (Botvinick et al., 2001; Botvinick et al., 2004; Carter

et al., 1998; Kerns et al., 2004; van Veen & Carter, 2002a; Yeung et al., 2004). This proposition, however, is unable to adequately explain ACC activation in instances that do not involve response conflict. In particular, the observation that ACC is activated upon presentation of information about performance through augmented feedback (Miltner et al., 1997), and during the observation of third-party errors (van Schie et al., 2004) suggests that the ACC is involved in different monitoring processes other than, or in addition to, monitoring response conflict. While it is generally well accepted that ACC acts in conjunction with other areas in the prefrontal cortex to modulate cognitive control[9] (Bush et al., 2000; E. K. Miller & Cohen, 2001; Ridderinkhof et al., 2004; Ridderinkhof & van den Wildenberg, 2005) in what has been generically termed attention for action (Allport, 1987; Norman & Shallice, 1986; Passingham, 1996), the broad spectrum of monitoring events that are associated with ACC activity, and the large number of cortical and sub-cortical structures that have afferent connections with ACC (cf., Vogt, Rosene, & Pandya, 1979) have made it difficult for neuroscientists to define what specifically triggers the activation of the ACC in performance monitoring. In other words, there is general agreement on what the activation of ACC does, but not in what gives rise to this activation. It is possible that ACC is functionally related to several tasks. Paus and colleagues suggest that ACC is activated by information about the difficulty of tasks (Paus, Koski, Zografos, & Westbury, 1998), Carter and colleagues suggest that ACC detects conditions in which errors are likely to occur (Carter et al., 1998), and similarly Brown and Braver (2005) propose that "ACC learns to predict error likelihood in a given context, even for trials in which there is no error or response conflict". Holroyd

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[9] The term 'cognitive control' is used by neuroscientists to describe cognitive processes that are conceptually similar to what has been referred to as 'cognitive effort' by motor behaviourists (cf., Lee, Swinnen, & Serrien, 1994; Oliveira & Goodman, 2004; Sherwood & Lee, 2003).

and Coles (2002), on the other hand, suggest that ACC is activated by the recognition that events are worse than expected, and Mai and colleagues present evidence indicating that ACC is also activated when a mental set is broken in 'Eureka-like' moments (Mai et al., 2004). Apart from these highly specialized functions, ACC activity has also been observed in response to simpler event characteristics such as stimulus novelty (Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005), and infrequency (Luu & Pederson, 2004; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003). Based on the evidence described above, one might be compelled to conclude that ACC is thus involved in multiple specialized monitoring functions and that many different classes of events give rise to ACC activity. However, linking ACC function to the events that trigger its activity is a descriptive approach that does not target the more fundamental question of what is *necessary* to activate the ACC. A different approach would be to try to find a common denominator in the tasks that are shown to activate ACC that would summarize its function. Indeed, it would be enlightening to be able to describe the eclectic responsivity of ACC in performance monitoring through a single class of events.

Although the goal of the two experiments presented in this thesis was not to accomplish this complex task, I sought to take a small step in this direction by attempting to include error processing within a larger class of possible ACC functions, namely the detection of expectancy-deviation (Luu & Pederson, 2004; Pritchard et al., 1991). In Experiment 1, I tested this hypothesis by recording participants' judgement of their performance and matching it to the actual performance. This procedure enabled a separation of trials not just based on the valence of the feedback about performance, but also on whether feedback represented a match or mismatch with participants'

expectations. The results showed that the valence of feedback might not be the determining factor that gives rise to f-ERN (and ACC activity), but rather that the presence or absence of mismatches between expected and actual feedback might be the necessary component to elicit the f-ERN. The observation that error feedback elicits a larger f-ERN might be an artefact caused by overoptimistic expectations from participants (D. T. Miller & Ross, 1975), in conjunction with methodological limitations of event-related procedures (Coles & Rugg, 1995; Picton et al., 1995). Specifically, the results of Experiment 1 suggest that error feedback accompanies more trials than correct feedback in which a mismatch between expected and actual feedback is observed. The result that error feedback elicits larger f-ERNs could thus be a reflection of the unequal weight that mismatches bear in error and correct feedback trials after trials are averaged together into these conditions. This view is in opposition to a frame of reference that considers the amplitude of the f-ERN being directly related to the valence of the feedback. Indeed, this appears to be the case as differences between error and correct feedback disappear when they are compared with the amount of mismatch equated. Notwithstanding, while unlikely, the possibility exists that the results of Experiment 1 might be confounded by the fact that the task that participants performed involved a secondary requirement, namely estimating their performance, that could have influenced their perception of what constituted an error. Eliminating the estimation requirement and still being able to test the expectancy-deviation hypothesis was not a simple problem to solve, however, as the lack of a direct measure of expectancy severely complicates this accomplishment. Experiment 2 was nevertheless an attempt to do so with the use of false feedback as the means to generate expectancy-deviations. I acknowledge several

limitations to this study, among which I highlight the fact that the anticipation-timing task proved to be somewhat unfitting, as it does not provide participants with unambiguous cues of whether their response was correct or erroneous. This complicates testing the expectancy-deviation hypothesis even further, as the recognition of error in trials followed by false correct feedback is a prerequisite to generating mismatches between expected and actual feedback. Moreover, the relatively long testing sessions along with the repetitiveness of the task may have contributed to an overall low motivational state shown by the participants. Although not unanimous (see Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001 for conflicting results), ERN and ACC activity have been generally thought to depend on consciousness (Mayr, 2004), motivation (Rodriguez-Fornells et al., 2002; Swick & Turken, 2002), intention (Stemmer et al., 2001) and the affective importance of behaviour (Bush et al., 2000; Holroyd et al., 1998; Ruchsow et al., 2002; Vidal et al., 2000). Therefore, low levels of motivation and engagement could affect the results of the study by decreasing activity in the monitoring system.

Despite these limitations, however, the results found in Experiment 2 provided support for the hypothesis that false correct feedback would elicit a larger ERN than correct feedback. More importantly, Experiment 2 provided a test of a specific prediction of the expectancy-deviation hypothesis, namely that correct feedback would elicit a f-ERN if it constituted a mismatch between expected and actual feedback, that is incompatible with current views of the f-ERN (Holroyd & Coles, 2002; Miltner et al., 1997). Also, while false error feedback had been used previously in f-ERN research, to the best of my knowledge Experiment 2 was the first study to use false *correct* feedback in the study of f-ERN. Given that I found compatible results to those of Experiment 1, but

in this case without the estimation requirement, it seems reasonable to say that the results of Experiment 1 cannot be explained solely by the potential confound that requiring participants to estimate their performance might have caused. Instead, the results of Experiments 1 and 2 together suggest that expectancy-deviation can indeed be used as a common denominator to provide a functional link between the f-ERN elicited by error feedback and the MFN elicited by correct feedback. Moreover, it is possible that other ERP components that have been attributed to ACC activity and that are associated with different instances of context violation could also be attributed to this general expectancy-deviation monitoring system.

In the early 1990's Pritchard, Shappell and Brandt (1991) published an extensive review of electrophysiological studies reporting negative-going deflections recorded in the fronto-central scalp. They suggested that despite being observed under different experimental paradigms and having differences in scalp distribution and latency, several of those ERP components might be functionally related and thus represent the same underlying cognitive processes. They used the example of the motor potential and of the late positive component (LPC) to illustrate that having the same scalp distribution and latency should not be a requirement to classify two or more ERP components as representing the same cognitive processes. The motor potential is known to differ substantially in scalp-distributions depending on the effectors in use but is nevertheless considered to represent the same cognitive process. The LPC is thought to represent similar cognitive processes across a multitude of tasks despite having latency variations of over 300 ms between different experimental paradigms. At the time the Pritchard et al. paper was published, little information was available about the neural sources responsible

for ERP components. Findings from spatially precise measures locating the activity of functionally similar ERP components to the same neural generators should only strengthen their proposition. Single cell recording, fMRI and MEG data along with a functional commonality should be taken as stronger evidence that the same cognitive processes are represented by different ERP components than more crude measures such as latency and scalp distribution.

One important limitation of both studies was therefore the fact that dipole modelling was not performed and thus activity in the ACC was implied by previous studies showing that the MFN observed in response to feedback is indeed generated in the ACC. However, this is a well-accepted approach (Hajcak et al., 2005; Mars et al., 2004; Yeung & Sanfey, 2004).

Pritchard and colleagues already hinted in 1991, that a general class of fronto-central negative components happening around the 200 and 400 ms latencies might be related to context violations. Following the same logic, I propose that several medial frontal negativities (MFNs) that have been viewed as distinct might in fact represent the same cognitive process—the detection of expectancy-deviations—represented by ACC activity. It is possible that in different tasks, distinct processes might happen prior, concurrently or subsequent to a common ACC-mediated process, changing latency and scalp distribution slightly. For instance, while expectancy-deviation is a common denominator between f-ERN and the oddball N200 (Holroyd, 2004), the Go/NoGo N2 (Bokura et al., 2001; Nieuwenhuis et al., 2003), the Aha! N380 (Mai et al., 2004), and the sequence violation N2 observed in serial reaction time (SRT) paradigms (Eimer et al., 1996), the modulation of expectancy occurs through different processes. Whereas

expectancy is set by predictions of success and failure in the case of f-ERN, it is set by the frequency of events in the case of oddball N200 and Go/NoGo N2; learned contingencies in the case of the N2 in SRT paradigms; and the failure to find a suitable solution to a problem in the Aha! N380. Thus, in addition to activity in the ACC related to the identification of expectancy-deviation, it would be presupposed that activity in distinct cortical areas, and with distinct latencies, would be associated with processes specific to the context of each experimental paradigm.

4.2   Conclusion

In summary, in this thesis I proposed a novel account for the f-ERN based on expectancy-deviation. The results of two experiments corroborated the expectancy-deviation hypothesis and presented a challenge to current explanations of the f-ERN. The observation of a f-ERN elicited by correct feedback, when this feedback also signalled a violation in expectancy cannot be accounted for by the reinforcement-learning theory (Holroyd & Coles, 2002), or any other present theories that attempt to explain what gives rise to the f-ERN. The findings presented here represent a small step in trying to find a common denominator that might explain what is necessary to give rise to ACC activity in performance monitoring. I suggest a revision in theories that explain the f-ERN and ACC function.

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