Hot cognition and activation of the medial prefrontal cortex: Self-regulating in contexts involving motivational pressures

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Abstract

The medial prefrontal cortex (mPFC) is involved in performance-monitoring and has been implicated in the generation of several electrocortical responses associated with self-regulation. The error-related negativity (ERN), the inhibitory Nogo N2 (N2), and the feedback-related negativity (FRN) are event-related potential (ERP) components which reflect mPFC activity associated with feedback to behavioural (ERN, N2) and environmental (FRN) consequences. Our main goal was to determine whether or not mPFC activation varies as a function of motivational context (e.g., those involving performance-related incentives) or the use of internally versus externally generated feedback signals (i.e., errors). Additionally, we assessed medial prefrontal activity in relation to individual differences in personality and temperament.

Participants completed a combination of tasks in which performance-related incentives were associated with task performance and feedback generated from internal versus external responses. MPFC activity was indexed using both ERP scalp voltage peaks and intracerebral current source density (CSD) of dorsal and ventral regions. Additionally, participants completed several questionnaires assessing personality and temperament styles.

Given previous studies have shown that enhanced mPFC activity to loss (or negative) feedback, we expected that activity in the mPFC would generally be greater during the Loss condition relative to the Win condition for both the ERN and N2. Also, due to the evidence that the (vmPFC) is engaged in arousing contexts, we hypothesized that activity in the ventromedial prefrontal cortex (vmPFC) would be greater than activity in the dorsomedial prefrontal cortex (dmPFC), especially in the Loss condition of the Go-Nogo task (ERN). Similarly, loss feedback in the BART (FRN) was expected to engage the vmPFC more than the dmPFC. Finally, we predicted that persons rating themselves as more willing to engage in approach-related behaviours or to exhibit rigid cognitive styles would show reduced activity of the mPFC.

Overall, our results emphasize the role of affective evaluations of behavioural and environmental consequences when self-regulating. Although there were no effects of context on brain activity, our data indicate that, during the time of the ERN and N2 on the MW Go-Nogo task and the FRN on the BART, the vmPFC was more active compared to the dmPFC. Moreover, regional recruitment in the mPFC was similar across internally (ERN) and externally (FRN) generated errors signals associated with loss feedback, as reflected by relatively greater activity in the vmPFC than the dmPFC.

Our data also suggest that greater activity in the mPFC is associated with better inhibitory control, as reflected by both scalp and CSD measures. Additionally, deactivation of the subgenual anterior cingulate cortex (sgACC) and lower levels of self-reported positive affect were both related to increased voluntary risk-taking on the BART. Finally, persons reporting higher levels of approach-related behaviour or cognitive rigidity showed reduced activity of the mPFC.

These results are in line with previous research emphasizing that affect/motivation is central to the processes reflected by mediofrontal negativities (MFNs), that the vmPFC is involved in regulating demands on motivational/affective systems, and that the underlying mechanisms driving these functions vary across both individuals and contexts.

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Anterior Cingulate Cortex - (ACC)

Balloon Analogue Risk Task - (BART)

Behavioral Inhibition System - (BIS)

Behavioral Activation System - (BAS)

Brodmann Area - (BA)

Current Source Density - (CSD)

Dopamine - (DA)

Dorsal Anterior Cingulate Cortex (dACC)

Dorsomedial Prefrontal Cortex- (dmPFC)

Electroencephalography- (EEG)

Error-negativity - (Ne)

Error-related Negativity - (ERN)

Feedback-related Negativity - (FRN)

Functional Magnetic Resonance Imaging - (fMRI)

HEXACO Personality Inventory - (HEXACO)

Low Resolution Brain Electromagnetic - (LORETA)

3,4-Methylenedioxymethamphetamine (MDMA)

Medial Prefrontal Cortex - (mPFC)

Mediofrontal Negativities - (MFNs)

Nogo Inhibitory N2 - (N2)

Positive and Negative Affect Schedule - (PANAS)

Prefrontal Cortex - (PFC)

Reinforcement Learning Theory - (RLT)

Standardized Low Resolution Brain Electromagnetic Tomography - (sLORETA)

Subgenual Anterior Cingulate Cortex - (sgACC)

Ventral Anterior Cingulate Cortex (vACC)

Ventromedial Prefrontal Cortex - (vmPFC)

Zuckerman Sensation Seeking Scale – Form V - (SSS-V)

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Introduction

The prefrontal cortex as a neural substrate for self-regulation

A hallmark of self-regulation is flexibility - the ability to maintain or disengage and re-establish new patterns of behaviour in pursuit of adaptive outcomes (Baumeister & Vohs, 2007). Self-monitoring involves the detection and evaluation of behavioural and environmental consequences which signal that an adjustment needs to be made, and involves the coordination of activity across multiple neural systems. Regions of the prefrontal cortex (PFC) are involved in regulating the timing (Forster & Brown, 2011; Luu, Flaisch, & Tucker, 2000) and evaluation of behaviours (Holroyd & Coles, 2008), a capacity which takes considerable time to develop as reflected by the prolonged structural maturation of the PFC (Dumontheil, Burgess, & Blakemore, 2008; Nair, Berndt, Barrett, & Gonzalez-Lima, 2001). Key regions include dorsal and lateral regions of the PFC which are involved in the cognitive control of motor behaviour (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004), and ventral and medial regions which are recruited during the rapid evaluation of behavioural and environmental consequences.

Functionally, activity in the medial prefrontal cortex (mPFC) has been shown to predict learning of optimal choice behaviour (Amiez, Joseph, & Procyk, 2005) and has been implicated in the control of motor responses (Rubia et al., 2001) such that greater activation in these regions is associated with greater success at inhibiting behavioural responses (Forstmann, Jahfari, Scholte, Wolfensteller, van den Wildenberg, & Ridderinkhof, 2008). Additionally, activity in the mPFC is also associated with representing value signals in relation to cognitive goals (Koechlin, Corrado, Pietrini, & Grafman, 2000), suggesting that self-regulation is not exclusive to the control of motor responses.

The role of prefrontal regions in self-regulation can also be determined from lesion studies. Injury to dorsal and lateral regions of the frontal lobes can impair working memory, as well as the planning and executing of flexible behaviour (Picton, Stuss, Alexander, Shallice, Binns, & Gillingham, 2007; Gehring & Knight, 2000). Conversely, injuries isolated to the medial and ventral portions of the frontal lobes are associated with marked deficits in the modulation of arousal (Pardini, Kreuger, Raymont, & Grafman,

2009) and judgments related to the evaluation of behavioural and environmental consequences (Bechara, 2004; Bechara & Naqvi, 2009; Damasio, 1996).

The contribution of the mPFC in self-regulation can also be inferred from studies investigating the association between changes in arousal and mPFC functioning. Increases in stress and arousal are associated with a rise in catecholamine levels (e.g., dopamine; DA) in the PFC (Arnsten, 1998). Even mild and acute changes in arousal introduce modulatory effects of DA and norepinephrine within the PFC (Arnsten, 1997) which, if excess, can seriously undermine top-down control over arousal and behaviour (Murphy, Arnsten, Goldman-Rakic, & Roth, 1996). For example, rhesus monkeys completing a working memory task were found to be impaired when simultaneously exposed to white noise with their stress response being augmented via pharmacological blockade of dopaminergic receptors (Arnsten & Goldman-Rakic, 1998). In humans, Liston, McEwen, and Casey (2009) found that individuals exposed to a psychosocial stressor, compared to non-stressed controls, presented with decreased functional connectivity in frontal regions when performing an executive control task. These studies illustrate that increased arousal/stress affects the functioning of the mPFC, and that this dysregulation manifests as limitations in self-regulation.

A large body of data implicates the mPFC as a core neural substrate for self-monitoring and self-regulation, and further suggests that these processes are influenced by the arousing nature of task context. Although considerable cognitive neuroscience literature suggests that regions of the mPFC are associated with self-regulation, little research has focused on how recruitment of medial prefrontal regions varies as a function of motivational context (e.g., those involving performance-related incentives, such as monetary outcomes) or the use of internally versus externally generated feedback signals (i.e., errors). Consequently, our goal was to investigate whether the engagement of the mPFC is influenced by the arousing nature of the contexts in which behavioural and environmental consequences occur. We used a combination of tasks in which performance-related incentives were associated with task performance and feedback generated from internal versus external responses.

The mPFC and the generation of Event-Related Potentials (ERPs) related to performance-monitoring and self-regulation

The cognitive and affective neuroscience literature implicates the mPFC in generating various ERPs which are functionally useful for understanding self-monitoring and self-regulation. These electrocortical responses belong to a family of ERPs which are collectively referred to as mediofrontal negativities (MFNs). Findings to date suggest that the error-related negativity (ERN) reflects activation of the mPFC in response to internal feedback (i.e., awareness of error that is not contingent on external feedback) indicating that goal-directed behaviour has failed, and that affective, behavioural, and cognitive adjustments are necessary. Conversely, the Nogo N2 (N2) reflects activation of similar frontal regions, and is elicited when a person successfully withholds a prepotent response to a target item. Finally, the feedback-related negativity (FRN) reflects medial frontal activation to external feedback regarding the nature/significance of an environmental or behavioural consequence.

ERN. The ERN, or error-negativity (Ne; Falkenstein, Hohnsbein, Hoorman, & Blanke, 1991), was first identified in the early 1990s, and was thought to reflect the activation of a neural system sensitive to discrepancies between intended and actual responses. This ERP component can be observed as a negative-going deflection over central and frontal midline sites, peaking between 50 and 100 ms after an erroneous response has been delivered (Gehring, Goss, Coles, Meyer, & Donchin, 1993). The ERN is traditionally examined in speeded response tasks where conflicting stimulus-response mappings are equally likely to occur (e.g., spatial discrimination, target item surrounded by flanking stimuli), or when prepotent responses to target stimuli must be inhibited, as is the case in a Go-Nogo task. The elicitation of the ERN is not specific to errors committed with the hand, as it has been observed after vocal (Masaki, Tanaka, Takasawa, & Yamazaki, 2001) and saccadic motor errors (Van't Ent & Apkarian, 1999). Using both functional neuroimaging and electroencephalography (EEG) methods (van Veen & Carter, 2002a), error-related responses have been localized to the dorsomedial prefrontal cortex (dmPFC) (Gehring et al., 1993; Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004) and, in some studies, ventral/rostral regions (Kiehl, Liddle,& Hopfinger, 2000; Luu & Tucker, 2003; Menon, Adleman, White, Glover, & Reiss, 2001). Corroborated by functional magnetic resonance imaging (fMRI) data, activity in dorsal and ventral regions has been shown to correlate with error-related scalp potentials (Mathalon, Whitfield, & Ford, 2003).

Nogo N2. Several negativities occurring in the 200-350 ms latency range have been identified (Luck, 2005), some of which are associated with executive functioning (Kopp, Rist, & Mattler, 1996), and possibly reflect the similar engagement of frontal systems mediating self-regulation (Holroyd, 2003). In the present study, the Nogo (or inhibitory) N2 is the focus. The N2 is an electrocortical response associated with the successful inhibition of conflicting or prepotent motor representations (Falkenstein, Hoormann, & Hohnsbein, 1999; Jodo & Kayama, 1992; Luu & Tucker, 2003), and is traditionally studied using Go-Nogo tasks. Whereas the ERN is time-locked to response onset, the N2 is locked to the stimulus signalling that a response is to be withheld. The N2 shares a similar scalp distribution as the ERN, peaking maximally over central and frontal midline sites and, using source analysis, has been shown to share overlapping neural generators in the medial frontal cortex (Bokura, Yamaguchi, & Kobayashi, 2001; van Veen & Carter, 2002a; van Veen & Carter, 2002b). As with the ERN, fMRI activation in the mPFC has also been shown to relate to N2 amplitude (Mathalon et al., 2003).

FRN. The FRN is similar to the N2 in that it is a stimulus-locked component, negative in polarity, and peaks in a similar latency range (approximately 250 ms post-feedback). Whereas the ERN reflects the activation of an internal monitoring system, the FRN is time-locked to the presentation of a feedback stimulus, and thus reflects the activity of an external monitoring and evaluative system. The evaluative processes are reflected in the amplitude of the FRN, such that larger signals are elicited when feedback indicates that behaviour was incorrect (Miltner, Braun, & Coles, 1997; Sato et al., 2005) or that an outcome has resulted in a loss or punishment (Gehring & Willougby, 2002; Pfabigan, Alexopoulos, Bauer, & Sailer, 2011). Typically, the FRN is investigated using gambling (Gehring & Willoughby, 2002) or associative learning paradigms (Nieuwenhuis, Holroyd, Mol, & Coles, 2004) in which individuals make choices between stimuli characterized by differing features (e.g., riskiness, magnitude, probability), or attempt to learn action-outcome contingencies on the basis of feedback information (Holroyd & Coles, 2008).

Additionally, FRN amplitude has been shown to be sensitive to unexpected outcome deviations (e.g., false-positive feedback; Oliveira, McDonald, & Goodman, 2007), outcome prediction errors (Holroyd & Coles, 2002), and predict adaptive behavioural responses (i.e., the avoidance of choices which were previously incorrect; van der Helden, Boksem, & Blom, 2010). Overall, considerable evidence suggests that the FRN reflects, to some extent, the motivational/affective significance of outcomes (Holroyd, Hajcak, & Larsen, 2006; Luu, Tucker, Derryberry, Reed, Poulsen, 2003), particularly in the context of reinforcement learning (Pfabigan et al., 2011; Yeung, Holroyd, & Cohen, 2005). Scalp distributions for the FRN often show peak activation at sites slightly more anterior to those at which the ERN and N2 are often found to be maximal (Gehring & Willoughby, 2004; Müller, Möller, Rodriguez-Fornells, & Münte, 2005), suggesting the possibility of additional underlying cortical generators (Gehring & Willoughby, 2004).

Theoretical accounts regarding the functional significance of MFNs. There are several prominent theories regarding the functional significance of MFNs that focus on error-detection, conflict-monitoring, reinforcement learning, and evaluative processes in the context of action monitoring.

According to error-detection theory, the ERN and FRN represent the activation of a generic performance monitoring system which is involved in detecting mistakes in performance (Miltner et al., 1997). It has been established that changes in ERN amplitude are associated with behavioural adjustments (e.g., post-error slowing) (Ghering et al., 1993), and that trial-by-trial fluctuations systematically relate to future response patterns mediated by the dorsolateral PFC (Debner, Ullsperger, Siegel, Fiehler, von Cramon, & Engel, 2005). Moreover, damage to the anterior cingulate cortex (ACC) has been shown to hinder the ability of this region to produce signals that correspond with the need for behavioural adjustment (Gehring & Knight, 2000), resulting in a slower correction of errors (di Pellegrino, Ciaramelli, & Làdavs, 2007; Modirrousta & Fellows, 2008). Whereas ACC activation is sensitive to information indicating performance errors and is associated with subsequent behavioural adjustments (Miltner et al., 1997; Miltner, Lemke, Weiss, Holroyd, Scheffers, & Coles, 2003), recent evidence suggests a more general monitoring function (Botvinick & Matthew, 2007; Krug & Carter, 2010). This is not to say that the mPFC does not respond to error detection, per se, but rather that error commission represents a salient event which a general monitoring system would detect as reflecting a need for the on-line control of behaviour.

Botvinick and colleagues (Botvinick, Cohen, & Carter, 2004; Botvinick & Matthew, 2007) have proposed that the ACC and regions of the PFC are involved in conflict monitoring, which includes detecting the potential for discrepancies between intended and actual behaviours, inhibiting prepotent response patterns, selecting a behaviour between equally permissible options, or in situations involving the potential for error (Botvinick et al., 2004; Botvinick & Matthew, 2007). Specifically, this theory suggests that ACC activity is sensitive to conflict and indirectly recruits control mechanisms of the dorsolateral PFC to deal with contextual and task demands. In support of this theory, it has been shown that greater ACC activation in tasks that are more cognitively demanding than those placing lower demands on cognitive control (Hester et al., 2004). Moreover, activity in the ACC during conflict processing positively relates to activation of the dorsolateral PFC and behavioural adjustments on subsequent trials (Kerns, 2004; Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2006). Finally, this theory accounts for the similar patterns of activation associated with inhibition of prepotent responses

(Falkenstein et al., 1999) which, similar to errors, involve high levels of conflict in streams of information processing.

A further extension of the role of the medial frontal cortex in performance monitoring and self-regulation suggests that engagement of this region is not exclusive to the monitoring of conflict at the response-outcome level (Botvinick et al., 2004; Potts, Martin, Burton, & Montague, 2006), but that mediofrontal activation is associated with the evaluation of behavioural and environmental consequences. As such, researchers have incorporated these data into a model of reinforcement learning (Holroyd & Coles, 2002; Holroyd & Coles, 2008; Holroyd et al., 2004). According to the reinforcement learning theory (RLT), phasic midbrain DA responses to unexpected events are conveyed to the ACC and utilized by the basal ganglia and frontal cortex to revise outcome predictions and channel future behaviour toward advantageous outcomes (Holroyd & Coles, 2002).

Considerable evidence suggests that the FRN is associated with violations in expectancy regarding action-outcome contingencies. For example, Moser and Simons (2009) found that FRN amplitude is minimal when outcomes are consistent with predictions, a result which has been confirmed by other studies reporting modulation of FRN amplitude in response to the magnitude of deviations from expected outcomes (Bellebaum, Polezzi, & Daum, 2010). Additionally, the FRN has been shown to relate to adaptive changes in behaviour (Cohen & Ranganath, 2007; Yasuda, Sato, Miyawaki, Kumano, & Kuboki, 2004), particularly when tasks involve active, compared to observational, learning (Bellebaum, Kobza, Thiele, & Daum, 2010), require overt responding (Yeung et al., 2005), or when information can actually be learned/used to guide future behavioural adjustments (Gentsch, Ullsperger, & Ullsperger, 2009; Holroyd, Krigolson, Baker, Lee, & Gibson, 2009). Further support comes from neurochemical studies that implicate midbrain DA transmission in the signalling of reward prediction errors, which reflect differences between expectations and actual outcomes (Schultz, 1998; Schultz & Dickinson, 2000).

A more parsimonious account of mediofrontal activation associated with the ERN and FRN has been proposed by Luu, Tucker, and colleagues. These researchers suggest that, in the context of self-regulation, activation patterns of the mediofrontal cortex reflect the monitoring and evaluation of context and action consequences (Luu et al., 2000a; Luu, Tucker, & Makeig, 2004). Additionally, self-regulation in the context of action monitoring involves the engagement of the mPFC in the modulation of visceral responses which support adaptive changes in behaviour (Luu, 2003). For example, in addition to predicting adaptive behaviour (Cohen & Ranganath, 2007; Genstch et al., 2009; van der Helden et al., 2010), activity in the mPFC has been shown to reflect the motivational significance of internal and external feedback (Luu et al., 2003). Further support comes from evidence indicating that MFNs involve multiple neural sources (Luu, Tucker, & Stripling, 2007), which mediate the monitoring, evaluation, and regulation of rapid behavioural changes (Luu & Tucker, 2003), as well as convey details regarding the autonomic state of the organism (Luu, 2003). As such, both dorsal and ventral regions of the mPFC are involved in the monitoring of actions in context, as well as the affective evaluation of these actions (Luu & Tucker, 2003). Overall, these authors suggest that the entrainment of corticolimbic circuits, which are core to self-regulation, is reflected by the oscillatory patterns of medial prefrontal neurons (Luu, 2003; Luu et al., 2003; Luu & Tucker, 2003).

The similarity in the various theories regarding the functional significance of these MFNs is that they generally reflect the activation of a system (or systems) involved in monitoring the need to change the current state of neural processing, and integrating information from internal and external systems (Holroyd et al., 2004; Luu & Tucker, 2003; Segalowitz & Dywan, 2009). Also, the activation of the mPFC in the context of self-regulation involves the coordination of autonomic responses to augment changes in adaptive behaviour (Critchley, 2005; Luu & Tucker, 2003; Luu et al., 2007). Thus, depending on the context and systems involved (e.g., sensorimotor, cognitive, affective, etc.), separate regions of the prefrontal cortex may differentially respond to internal and external feedback regarding successful and unsuccessful outcomes, any of which may indicate that the current repertoire being used to process information is insufficient (i.e., committing errors, discrepancies in reward predictions, outcome deviations from expectancy, novelty, and/or desirability). This differential engagement is important to consider, given the structural and functional data evincing specific divisions within the mPFC.

Self-regulation and the prefrontal cortex: Structural and functional divisions

Various techniques used to map structural differences in neural tissue indicate that distinctions can be made along anatomical planes (e.g., dorsal-ventral), which can be used further to characterize differences in functional recruitment during performance monitoring and self-regulation. Based on cytoarchitectural data, distinct structural features have been found both between and within dorsal and ventral sub-regions of the ACC (Vogt, Berger, Derbyshire, 2003; Vogt, Nimchinsky, Vogt, & Hof, 1995; Vogt & Vogt, 2003). Devinsky, Morrell, and Vogt (1995) suggest that a division between dorsal and ventral areas can be made caudal to Brodmann Area (BA) 32, approximating the genu of the corpus callosum. In a more recent study, using several techniques to map the structure of the human cortex, Hagmann et al. (2008) report separate anatomical sub-regions in the frontal cortex which closely parallel, the dorsal and ventral sub-regions which are based on cytoarchitectural data reported by other researchers (Devinsky et al., 1995; Vogt et al., 1995; Vogt et al., 2003).

Of particular importance to the current study are the functional differences which have been found between dorsal and ventral regions of the frontal cortex, specifically in the context of monitoring, evaluating, and adjusting behaviour (see Figure 1).

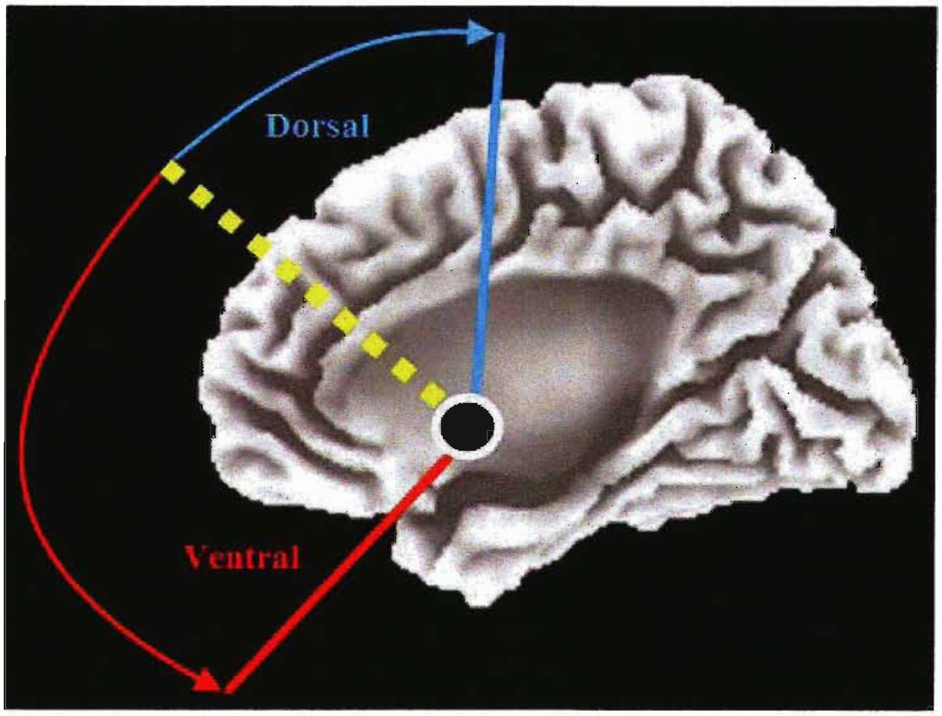

Figure 1. Approximate division between dorsal and ventral planes in the medial prefrontal cortex. Division is based on based on structural (Bush et al., 2000; Devinsky et al., 1995; Hagmann et al., 2008; Vogt et al., 1995; 2003) and functional data (Botvinick et al., 2004; Bush et al., 2000; Steele & Lawrie, 2004; Vogt et al., 2003).

A distinction between ventromedial and dorsomedial/dorsolateral prefrontal regions is a useful heuristic for characterizing cognitive-behavioural functions which involve affective or emotionally neutral processes, respectively. Evidence suggests that medial and ventral regions are recruited for the evaluation and prediction of outcomes (Hare, Camerer, & Rangel, 2009), whereas dorsomedial and dorsolateral regions modulate the cognitive control of behaviour.

Hot cognition: Engagement of the medial and ventral frontal lobes. The dorsal-ventral distinction of prefrontal functioning maps onto the cognitive and affective demands on goal-directed behaviour (Drevets & Raichle, 1998), such that ventromedial regions are preferentially recruited to process and deal with emotional content. Performing semantic tasks with affective stimuli was found to increase activation in ventral regions of the PFC compared to tasks with neutral content (e.g., such as syllogistic arguments (Goel & Dolan, 2004) and incongruent colour-word combinations (Mohanty et al., 2007), which are associated with greater neural activity in the dorsal PFC. A robust finding in the literature is that the activation of dorsomedial and lateral areas of the PFC is greater during cognitive and motor goal-directed tasks, whereas the ventromedial regions of the PFC are more likely to be engaged in arousing cognitive contexts, or when processing affective information is required (Steele & Lawrie, 2004). As reviewed by Bush et al. (2000), several studies show that both the dorsal anterior cingulate cortex (dACC) and dorsolateral PFC are more active when individuals engage in cognitive and/or behavioural-control processes with minimal affective influence, but that the ventromedial prefrontal cortex (vmPFC) shows greater activation when tasks involve the processing of affective information and/or occur in contexts of motivational pressure.

The mPFC (and ACC, including subgenual anterior cingulate cortex [sgACC]) is involved in integrating affective/autonomic states in support of goal-directed behaviour. The role of the medial and ventral regions of the PFC is emphasized during "hot cognition" (e.g., the engagement of executive functions or mental processes that are exposed to influences from arousing contexts, affective stimuli, or personally motivated goals). As studies have shown, ventral prefrontal regions and the ACC are involved in modulating affective responses and are reciprocally connected to thalamic nuclei, and subcortical areas which innervate sympathetic ganglion (Barbas, Saha, Remepel-Clower, & Ghashghaei, 2003; Paus, 2001; Vogt et al., 2003). Electrical stimulation of the human ACC has been shown to increase blood pressure, heart rate, and respiration (Pool & Ransohoff, 1949). These findings have been corroborated by Critchley and colleagues, who found that patterns of activation in the ACC are associated with changes in heart rate (Critchley et al., 2003) and the dilation of pupils (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005). In another study, volume of the insular and anterior cingulate cortices, along with subjective reports of emotional state, were shown to correlate with accuracy in the prediction of one's own heart rate (Critchley et al., 2004), suggesting a role of these regions in generating, accessing, and modulating physical states of affect (Critchley, 2005). Similarly, other studies have found that vmPFC activation is associated with changes in autonomic arousal (e.g., blood pressure; Gianaros, Derbyshire, May, Siegle, Gamalo, & Jennings, 2005) and improved task performance in the presence of motivational pressures (Krug & Carter, 2010; Kanske & Kotz, 2011; Matthews, Paulus, Simmons, Neleson, & Dimsdale, 2004) and stimuli containing emotional content (Kanske & Kotz, 2011). Not only has selective engagement of ventral prefrontal regions to emotional stimuli been observed at the level of single neuronal responses (Kawasaki et al., 2001), but also at a network level such that greater recruitment of ventral prefrontal areas has been associated with the suppression of subcortical limbic activity (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; van Reekum et al., 2009) and motor responses to emotional stimuli (Chiu, Holmes, & Pizzagalli, 2008). Taken together, there is considerable evidence that the ACC and vmPFC are involved in regulating the autonomic nervous system to align with the motivational demands of the environment.

It is well established that cognitive processing and behavioural responses are influenced by arousing stimuli and contexts. For example, viewing emotional images during a delayed working memory task is associated with poorer recall (Dolcos & McCarthy, 2006), source memory can be impaired due to arousing images (Mather, Mitchell, Raye, Novak, Greene, & Johnson, 2006), and negative feedback can interfere with the ability to inhibit motor responses to target items (Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006). Whereas the influence of arousing stimuli or contexts on behavioural responding and cognitive performance has been demonstrated, how the medial frontal cortex may differentially respond to internal (ERN) and external (N2; FRN) information due to the arousing nature of the context is less clear. Turning to the ERP literature, parallels can be drawn between differences observed in the characteristics and neural generators of the ERN, N2, and FRN, and the structural and functional features of the mPFC described above. These functional subdivisions indicate that dorsal and ventral regions of the mPFC could be differentially engaged when contributing to ERN, N2, and FRN (Ghering & Willoughby, 2004; Luu & Tucker, 2003), especially when elicited in contexts involving performance-related/motivational pressures.

Cortical generators of the MFNs

Regions of the medial prefrontal cortex are consistently implicated as neuronal generators of the ERN, N2, and FRN. While overlapping neuronal generators have been found for these MFNs (Gründler, Ullsperger, Pantev, & Huster, 2009; Holroyd et al., 2004), there is some evidence to suggest that regions of the mPFC may differentially contribute to these ERPs (Gehring & Willoughby, 2004; Luu & Tucker, 2003; Mathalon et al., 2003; Segalowitz, Santesso, Murphy, Homan, Chantziantoniou, & Khan, 2010). Generally, studies have failed to consider that the regional contribution from areas of the PFC (e.g., dorsal-ventral) in generating these ERPs may differ due to contextual influences, such as those impacting arousal and affect.

Results from dipole modeling implicate the dACC in the generation of the ERN (Gehring et al., 1993; Luu et al., 2003), with a single dipole often accounting for more than 90-95% of the variance in scalp topography (O'Connell et al., 2007; van Veen & Carter, 2002a; 200b). Other studies also suggest that the ERN is associated with increased activation in dorsal ACC and motor areas responsible for planning the execution of relevant behaviours (Dehaene, Posner, & Tucker, 1994; Herrmann et al., 2004; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). Other imaging methods, such as standardized low resolution brain electromagnetic tomography (sLORETA), also implicate dorsal regions of the ACC as generators of the ERN (Herrmann, et al., 2004). Similar regions have been implicated in generating the inhibitory N2 (van Veen & Carter, 2002a), with dipoles in medial prefrontal regions reliably explaining the distribution of electrical activity at the scalp (Bekker, Kenemans, & Verbaten, 2005; Jonkman, Sniedt, & Kemner, 2007), fMRI localizations to dmPFC (Mathalon et al., 2003), and sLORETA analyses localizing the N2 to the medial walls of the PFC (Gründler et al., 2009).

Although various regions of the ACC have been implicated in the generation of the FRN, evidence suggests that the ventral anterior cingulate cortex (vACC) and other ventromedial prefrontal structures are also involved in the production of this component in addition to dorsomedial regions (Luu et al., 2003).

For example, dipole models point toward a medial prefrontal generator (Müller et al., 2005), and results from sLORETA analyses indicate that the outcomes which carry affective or motivational significance are associated with activation of the ventromedial and rostral areas of the PFC (Kamarajan et al., 2009; Ogawa, Masaki, Yamazaki, & Sommer, 2011). A study which combined EEG and fMRI methods showed that not only does ventral PFC activation increase as outcomes become more motivationally significant, but also no areas in or near the dACC could reasonably account for the FRN (Nieuwenhuis, Slagter, Geusau, Heslenfeld, & Holroyd, 2005). Recent results from low resolution brain electromagnetic (LORETA) source analysis indicated that the rostral ACC best accounted for FRN activation at the scalp (Polezzi, Satori, Rumiati, Vidotta, & Daum, 2010), and findings from our lab using LORETA suggest that the ERN and FRN are accounted for by dmPFC and vmPFC regions, respectively (Segalowitz et al., 2010). It should be noted that, although evidence supports ventromedial prefrontal regions in the generation of the FRN, there is evidence for functional overlap in the neuronal generators of the ERN, FRN, and the N2 (Gehring & Willoughby, 2002; Gründler et al., 2009; Luu & Tucker, 2003). Together, the evidence indicates that the mPFC is involved in the generation of MFNs, while contributing sources located more ventrally are found when tasks involve motivational pressures and/or emotional content.

Medial prefrontal activity in response to motivation manipulations

Researchers who have investigated the effects of arousal and/or contextual manipulations on mPFC activation have found increased engagement of the mPFC, particularly for negative affect, with additional neuronal generators in ventral and rostral regions. For example, Taylor et al. (2006) found that, compared to a non-incentive condition, hemodynamic error responses in rostro-ventral regions of the ACC were significantly greater when errors produced a monetary loss. In a more recent study, similar fMRI results were found using a Go-Nogo task which involved a neutral condition and a punishment condition where errors resulted in monetary loss (Simões-Franklin, Hester, Shpaner, Foxe, & Garavan, 2010). Whereas the dorsal ACC did not show different activation profiles across conditions, in the punishment condition, phasic activity to errors of commission was significantly greater in the rostral ACC as compared to the neutral condition (Simões-Franklin et al., 2010). In another study, Kanske and Kotz (2011) had participants perform a gender voice decision task, involving congruent (i.e., auditory presentation and response side match for gender) and incongruent (i.e., auditory presentation and response side non-match for gender) trials, where the words spoken were neutral or emotional in content. Resolving conflict between stimulus-response mappings for emotional words was associated with additional recruitment of a vACC source.

Similar results have been reported in several EEG studies. For example, Luu et al. (2003) identified an additional neural source in the rostral mPFC when delaying feedback to render it uninformative to immediate performance, but allowing it to retain its affective significance. Compared to verbal encouragement, derogatory feedback has been shown to enhance medial frontal activation, where the magnitude of this increase is associated with greater self-reports of negative affect (Wiswede, Münte, & Rüsseler, 2009). More recently, researchers found that, compared to encouragement and neutral conditions, verbal admonishment following erroneous responses was associated with additional activation of ventromedial prefrontal regions (Ogawa et al., 2011). Inhibitory N2s are also sensitive to changes in arousal, as revealed by larger amplitudes and additional ventral sources during conditions of distress and anxiety as compared to neutral and positive conditions (Lewis et al., 2006). Overall, evidence suggests a functional overlap in the cell assemblies generating these MFNs, with additional activation and recruitment of ventral sources of the mPFC when tasks involve responding to emotional content, increased arousal, or motivational pressures.

Individual differences in mPFC function

A growing body of literature supports the view that individual differences in personality and cognitive style relate to the functioning of the mPFC. Cognitive styles characterized by rigidity have been found to relate to reduced mPFC activation in the context of self-regulation. For example, smaller ERNs have been observed in individuals who rate themselves as having more conservative orientations (Amodio, Jost, Master, & Yee, 2007), as well as in individuals rated higher in right-wing authoritarianism and social dominance orientation compared to those scoring higher in egalitarianism (Weissflog, van Noordt, Choma, Dywan, & Segalowitz, 2009). Evidence from a series of fMRI studies using Go-Nogo tasks indicates that general error-related activity in the mPFC is negatively associated with self-reported absentmindedness (Hester et al., 2004). In addition to associations with cognitive styles, relationships between temperament style and mPFC activation are informative for understanding individual differences in temperament, especially in relation to self-control.

Several research groups report that individuals who have a greater tendency to internalize and exhibit withdrawal-related behaviours show hyperactivation of the mPFC, as indexed by MFN amplitude. For example, individuals scoring higher on conscientiousness and low in neuroticism have been found to elicit smaller ERNs than those with the inverse temperamental profile (Pailing & Segalowitz, 2004), and greater levels of externalizing behaviours are related to reductions in ERN amplitude and oscillatory brain responses following errors (Hall, Bernat, & Patrick, 2007). Conversely, persons scoring high on measures of behavioural inhibition have been shown to generate larger ERNs (Boksem, Tops, Wester, & Merijam, Lorist, 2006), especially when errors are associated with overt punishments, such as losing money (Boksem, Tops, Lostermans, & Cremer, 2008).

With respect to the FRN, amplitude differences to feedback associated with and without overt actions have been shown to correlate with ratings of task involvement (Yeung et al., 2005). Some researchers have found that higher self-reports of inhibition (Santesso, Dyzundzyak, & Segalowitz, 2011) and negative affect relate to increased neural responses to feedback indicating errors or losses (Sato et al., 2005; Yasuda et al., 2004), indicating that sensitivity to negative feedback varies across individuals. In a sample of children, Stieben, Lewis, Granic, Zelazo, Segalowitz, and Pepler (2007) found reduced inhibitory- and error-related activation in the mPFC of persons presenting with pure externalizing symptomatology, as compared to controls and those comorbid for externalizing and internalizing tendencies. Similar results have been reported in a recent study by Moadab, Gilbert, Dishion, and Tucker (2010), in which individuals higher in externalizing showed reduced mPFC responses to errors as well as during response inhibition (i.e., N2). Taken together, differences in temperament styles are reflected by the variability in mPFC activity across persons. Thus, examining the associations between brain function, temperament, and personality can be seen as relevant to understanding the neural underpinnings of real-world behaviours.

One set of real-world behaviours which are particularly relevant in the context of temperament and brain function is that of risk-taking. Approach-related behaviours are core to risk-taking, and results from our lab and others implicate deactivation of the mPFC during performance monitoring as a neural correlate of approach-related dispositions. In a sample of young men Santesso and Segalowitz (2009) found that individuals scoring higher on scales assessing approach-related behaviours (i.e., sensation-seeking, reward sensitivity) displayed reduced mediofrontal activity following erroneous behavioural responses. In a more recent study, Polezzi et al. (2010) found that risk-taking styles can be characterized by specific reductions in mPFC activation, whereby reduced FRN amplitudes are found specifically in conditions in which persons are prone to take risks. Contextual influences in relation to mPFC activation and approach-related behaviours have also been examined. Segalowitz et al. (2011) found that FRN amplitude was reduced when individuals engaged in risk-taking in the presence of their peers as compared to alone. These relationships were confirmed using source measures of CSD in the dmPFC and vmPFC, such that larger mPFC responses predicted lower scores of sensation-seeking and risk-taking. Given the evidence that individual differences in personality and temperament are reflected in the variability of medial prefrontal function, we were further interested in examining these associations.

The Current Study

The mPFC is a key neural substrate mediating self-regulation, and strong evidence implicates regions of the mPFC as cortical generators of the ERN, N2, and FRN (Gehring & Willoughby, 2002; Genstch et al., 2009; Gründler et al., 2009; Nieuwenhuis et al., 2005; Segalowitz et al., 2010; van Veen & Carter, 2002a; 2002b). It has also been established that recruitment of medial prefrontal regions differs across contexts involving emotional content/stimuli (Kanske & Kotz, 201; Ogawa et al., 2011; Wiswede et al., 2009) or motivational pressures (Luu et al., 2003; Simões-Franklin et al., 2010; Taylor et al., 2006). Although some researchers have examined scalp and source activity of the MFNs when manipulating task context (Simões-Franklin et al., 2010; Taylor et al., 2006), there are no known studies that have considered these effects in terms of regional activation of the mPFC, based on high-density EEG data. Given the lack of studies designed to investigate the ways in which regional mPFC activity responds to task context issues, our goal for the present study was to examine whether mPFC activation was sensitive to the arousing nature of the contexts in which behavioural and environmental consequences occur. If mPFC activity is influenced by contexts involving performance-related incentives, this sensitivity should be reflected by changes in ERP amplitude and the relative activation of medial prefrontal regions.

In order to address whether or not mediofrontal activation differs across contexts involving motivational pressures, we used two tasks which involved performance-related incentives. The ERN and Nogo N2 were collected using a standard Go-Nogo task, whereas the FRN was collected using the Balloon Analogue Risk Task (BART). The Go-Nogo task requires that participants deliver a response to a 'Go' stimulus, which is presented disproportionally more often than the 'Nogo' stimulus, which indicates that the response is to be withheld. Errors of commission (i.e., motor response to a Nogo stimulus; ERN) and successful inhibition (i.e., withheld motor response to Nogo stimulus; N2) were the focus for this task.

In our study, we had participants complete two separate versions of the task, one in which they could gain points (Win condition) and one where they could avoid losing points (Loss condition). In the Win condition, successful inhibition was rewarded with an increase in points, whereas errors resulted in a missed opportunity to accrue points. Conversely, successful inhibition in the Loss condition resulted in loss aversion, with errors being associated with a reduction in points. ERPs are often used in Go-Nogo studies in order to capture brain function occurring at a high temporal resolution. Our manipulation provided us the opportunity to compare indices of medial prefrontal activation associated errors and inhibition across contexts involving rewards (gain, missed gain) and punishments (averted loss, loss).

The BART was used to elicit FRNs because voluntary risk-taking on this task is associated with reward and punishment outcomes. On this task, the inflation of the balloon is tied to an increase in points which can be banked once the participant decides to stop the inflation and collect the accrued points. Eventually, during the inflation process the balloon bursts and the accrued points for that trial are lost. Thus, although participants know that the balloon will burst on every trial if they do not intervene, they do not know the exact point at which the balloon will burst from trial to trial. Risk-taking on this task is indexed by the number of inflations participants allow on trials where the balloon does not burst.

In the 10 years since its introduction, considerable research has been focused on the construct validity and reliability of the BART as a behavioural index of risk-taking. Risk-taking propensity on the BART has been found to positively correlate with approach-related behaviours (e.g., sensation seeking, impulsivity) as well as self-reports of addiction and detrimental health behaviours (Lejeuz et al., 2002). For example, higher levels of risk-taking have been shown to predict the use of cigarettes (Lejeuz et al., 2003), as well as the use controlled substances (e.g., 3,4-Methylenedioxymethamphetamine (MDMA); Hopko et al., 2006) and, in combination with measures of impulsivity and self-esteem, has been found to uniquely predict risky sexual behaviours (Lejuez, Simmons, Aklin, Daughters, & Dvir, 2004). Others have found that individuals with higher ratings of antisocial behaviour and authority problems exhibit riskier behaviour on the BART (Hunt, Hopko, Bare, Lejuez, Robinson, 2005). Adolescents with conduct disorder and substance use problems exhibit riskier behaviour and suffer greater losses on the BART as compared to controls (Crowley, Raymond, Mikulich-Gilbertson, Thompson, & Lejuez, 2006). Other studies have replicated these findings in a sample of adolescents (Lejeuz, Aklin, Zvolensky, & Pedulla, 2003). A youth version of the BART has also been validated (Lejeuz, Atkin, Daughters, Zvolensky, Kahler, & Gwadz, 2007).

Although few studies have examined the associations between neural responses and risk-taking on the BART, there is evidence to suggest that the BART engages regions of the mPFC associated with evaluation and self-regulation. Using ERPs, Fein and Chang (2008) found that FRN amplitude was larger for active versus passive risk-taking, and that peak FRN amplitude was negatively associated (i.e., reduced negativity) with a family history of alcohol problems. Neuroimaging data also suggest that voluntary risk-taking on the BART is associated with increased activity in several medial prefrontal regions (Rao, Korczykowski, Pluta, Hoang, & Detre, 2008). Thus, this task allows us to examine regional differences in mediofrontal activation during a time of negative feedback which results from an individual's propensity to take risks.

Hypotheses.

MFN amplitudes. We expected that amplitude of the ERN and N2 would be larger (i.e., more negative) in the Loss condition as compared to the Win condition on the Go-Nogo task. Given the FRN was tied to loss feedback, our only expectation was that the feedback would elicit an ERP component exhibiting a negative deflection between 200 and 350 ms post-feedback stimulus. These findings were expected because previous studies have shown that negative feedback or punishment/loss conditions are associated with evoked mediofrontal activity.

Regional activity. Based on the data from the Go-Nogo task, we predicted that activity in the mPFC during the Loss condition would be relatively greater than in the Win condition for both the ERN and N2. Furthermore, given the mixed evidence regarding dorsal and ventral generators contributing to the ERN, along with the large body of evidence that ventral regions are recruited in contexts that are arousing, it was expected that the vmPFC would become significantly more active than the dmPFC during the Loss condition, as compared to the Win condition. The FRN to negative feedback in the BART was expected to be associated with greater activity in the vmPFC than in more dorsal regions. Such findings would confirm data indicating that ventromedial regions are sensitive to task engagement in contexts involving motivational pressures.

A final prediction was made regarding regional recruitment during punishment and negative feedback. Comparing activity associated with the ERN from the Loss condition of the Go-Nogo task, and the FRN to negative feedback on the BART, we expected that regional recruitment would show more activity in the vmPFC than the dmPFC for both ERPs. These findings would not only support previous research implicating ventromedial engagement in arousing contexts, but would further confirm a model of medial prefrontal function in which error feedback associated with internally and externally generated responses similarly recruit medial prefrontal regions.

Individual differences. Personality and temperament were assessed in relation to the various indices of mPFC activation. Generally, it was expected that individuals scoring higher on approach-related tendencies would present with reduced mPFC activation because previous research has shown that deactivation of the mPFC is greater in persons scoring higher on indices of behavioural approach (e.g., sensation-seeking, risk-taking). Conversely, greater self-reports of inhibitory/withdrawal-related behaviour were expected to be associated with increased mPFC activation. Moreover, individuals self-reporting a greater tendency to exhibit rigid cognitive styles were expected to show reduced medial prefrontal activation. These findings could be related to previous studies reporting lower levels of medial prefrontal activity in relation to cognitive styles characterized by rigidity, such as political conservatism or religious zeal.

Methods

Participants

Twenty-eight Brock University students (*M* age = 21.0 years, *SD* = 3.71 years, range = 18-35 years) participated in the current study. Recruitment was done through advertisements posted on campus, as well as with the use of an on-line registration system through which students can sign-up for psychology studies. In the current sample, 86% (*n* = 24) were female, and 89% (*n* = 25) reported right-hand dominance. One participant reported the use of neuroleptics to treat a clinically diagnosed mood disorder. However, the participant was not removed from the analyses as their scores were within the range of the other participants' scores.

Materials

Psychophysiological tasks.

All tasks were created and presented using E-Prime software, version 1.2 (Psychological Software Tools, Pittsburgh, PA).

MW Go-Nogo task. In this task, participants were instructed to either deliver or withhold a motor response, depending on the presented stimulus. Go and Nogo stimuli were counterbalanced across participants, and consisted of the uppercase letters 'M' and 'W'. Stimuli were white and presented centrally on a black background for 100 ms. Participants had to deliver a response within 500 ms in order for it to be logged as correct or incorrect. Responses falling outside of this window were followed with feedback (1000 ms duration) indicating that the response was 'Too Slow'. Responses to Nogo stimuli were followed with feedback indicating that the response was 'Incorrect'. An inter-stimulus interval of 250 ms was used.

In the Win condition, participants were rewarded with 50 points for each response that was successfully inhibited to Nogo stimuli. Participants would not lose points for erroneous responses, but would instead have lost an opportunity to gain points. In the Loss condition, the score was reset to zero and participants averted losing points by successfully inhibiting motor responses to Nogo stimuli; that is, they did not gain points for successful inhibition. However, each unsuccessful inhibition in the Loss condition resulted in a subtraction of 50 points.

It is important to note that participants were not awarded points for correct responses to Go stimuli in either condition. Conversely, errors on Go trials (i.e., responses which were too slow, or the absence of a response) were not punished with a reduction in points for either condition. Nonetheless, all participants cooperated with task instructions, as revealed by nearly perfect response rates to Go stimuli in both the Win (*M* = 98.91%, *SD* = 0.02, range = 83.86% - 100%) and Lose conditions (*M* = 98.61%, *SD* = 0.03, range = 88.61% - 100%).

Participants were informed that points secured would be translated into a monetary payout at the end of the experiment. Each condition consisted of 400 trials, 80% of which were Go trials. Each condition was performed in two rounds of 200 trials, separated by a 30 second break, and the running point total was presented every 20 trials. This task took approximately 25 minutes to complete, including instructions and breaks.

Balloon Analogue Risk Task (BART; Adapted from Lejuez et al., 2002). As mentioned previously, considerable research has been carried out on the ecological validity of risk-taking on the BART, and test-retest reliability of the risk-taking propensity measure has been found to be high(White, Lejuez, & de Wit, 2008; *r* = .77). In this task, participants are presented with a static image of a circle, covered in a checkerboard pattern, which symbolizes a balloon. The center of the circle contains a ‘point box’, in which the available points for the current trial are displayed in red text. On every trial the participant presses the response button which causes the balloon to increase in size (every 500 ms, by a factor of .35 for both height and width) and 10 points to be added, cumulatively, to the point box. This process continues until (i) the balloon pops, or (ii) the participant decides to end the inflation by pressing the button a second time. On every trial, the computer randomly selects a critical value for the maximum inflation (between pump 3 and 10), at which point the balloon will pop if the second response is not made. Given the need for negative feedback to produce the FRN, the balloon was set never to pop on the first two pumps in order to minimize the possibility that participants become hypersensitive to losing, and consequently adapting a strategy of ending the inflation immediately. Participants were told, however, that the points on a given trial would never exceed 100 and that the balloon would not exceed the visual area of the computer monitor.

The main objective in this task is to accumulate as many points as possible. If the participant decides to end the inflation before the balloon pops, any points currently in the point box are banked into a running total, and the presented feedback reads 'Win – X points', with the current running total displayed below. Conversely, if the balloon pops before the participant decides to end the inflation process, they would lose both the points currently in the point box, and 10% of their banked running total. The presented feedback for loss trials mirrored that of win trials, with the exception of the word 'Bust!' in place of the word 'Win!'. Screens for both types of feedback are presented for 1500 ms and consist of red text on a black background. Breaks were used to separate the task into three blocks, each containing 85 trials, with points being carried across blocks. This task took approximately 20 minutes to complete, including instructions and breaks.

To minimize order effect, the presentation of Win/Lose conditions in the Go-Nogo task were counterbalanced across participants, as was the ordering of the each of the two tasks.

Questionnaires.

Demographic and Health Screening Questionnaire. Prior to any testing, the researcher administered a short questionnaire in order to screen for any potential problems with participation and/or recording (Appendix A). The questionnaire was used to gather details regarding past or continuing issues in the domains of reading and/or number skills, mood, anxiety, sleep patterns, and concentration problems. Information was also gathered about appetite dysregulation, activity level, recent major stressors, surgery, and chronic health problems. In addition, participants were asked to provide details about the use of any prescription or over-the-counter medication, general consumption of caffeine, nicotine, and alcohol, as well as frequency and intensity of exercise practices. See Appendix B for this questionnaire.

HEXACO. Personality was measured using the HEXACO Personality Inventory (Lee & Ashton, 2004). For this questionnaire, twenty-four facet-level traits load onto six factors that characterize main aspects of personality. These factors include Honesty-Humility (H), Emotionality (E), Extraversion (X), Agreeableness (A), Conscientiousness (C), and Openness to Experience (O). Ratings are done on a 5-point scale (1 = Strongly Disagree, 5 = Strongly Agree) across 60 statements which characterize the various dispositional behaviours that load onto these six factors. Higher scores on the Honesty-Humility factor indicate little desire to control situations or others and that the respondent does not feel unique entitlement due his/her accomplishments. An item reflecting H is "I think that I am entitled to more respect than the average person is." Scoring high on the Emotionality factor suggests the desire for emotional support from others, as these individuals tend to experience anxiety and physiological response to stressors in their lives. An item from the E factor is "When it comes to physical danger, I am very fearful." High scores on Extraversion reflect confidence and enjoyment in engaging with others socially. An item from the X factor is "I prefer jobs that involve active social interaction to those that involve working alone." Agreeableness assesses an individual's cooperative tendencies, such that higher scores indicate a leniency in judging others and patience when engaging with others who disagree or have transgressed. An item from the A factor is "Even when people make a lot of mistakes, I rarely say anything negative." Conscientiousness is characterized by a tendency to organize time and surroundings in order to reach goals in a precise and disciplined manner. An item from the C factor is "I always try to be accurate in my work, even at the expense of time." Finally, the higher scores on the Openness to Experience factor are suggestive of a tendency to be immersed in one's surroundings, to be interested in novel or anomalous events, and to appreciate culture. An item reflecting O is "I like people who have unconventional views". See Appendix C for this questionnaire.

Both facet and factor levels have been shown to demonstrate high internal reliability, with alpha coefficients ranging from .75 to .92 (Lee & Ashton, 2004). Factor analysis indicates that these six factors explain nearly two-thirds of the total variance. Furthermore, convergent validity of each of the six factors has been demonstrated by their associations with other markers of these personality characteristics (Lee & Ashton, 2004).

BIS-BAS. Based on Gray's theory about the neural substrates of approach-avoidance behaviours, Carver and White (1994) developed a brief questionnaire to characterize the degree to which individual's showed a preference for approach (Behavioral Activation Scale; BAS) or withdrawal (Behavioral Inhibition Scale; BIS) related behaviours. A total of 20 items are rated on a 4-point scale (1 = Strongly Disagree, 4 = Strong Agree). Factor analysis on over 700 college students has yielded four factors which reflected differences in the sensitivity of the BIS-BAS systems. Specifically, while BIS reflects a single factor, BAS consists of subscales reflecting Drive, Reward Responsiveness, and Fun Seeking. As examples, a BIS item is "Criticism or scolding hurts me quite a bit.", a BAS-Drive item is "I go out of my way to get things I want.", a BAS-Reward Responsiveness is "When I get something I want, I feel excited and energized.", and a BAS-Fun Seeking item is "I'm always willing to try something new if I think it will be fun." Test-retest reliability of this scale has been shown to range from .59 to .69, and convergent validity with several well-established measures of personality and temperament has been demonstrated (Carver & White, 1994). See Appendix D for this questionnaire.

PANAS. In order to acquire a global measure of state affect, the Positive and Negative Affect Schedule (Watson, Clark, & Tellegen, 1988) was administered. Comprised of 20 descriptors of mood, on a 5-point scale (1 = Very Slightly/Not at All, 5 = Extremely) individuals rate the degree to which they have felt the descriptor that day. Ten items are summed to create the Positive Affect scale, with the other

10 items being summed to create the Negative Affect scale. Examples of items belonging to the PA scale include "excited", "enthusiastic", and "active". Examples of items belonging to the NA scale include "irritable", "hostile", and "ashamed". Cronbach's alpha for the PA scale has been shown to range from .86 to .90, and the NA scale from .84 to .87 (Watson et al., 1988). Moreover, test-test reliability indicates that, across different time assessments (i.e., how do you feel 'x' (i) today, (ii) past few weeks, (iii) year), the PANAS shows appreciable stability in assessing PA and NA across time (Watson et al., 1988; *r*'s range from .39 to .70). See Appendix E for this questionnaire.

SSS-V. The Zuckerman Sensation Seeking Scale Form V has been characterized as a need to seek out, and engage in, a variety of novel environments and complex situations, with a willingness to be exposed to physical and/or social risks in order to achieve these experiences (Zuckerman, 1979). The assessment of sensation-seeking was done using the Zuckerman Sensation Seeking Scale Form V(Zuckerman, 1994). Initially developed in the 1960s (Zuckerman, Kolin, Price, & Zoob, 1964), this scale has being used extensively to examine four factors (10 items each) related to the overall construct of sensation-seeking. Ratings are dichotomous choices between one of two statements about a specific behaviour/task, such that individuals choose which of the two they would prefer. Specifically, willingness to engage in activities or sports which carry a high risk for physical harm (e.g., "I often wish I could be a mountain climber" versus "I can't understand people who risk their necks to climb mountains") reflect 'Thrill and Adventure Seeking'. The Experience Seeking factor taps into cognitive and sensory sensation-seeking, whereby individuals feel the need to seek out new experiences (e.g., "I would not like to try any drug which might produce strange and/or dangerous effects on me" versus "I would like to try some of the drugs that produce hallucinations"). The Disinhibition factor reflects an individual's motivation to engage in uninhibited social activities (e.g., I dislike people who are uninhibited and free about sex" versus "I enjoy the company of people who are uninhibited and free about sex"). Finally, the Boredom

Susceptibility factor includes the desirability for novelty and unpredictability as opposed to monotony (e.g., "I get bored seeing the same old faces" versus "I like the familiarity of everyday friends").

In a large sample of undergraduate students Roberti, Storch, and Bravata (2003) have shown the SSS-V to be supported by a four-factor model, reliability with Cronbach's alphas for the subscales ranging from .75 to .80, as well as convergent validity with the Impulsive Sensation Seeking subscale of the Zuckerman-Kuhlman Personality Questionnaire (coefficients ranges from .43 to .61). See Appendix F for this questionnaire.

Procedure

Once participants arrived and were familiarized with the testing room and psychophysiological recording equipment, consent forms were read and signed (see Appendix G). Next, a brief health and demographic questionnaire was administered (see Appendix B). Additionally, the initial screening ensures safety of the recording equipment (e.g., use of non-permanent hair dyes), as well as the integrity of the data given that a host of factors can influence synaptic transmission which, in turn, influence EEG signals (e.g., history of head trauma, nervous system disorders, neuroleptic medications). Once the EEG sensor net was secure and participants were comfortable, the quality of the signals were checked (i.e., zeros, gains, impedance), after which administration of the experimental tasks commenced.

After both experimental tasks were complete, the sensor net was removed from participants, who were then offered the use of hair cleaning and styling products. Participants then completed a package of self-report personality questionnaires which included those described above, as well as others which were not the focus of the current study. Upon completion of the questionnaires, participants were fully debriefed as to the purposes and expectations of the study (see Appendix H). In compensating participants for their time, each received a maximum of two participation hours to be used towards the completion of course requirements. Additionally, each participant was given a monetary payment of $10 for points won during the tasks.

Procedures and measures used in the current study received clearance from the Research Ethics Board at Brock University (File # 10-101; See Appendix I).

EEG recording and data reduction.

EEG signals were recorded continuously at a sampling rate of 500 Hz using a 128-channel HydroCel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, Oregon), with 0.1-100 Hz band-pass filter, referenced to Cz. Impedance ≤ 50 kΩ was maintained on all channels and signals were amplified using a Net Amps 200 amplifier. Activity generated by ocular movements was recorded by bi-polar electrode pairs, above, below, and on the outer canthus of each eye.

Offline, all data processing was done using MATLAB (version 2007b) and EEGlab (version 10.0). A band-pass filter of 1-30 Hz (48dB/oct) was applied and ocular movements were corrected by regressing out, from all other channels, the activity indexed by one pair of bi-polar eye channels. Continuous EEG was visually inspected to identify bad channels and artifact-laden epochs, all of which were marked for removal. The data were re-referenced to the average reference, and all epochs and channels identified as bad were subsequently removed. Epochs were extracted from 600 ms before and ending 600 ms after the response for the ERN. For the N2, epochs were from -200 to +600 ms time-locked to the Go-Nogo stimuli. For the FRN, the epoch extracted was from -200 to +800 ms with respect to the feedback stimulus. The baseline correction included the 200 ms preceding stimulus onset, for the N2 and FRN, and from 600 to 400 ms before the response for the ERN.

Epochs were further examined for any residual artifact before averaging trials together. Removal of bad channels results in an unequal number of channels across participants, which becomes problematic when trying to apply an averaging reference across individuals. In order to ensure that a symmetrical reference is used for each participant, a standard 98-channel montage which covered the majority of the scalp was chosen (see Appendix J), onto which each subject's data was built. This method uses a spherical spline function to re-create each subject's data, onto the chosen 98 sites. In other words, whatever data is present at the scalp is mapped onto the 98 sites that symmetrically cover the scalp, as this will allow an unbiased representation of the average reference across participants.

ERP scoring.

Scoring of ERPs was done using an in-house computer-assisted peak-detection program (Segalowitz, 1999) which allows users to easily quantify peak amplitude and latency in ERP waveforms. The scoring was performed on a select cluster of frontal and posterior midline sites, at and around Fz, FCz, Cz, Pz, and Oz. Specifically, the maximum voltage for a given ERP was identified within the appropriate cluster (i.e., frontal and/or posterior) for each individual. This method is preferred as it does not rely on the assumption that a given ERP will be maximal at precisely the same site for each individual. In the present study, only data from frontal midline sites were analyzed given the focus on medial prefrontal activation (see Appendix K for chosen frontal sites).

The ERN was scored as the maximum frontal midline negativity between approximately 40-110 ms after response onset, the N2 as the maximum frontal midline negativity between approximately 200-350 ms after stimulus onset, and the FRN as the maximum frontal midline negativity between approximately 200-350 ms after feedback onset. Thus, any given MFN amplitude (ERN, N2, or FRN) used for analysis was taken from whichever frontal midline site was maximal for each subject.

sLORETA intracerebral current source density measurements.

Standardized Low Resolution Electromagnetic Tomography (sLORETA) is a way to examine variations in regional brain activity occurring at the time of ERP voltage peaks. Source analysis in LORETA, the precursor to sLORETA, was based on measurements of current density, which reflects the magnitude of convergent current flow through a square millimeter of tissue ($\mu A/mm^2$). The current *source* density (CSD) is subsequently calculated using vector calculus to obtain the spatial derivative reflecting the divergence of current flow ($\mu A/mm^3$). Although sLORETA still uses current density for source analysis, these values are standardized and thus reflect units of standardized current density (Musso et al., in press; Pascual-Marqui, 2002).

In modeling CSD distributions arising from post-synaptic transmission, sLORETA provides a solution for estimating neuronal activity based on electric potentials measured at the scalp (Fuchs, Kastner, Wagner, Hawes, Ebersole, 2002; Jurcak, Tsuzuki, & Dan, 2007; Pascual-Marqui, 2002).Mathematically, the density of a current source is reflected as the potential (Φ) at a radius (r) from a source (or sink), through which a current (I) passes in a medium with a given conductivity (σ)[1]. The 3-D distribution of CSD is calculated in 3-D Talairach space using all present scalp data (Musso et al., in press; Pascual-Marqui, 2002; 2007) within a given time frame, at each voxel of a given ROI.

For the purposes of the current study, six pre-defined regions of interest (ROIs), based on BA cytoarchitectural data were selected for sLORETA analysis on the basis of these regions capturing the PFC regions associated with our hypotheses. See Figures 2 through 6 for sLORETA images of the voxels corresponding to the predefined ROIs. These included BA10, BA11, BA24, BA25, BA32, and BA46. BAs 10 and 11 were divided into medial (x-coordinate = <20, >-20) and lateral (x-coordinate = >+/-20) portions. BA24 and BA32 were divided into dorsal (y-coordinate = <20, x-coordinate = >24) and ventral (y-coordinate = >20, x-coordinate = <24) regions. Using MATLAB, all 6,239 voxels were plotted into 3-D space, making sure that the voxels for a given BA were demarcated by colour. This method proved useful in obtaining a visual of which Cartesian coordinates would serve as reasonable cut-off points for dividing areas of the PFC across different anatomical planes (see Appendix L for voxel plots).

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[1] Formulaically, CSD is $\Phi(r) = \frac{1}{4\pi r\sigma}$

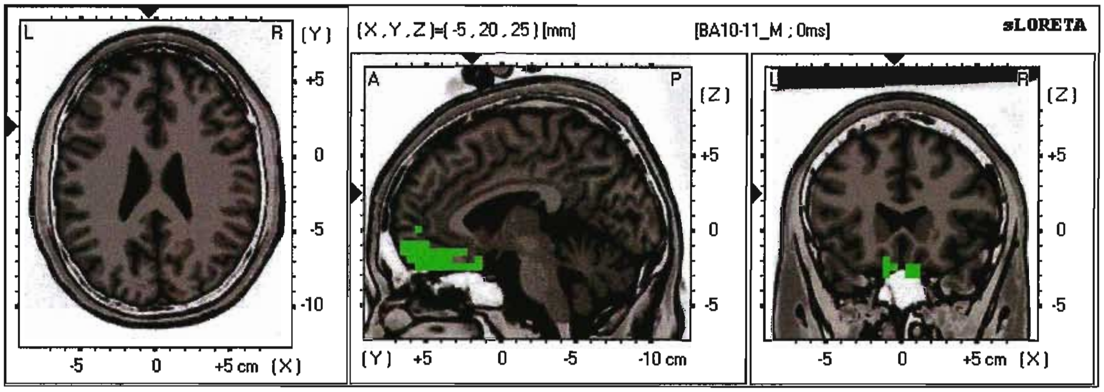

Figure 2. Voxels corresponding to medial portions of Brodmann Area 10 and 11 (green).

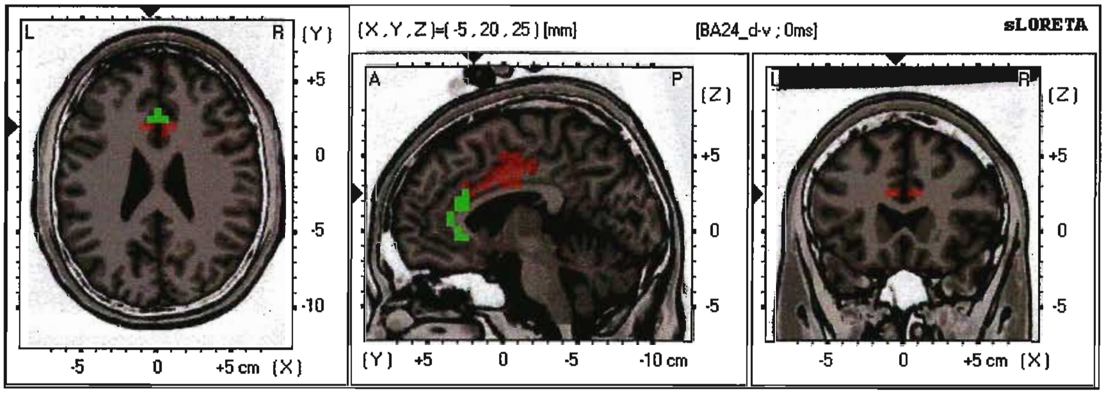

Figure 3. Voxels corresponding to dorsal (red) and ventral (green) portions of Brodmann Area 24.

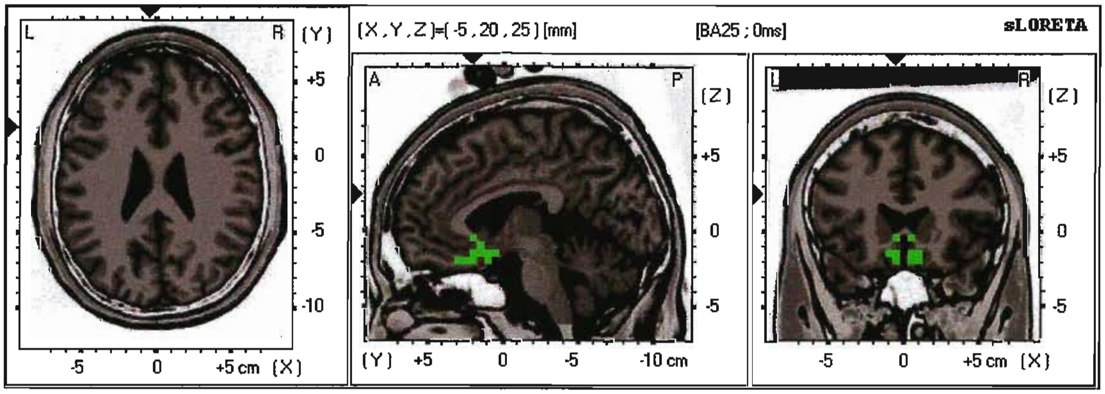

Figure 4. Voxels corresponding to Brodmann Area 25 (green).

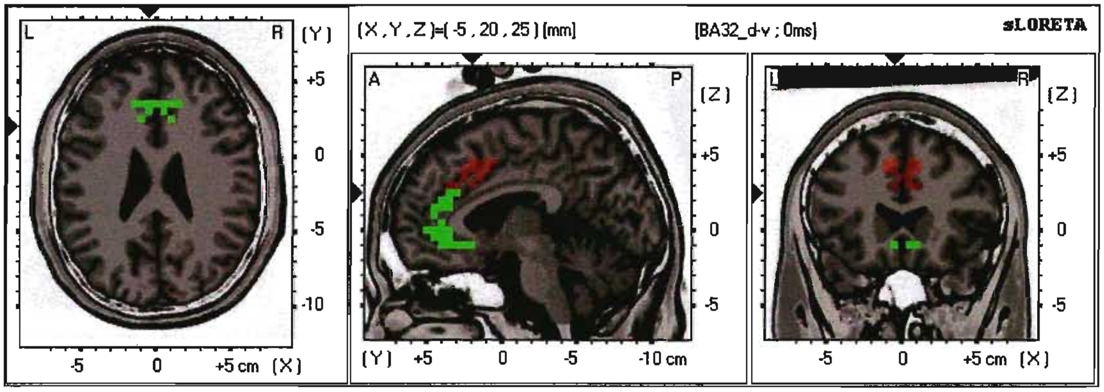

Figure 5. Voxels corresponding to dorsal (red) and ventral (green) portions of Brodmann Area 32.

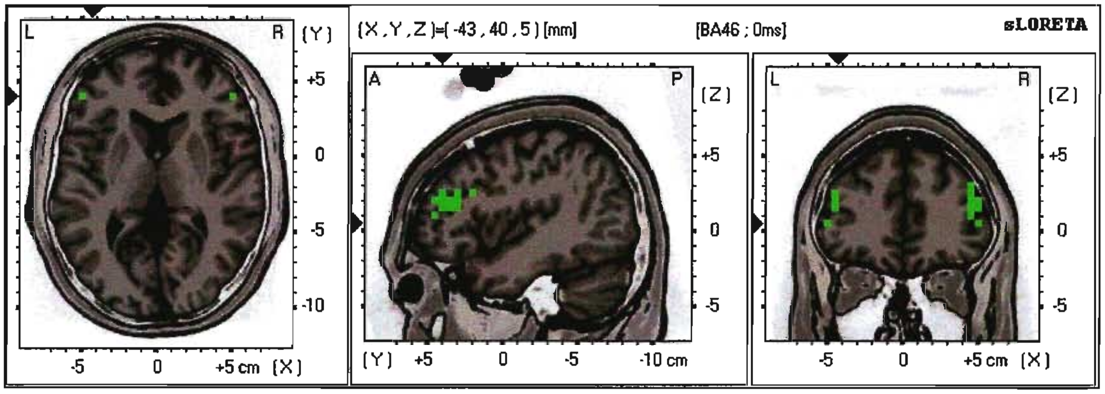

Figure 6. Voxels corresponding to Brodmann Area 46 (green).

These areas were selected because evidence has implicated their involvement as part of a larger network supporting self-regulation, they encompass neuroanatomical regions that occupy dorsal and ventral regions of the mPFC, and previous research has revealed meaningful associations between intracerebral CSD and self-regulation (Segalowitz et al., 2011). Given the evidence implicating several ventral prefrontal midline structures in coordinating self-regulation, for the purposes of the current study, an aggregate of vmPFC activation was created by averaging CSD values from BA10/11-medial, BA24/32-ventral, and BA25. For most the analyses in the current study, vmPFC activation was assessed in relation to dmPFC activation (average of BA24/32 dorsal regions).

CSD values were extracted across 20 ms occurring around the maximal peak of a given ERP. The latency window within which CSD values were extracted was based on the grand average ERP peak latency, as well as visual inspection of global field power. This visual inspection ensures that CSD values will be extracted from time frames that capture changes in power which are associated with the ERP of interest (Segalowitz et al., 2011), as the average peak latency may not directly correspond with peak increases in global field power.

CSD values for the ERN were extracted between 60-80 ms (Win condition; mean ERP peak = 69) and 65-85 ms (Loss Condition; mean ERP peak = 77 ms) following erroneous responses. For the N2, CSD values were extracted between 270-290 ms (Win condition; mean ERP peak = 285) and 262-282 ms (Loss condition; mean ERP peak = 277). Finally, CSD values for the FRN were extracted between 220-240 ms (mean ERP peak = 239 ms).

sLORETA source images. In order to create images of source activation using the group averaged CSD values, which were to be placed into voxels corresponding to a given ROI, a series of steps were carried out in MATLAB. First, Excel files containing the numerical indices of the voxels corresponding to the ROIs were created, from which .matlab files were generated. Next, MATLAB scripts were written which called the index values from the previously created .matlab files, into which activation values could placed (i.e., mean CSD values). Thus, .sLOR source activation files were created outside of the sLORETA interface, and were subsequently plotted using the sLORETA Viewer imaging tool. Activation data were plotted on the Colin 27 T2 magnetic resonance imaging template.

Data screening. Data used in the current study were screened for normality and possible outliers. Normality was assessed by examining skewness, kurtosis, and measures of central tendency. Distributions were considered to threaten normality if skewness and kurtosis exceeded an absolute value of three. Any cases exceeding 3 standard deviations from the mean were considered possible outliers and examined further with respect to the given variable on which they deviated considerably from the mean.

In the event that assumptions regarding homogeneity and/or sphericity of variance failed to be met, Greenhouse-Geisser corrections were made (Greenhouse & Geisser, 1959). Significant main effects and interactions were following with pair-wise t-tests with a 95% confidence interval, Bonferroni corrected for cases of multiple comparisons. Alpha level for all analyses was set at $\alpha = .05$. All statistical tests were performed using the Statistical Packages for the Social Sciences, version 17.

Measures of behaviour. Appendix M contains descriptive data pertaining to normality of the behavioural measures. Normality was not violated as indicated by skewness and kurtosis values all being less than an absolute value of 1.02.

Measures of neural activation. All measures of neural activation satisfied kurtosis and skewness criterion for normality. Appendix N displays normality statistics related to neural activation.

Measures of personality. The distributions of personality and temperament measures were generally within the acceptable range for normality. However, the distributions for the Conscientiousness subscale of the HEXACO, as well as the Negative Affect scale of the PANAS, were leptokurtic. All other skewness and kurtosis values for personality and temperament variables were below an absolute value of 1.71. Appendix O summarizes the descriptive and normality statistics for the personality and temperament questionnaires.

Results

Behavioural results

Only the Go-Nogo task provided behavioural results which could be compared across the Win versus Lose conditions. Accuracy was measured as the proportion of successfully withheld responses to the 20% of No-go stimuli. Across conditions, there was no difference in the proportion of successfully withheld responses to Nogo stimuli, $t(27) = 1.55, p = .13$, 95% CI [-.01, .09]. With respect to response time, a 2 (Response Type: Correct, Incorrect) x 2 (Condition: Win, Loss) repeated-measures ANOVA revealed a main effect of Response Type, $F(1, 27) = 494.81, p < .001, \eta^2 = .95$, 95% CI [50.63, 60.92], such that incorrect responses ($M = 242$ ms; $SD = 4.37$) were faster than correct responses ($M = 298$ ms; $SD = 4.52$). There was no effect of Condition, $F(1, 27) = .09, p = .77$, or interaction between Condition and Response Type, $F(1, 27) = .59, p = .46$. See Figure 7 for error and correct response times on the MW Go-Nogo task.

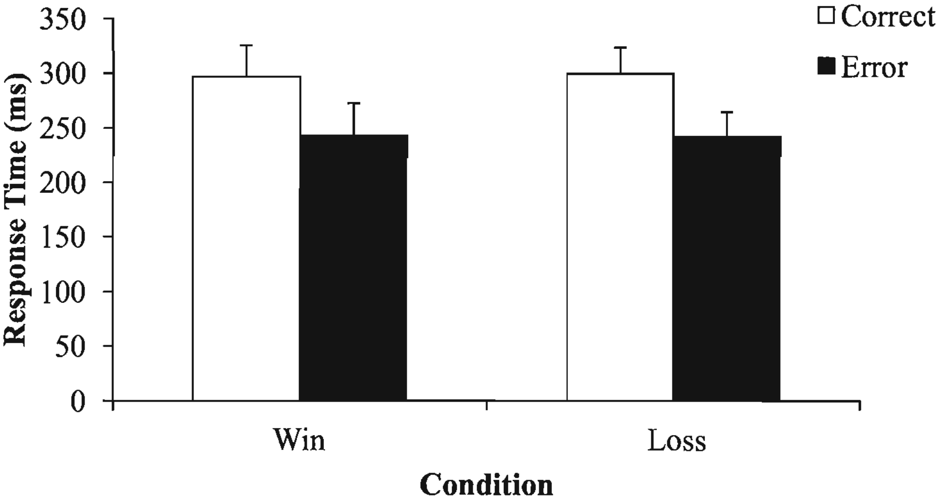

Figure 7. Average response time (ms) for correct and incorrect response to Nogo stimuli on the MW Go-Nogo task.

Intercorrelations among ERP components

The consistency of mediofrontal activation across MFNs was examined using bivariate correlations. As can be seen in Table 1, with the exception of non-significant associations between FRN amplitude and N2 amplitudes, all other MFN amplitudes were positively correlated. These data indicate that the various scalp measures are reliable in capturing evoked electrocortical responses. This is important given that, in some cases, we averaged MFN components to examine their relationship with task performance and personality.

Table 1.

Pearson r correlation coefficients for amplitudes of MFNs.

	1	2	3	4	5
1. ERN Amplitude (Win) [Go-Nogo]	1				
2. ERN Amplitude (Loss) [Go-Nogo]	.69**	1			
3. N2 Amplitude (Win) [Go-Nogo]	.79**	.62**	1		
4. N2 Amplitude (Loss)[Go-Nogo]	.57*	.64**	.63**	1	
5. FRN Amplitude (Loss) [B.A.R.T.]	.43*	.43*	.26	.27	1

Note: * $p \leq .05$, ** $p \leq .01$

Correlations between ERPs and CSD

As can be seen in Tables 2 through 6, MFN amplitudes were generally associated with mPFC activation as measured by CSD. With the exception of N2 amplitudes in the Loss condition, all other MFNs showed significant negative correlations with dorsal and ventral measures of mPFC activation, indicating that larger negativities (i.e., more negative) at the scalp were associated with increased activation in dorsal and ventral regions of the PFC. Furthermore, for a given MFN, measures of activation from dorsal and ventral regions of the PFC showed strong positive correlations (*r*'s .96 to .99).

Table 2.
Pearson r correlation coefficients between ERN amplitude and mPFC current source density in the Loss condition.

LOSS	ERN Amplitude
ERN Amplitude	1
dmPFC CSD	-.50**
vmPFC CSD	-.49**

Note: ** $p \leq .01$

Table 3.
Pearson r correlation coefficients between ERN amplitude and mPFC current source density in the Win condition.

WIN	ERN Amplitude
ERN Amplitude	1
dmPFC CSD	-.60**
vmPFC CSD	-.61**

Note: ** $p \leq .01$

Table 4.
Pearson r correlation coefficients between N2 amplitude and mPFC current source density in the Loss condition.

LOSS	N2 Amplitude
N2 Amplitude	1
dmPFC CSD	-.19
vmPFC CSD	-.26

Table 5.
Pearson r correlation coefficients between N2 amplitude and mPFC current source density in the Win condition.

WIN	N2 Amplitude
N2 Amplitude	1
dmPFC CSD	-.37*
vmPFC CSD	-.42*

Note: * $p \leq .05$

Table 6.
Pearson r correlation coefficients between FRN amplitude and mPFC current source density to loss feedback in the BART.

	FRN Amplitude
FRN Amplitude	1
dmPFC CSD	-.56**
vmPFC CSD	-.50**

Note: ** $p \leq .01$

Brain-behaviour relationships

Go-Nogo task. For the Go-Nogo task, average correct and incorrect response times were calculated for each participant, as well as overall Nogo accuracy (i.e., the proportion of successfully withheld responses to the 20% of Nogo stimuli). Response times were logged in reference to stimulus onset. In the Loss condition, accuracy was negatively related to ERN amplitude, $r(28) = -.50, p = .007$, indicating that larger ERNs were associated with increased accuracy (i.e., fewer errors). Similarly, activation in both the dmPFC, $r(28) = .60, p = .001$, and vmPFC, $r(28) = .57, p = .002$, was related to performance such that greater activity in these prefrontal regions during the ERN was associated with fewer errors. See Figures 8, 9 and 10 for the relations between Nogo accuracy in the Loss condition with ERN amplitude (Figure 8), CSD of dmPFC (Figure 9), and CSD for vmPFC (Figure 10).

The association between N2 amplitude and accuracy approached significance, suggesting that greater inhibitory signals (i.e., more negative) relate to more successful motor control, $r(28) = -.34, p = .082$. Neither vmPFC nor dmPFC CSD associated with the generation of the N2 were related to accuracy.

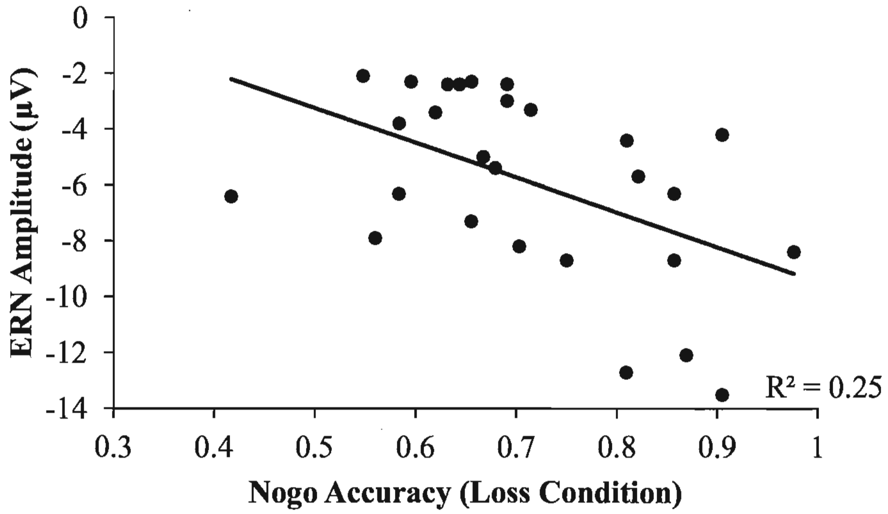

Figure 8. Scatter plot of ERN amplitude with Nogo accuracy in Loss condition of the MW Go-Nogo task.

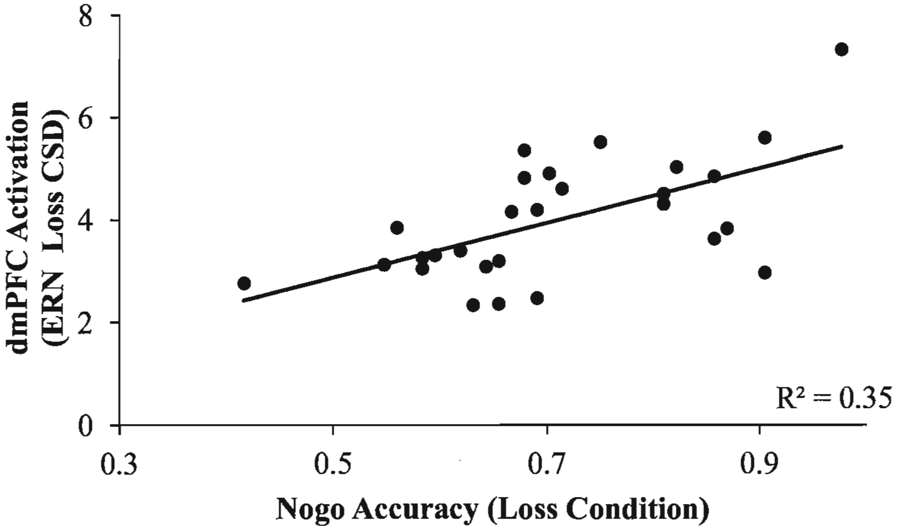

Figure 9. Scatter plot of Current Source Density (CSD) of dorsomedial prefrontal cortex (dmPFC) during error responses with Nogo accuracy in Loss condition of the MW Go-Nogo task.

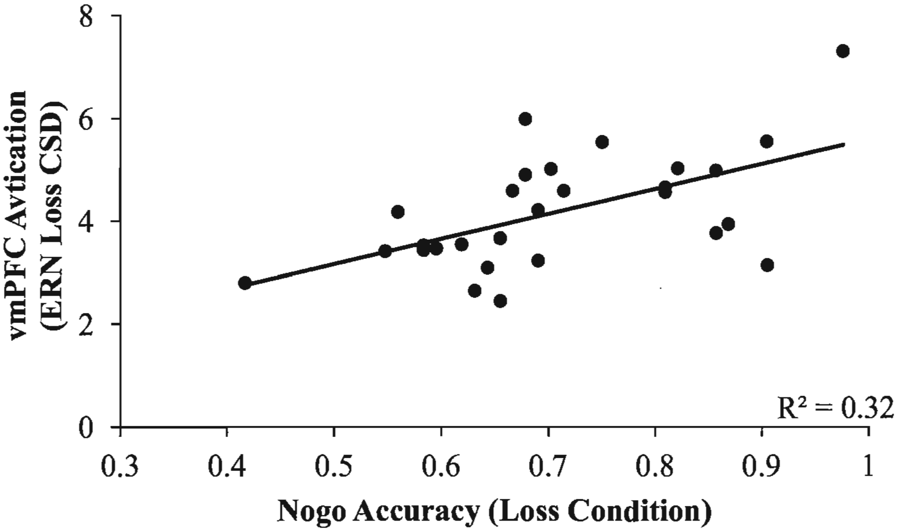

Figure 10. Scatter plot of Current Source Density (CSD) of ventromedial prefrontal cortex (vmPFC) during error responses with Nogo accuracy in Loss condition of the MW Go-Nogo task.

Although there was no relationship between ERN amplitude and performance in the Win condition (p>.15), neural activation levels mirrored those of the Loss condition. Accuracy was positively associated with activation in response to errors in the dmPFC, $r(28) = .43, p = .022$, and the vmPFC, $r(28) = .48, p = .011$ (see Figures 11 and 12).

For the N2, in the Win condition, larger amplitudes showed a trend towards being related to successful inhibitory control, $r(28) = -.34, p = .075$. Similar to the Loss condition, neither vmPFC nor dmPFC CSD were related to performance in the Win condition.

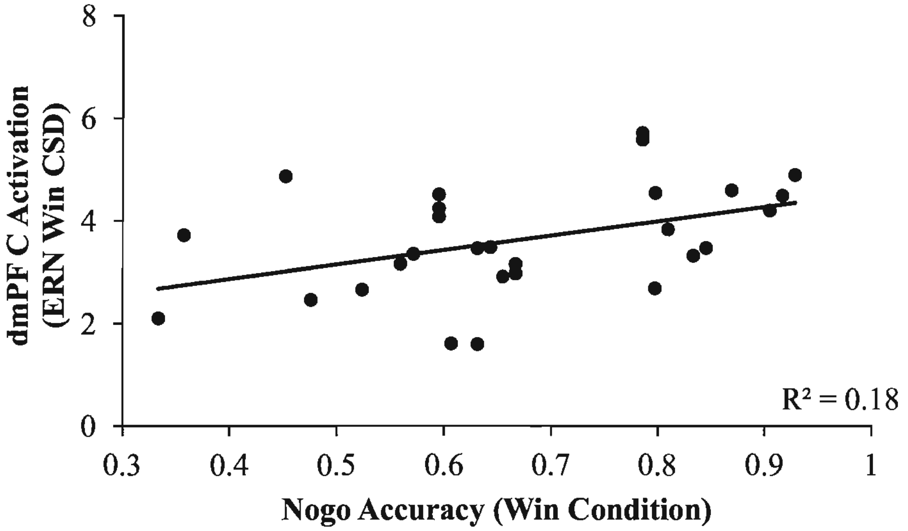

Figure 11. Scatter plot of Current Source Density (CSD) of dorsomedial prefrontal cortex (dmPFC) during error responses with Nogo accuracy in Win condition of the MW Go-Nogo task.

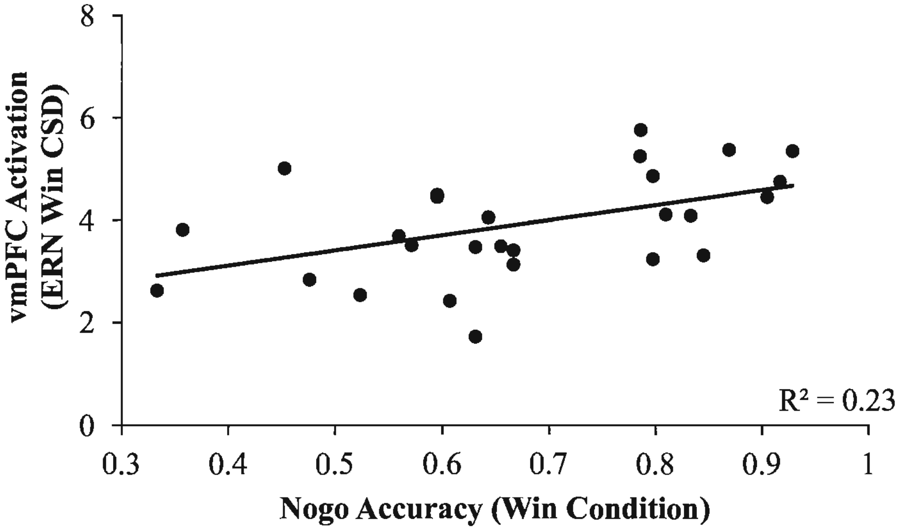

Figure 12. Scatter plot of Current Source Density (CSD) of ventromedial prefrontal cortex (vmPFC) during error responses with Nogo accuracy in Win condition of the MW Go-Nogo task.

BART. In the BART task, the only meaningful behavioural measure is risk-taking time, which was calculated as a weighted average of the amount of time that participants permitted the balloon to inflate for all trials during which the participant ended the inflation before the balloon popped. Thus, the risk-time was weighted for each participant by the number of Win trials as this is reflective of how risky the participant was willing to be over the course of the task. Higher values of risk-time indicate riskier behaviour as the possibility of losing increases with successive inflations.

Although the relationship between risk-taking on the BART and FRN amplitude to loss feedback was in the expected direction, the association did not reach significance, *r*(28)= .31, *p* = .11. See Figure 13 for the grand averaged ERP of the FRN to balloon pops. Given our version of the BART was novel, we averaged ERN, N2, and FRN amplitudes for each subject and across tasks. This aggregate of MFN amplitude was correlated with risk-taking on the BART, *r*(28)= .37, *p* = .05, indicating that reduced mPFC activation (i.e., less negativity in these scalp measures) was associated with greater voluntary risk-taking (see Figure 14). In relation to regional activation at the time of the FRN to negative feedback, risk-taking related to reduced levels of activation in the sgACC indicating that deactivation in this region was associated with a greater willingness to take risks, *r*(28) = -.46, *p* = .014 (see Figure 15).

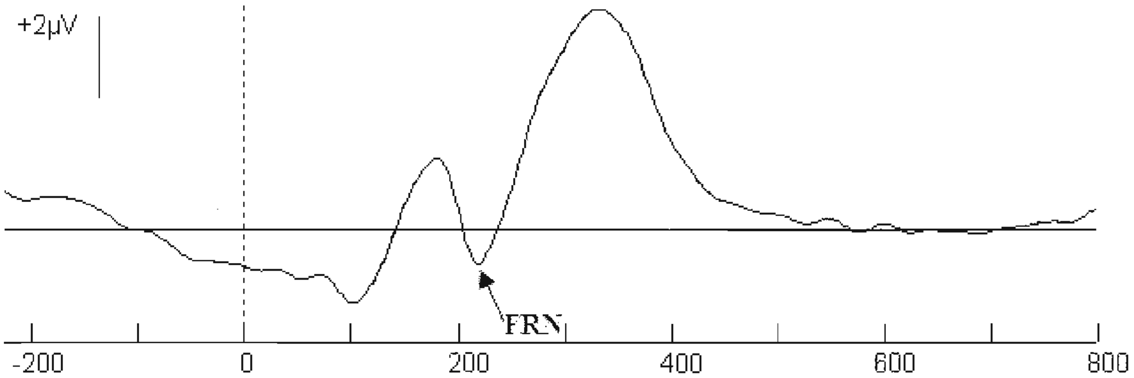

Figure 13. Grand average FRN to balloon pops on the BART, time-locked to Loss feedback onset (time = 0 ms).

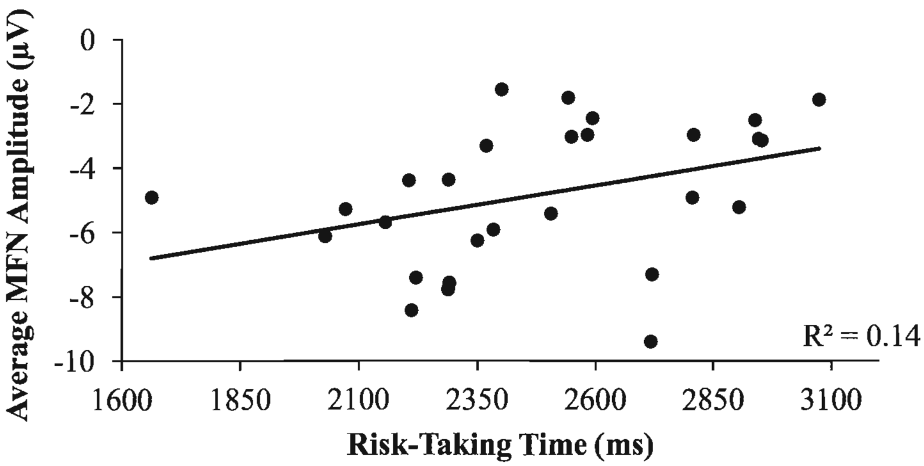

Figure 14. Scatter plot of average medial frontal scalp activity, averaged across the ERN, N2, and FRN, with voluntary risk-taking on the Balloon Analogue Risk Task (BART).

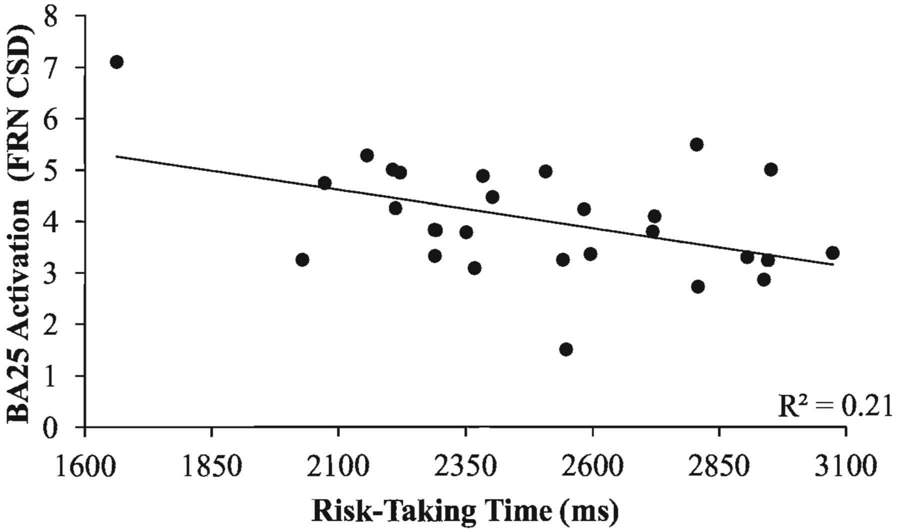

Figure 15. Scatter plot of Current Source Density (CSD) of BA25 during Loss feedback voluntary risk-taking on the Balloon Analogue Risk Task (BART).

Context effects on activity in the mPFC

We expected that mPFC activation would be greater in punishment contexts, for both scalp and intracerebral CSD measures. Furthermore, we expected the relative engagement of ventral regions to be greater than dorsal regions particularly in contexts involving punishment for failed self-regulation.

Scalp ERPs. In our data, the ERN was undifferentiated between the Win ($M = -5.81$ µv, $SD = 3.13$ µv) and Loss ($M = -5.86$ µv, $SD = 3.25$ µv) conditions, $t(27) = -.105, p = .92$. Mediofrontal activation to errors was no different whether associated with the loss of points or the lost opportunity to gain points (see Figure 16). Similarly, there was no difference in N2 amplitude between Win ($M = -4.66$ µv, $SD = 2.20$ µv) and Loss ($M = -4.55$ µv, $SD = 2.61$ µv) conditions, $t(27) = .278, p = .78$. As can be seen in Figure 17, mediofrontal activation to successfully inhibited responses was no different if associated with gaining points or the aversion of losing points.

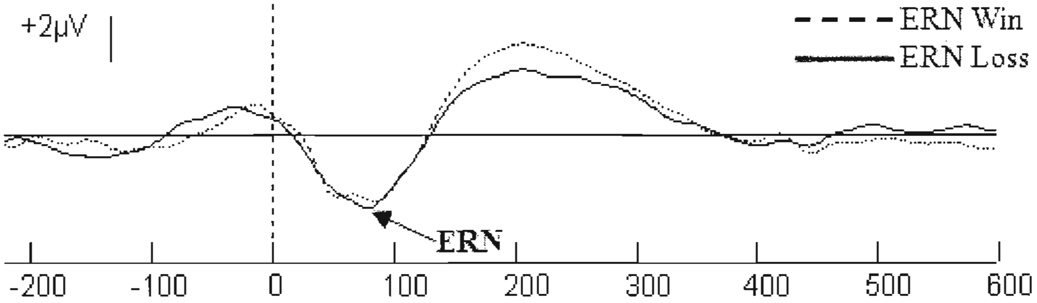

Figure 16. Grand averages of response-locked ERN for Win and Loss conditions of the Go-Nogo MW task.

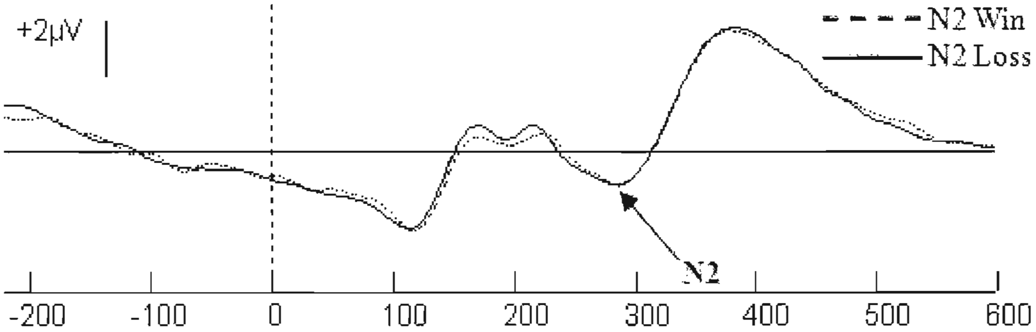

Figure 17. Grand averages of stimulus-locked Nogo N2 for Win and Loss conditions of the MW Go-Nogo task.

A 2 (ERP: ERN, N2) x 2 (Condition: Win, Loss) repeated-measures ANOVA on the number of trials used to generate grand averages revealed a significant main effect of ERP, *F*(1, 27) = 64.57, $p < .001$, $\eta^2 = .71$, 95% CI [23.07, 38.89], indicating that a larger number of trials were used to generate N2 averages (*M* = 53, *SD* = 2.12) as compared to ERN averages (*M* = 22, *SD* = 1.89). This is to be expected as the number of trials available for the ERN and N2 are mutually exclusive and exhaustive of all Nogo trials, and individuals generally perform well above chance which favours, further, the number of available trials for Nogo N2 ERPs. However, there was no significant main effect of condition, *F*(1, 27) = 0.43, $p = .52$, $\eta^2 = .016$, or an interaction between ERP and condition, *F*(1, 27) = 1.83, $p = .191$, $\eta^2 = .063$.

Intracerebral CSDs.

ERN. To examine whether CSD regional activation in the mPFC is differentiated as a function of task context when committing errors, a 2 (Condition: Win, Loss) x 2 (Region: dmPFC, vmPFC) repeated-measures ANOVA was performed on the ERN data. A trend towards a main effect of condition was found, *F*(1, 27) = 3.07, $p = .091$, $\eta^2 = .102$, such that activation of the mPFC during error commission was greater in the Loss condition (*M* = 4.81, *SD* = 1.16), as compared to the Win condition (*M* = 3.83, *SD* = 1.05), *t*(27) = 1.75, $p = .091$. A significant main effect of region was found, *F*(1, 27) = 44.16, $p < .001$, $\eta^2 = .621$, indicating that error-related activation was greater in the vmPFC (*M* = 4.14, *SD* = 1.09) than in the dmPFC (*M* = 3.81, *SD* = 1.12), *t*(27) = 6.65, $p <. 001$, 95% CI [-.44, -.23] (see Figure 18).

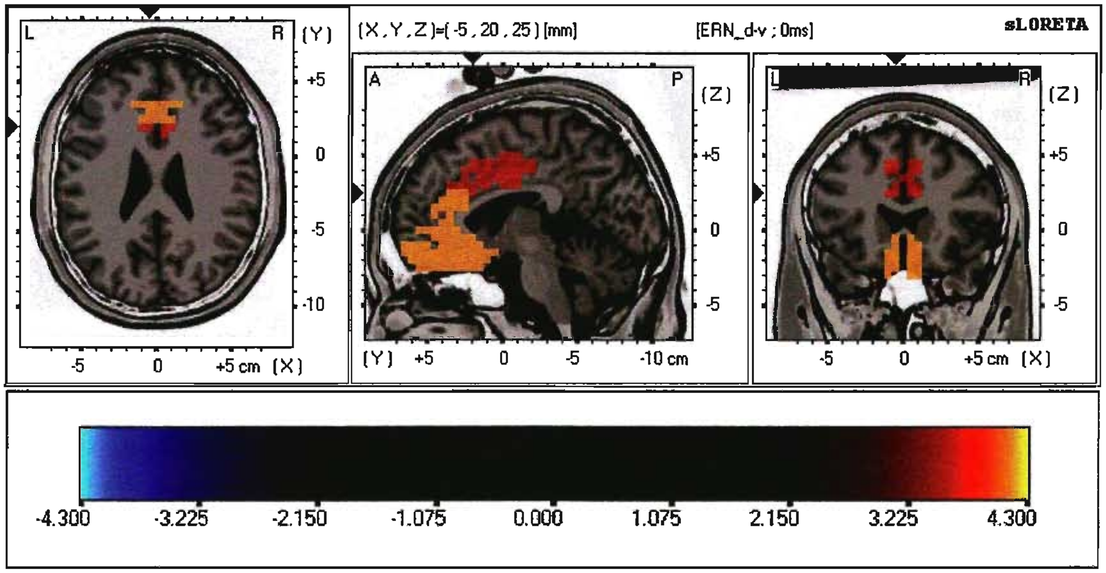

Figure 18. Relative activation of dorsal and ventral mPFC during error commission, collapsed across conditions of the MW Go-Nogo task. The vmPFC is significantly more active than the dmPFC (*p* <.001).

Similar to the main effect of condition, the interaction between condition by region was only a trend, *F*(1, 27) = 3.19, *p* = .085, η^2 = .106, where the dmPFC (Win: *M* = 3.63, *SD* = 1.07; Loss: *M* = 3.99, *SD* = 1.17) was more active than the vmPFC (Win: *M* = 4.04, *SD* = 1.02; Loss: *M* = 4.25, *SD* = 1.15) , particularly when errors are committed in the loss condition. See Figure 19 for activation in dmPFC and vmPFC during the time of the ERN, for Win and Loss conditions of the MW Go-Nogo task.

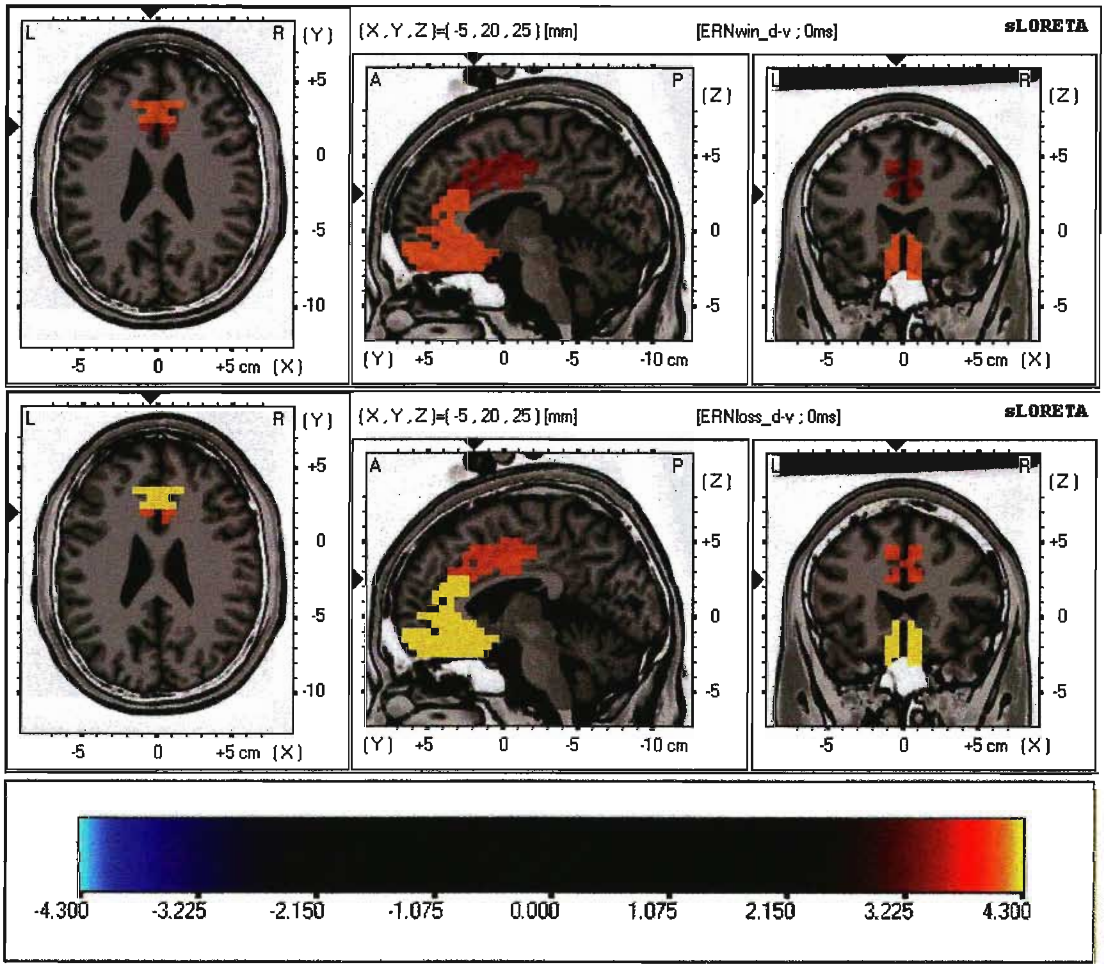

Figure 19. Relative activation of dorsal and ventral mPFC during error commission, across Win (top) and Loss (bottom) conditions of the MW Go-Nogo task.

N2. A subsequent 2 (Condition: Win, Loss) x 2 (Region: dmPFC, vmPFC) repeated-measures ANOVA was performed in order to examine whether or not regional activation in the mPFC was differentiated as a function of task context when individuals successfully inhibited responses to Nogo stimuli at the timing of the N2. Similar to the ERN results, there was a significant main effect of region, $F(1, 27) = 34.50, p < .001, \eta^2 = .56$, 95% CI [-.29, -.14], such that the vmPFC ($M = 3.11$, $SD = .83$) was more active than the dmPFC ($M = 2.89$, $SD = .85$). The effect of condition was not significant, $F(1, 27) = .18, p = .68, \eta^2 = .006$, nor was the interaction between condition and level, $F(1, 27) = .38, p = .54$. Figure

20 displays the relative activation in dorsal and ventral mPFC during inhibitory control (Nogo N2), collapsed across conditions of the MW Go-Nogo task.

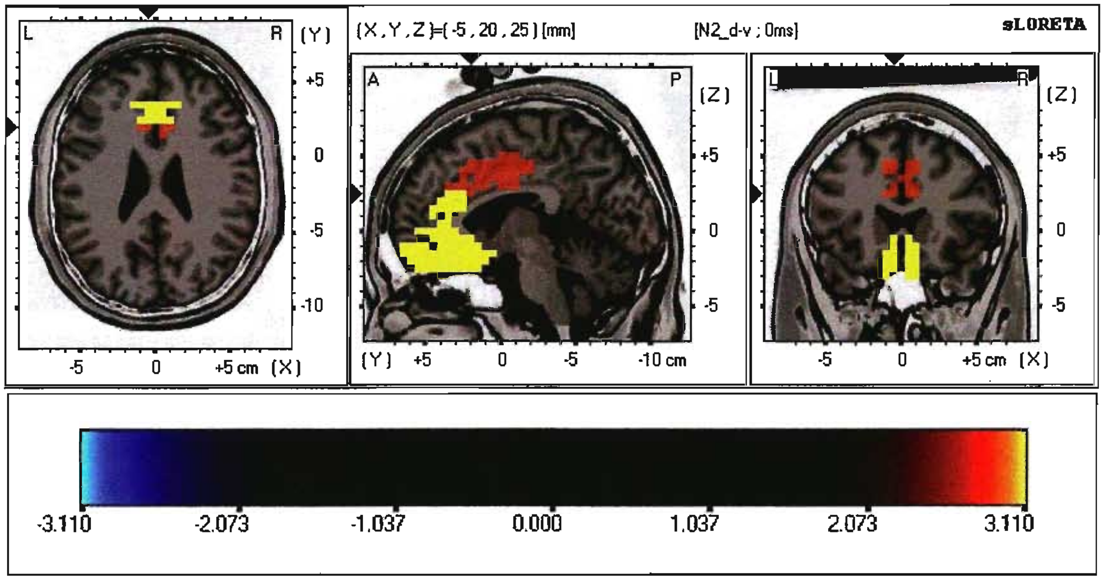

Figure 20. Relative activation in dorsal and ventral mPFC during successful inhibition, collapsed across conditions of the Mw Go-Nogo task. The vmPFC is significantly more active than the dmPFC (p <.001).

FRN. Using the data from the BART, a similar analysis was carried out to examine regional differences in activation during the presentation of negative feedback. Given that the FRN was collected specifically to loss trials, and not win, a series of paired t-tests were carried out to examine differences in regional activation. As expected, during the presentation of negative feedback in the BART, activity in the vmPFC (M = 3.54, SD = .91) was greater than activity in the dmPFC (M = 3.41, SD = .95), $t(27) = -2.92$, $p = .007$, 95% CI [-.23, -.04] (see Figure 21).

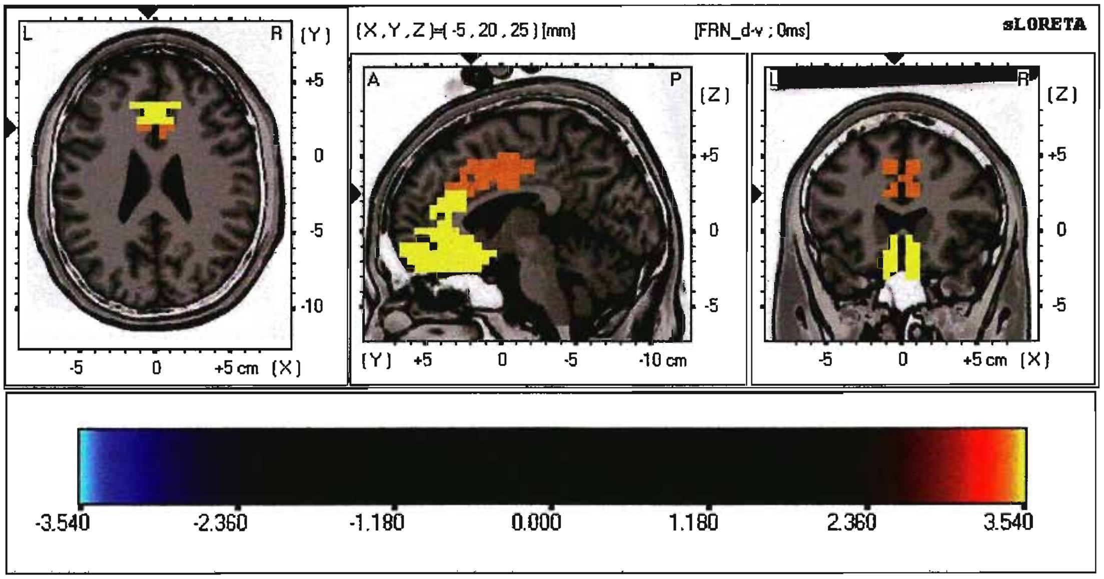

Figure 21. Relative activation of dorsal and ventral mPFC during loss feedback on the BART. The vmPFC is significantly more active than the dmPFC (*p* = .007).

Similarly, activation in the sgACC (BA25; *M* = 4.03, *SD* = 1.10) was greater than activity in the dorsolateral PFC (BA46; *M* = 3.56, *SD* = 1.15), *t*(27) = 3.19, *p* = .004, 95% CI [.17, .79], further validating the differences between dorsal and ventral regions of the PFC during the presentation/evaluation of negative feedback (see Figure 22).

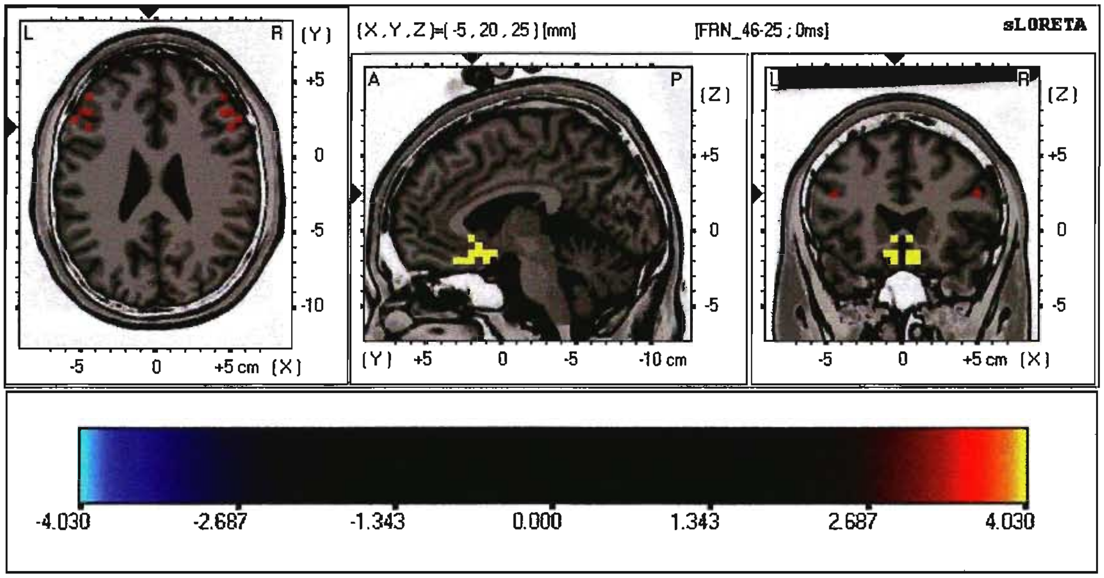

Figure 22. Relative activation of subgenual ACC and dorsolateral prefrontal cortex during loss feedback on the BART. Activity in the subgenual ACC is significantly greater than activity in dorsolateral regions ($p = .004$).

ERN and FRN. There is mixed evidence regarding regional differences in activation during the commission of error responses and the presentation of negative feedback. To address whether internally (ERN) or externally (FRN) generated responses can be differentiated on the basis of regional activation in the prefrontal cortex when losing/being punished, a 2 (ERP: ERN CSD, FRN CSD) x 2 (Region: dmPFC, vmPFC) repeated-measures ANOVA was performed. This analysis was based on the ERN data from the Loss condition of the MW Go-Nogo task, and FRN data from the BART task.

A main effect of ERP was found, $F(1, 27) = 7.91$, $p = .009$, $\eta^2 = .227$, 95% CI [.17, 1.06], such that activity in the mPFC was significantly greater during the commission of erroneous motor responses ($M = 4.10$, $SD = 1.14$) than during the presentation of negative feedback ($M = 3.47$, $SD = .93$). Figure 23 displays the relative activation of the mPFC during the ERN and FRN.

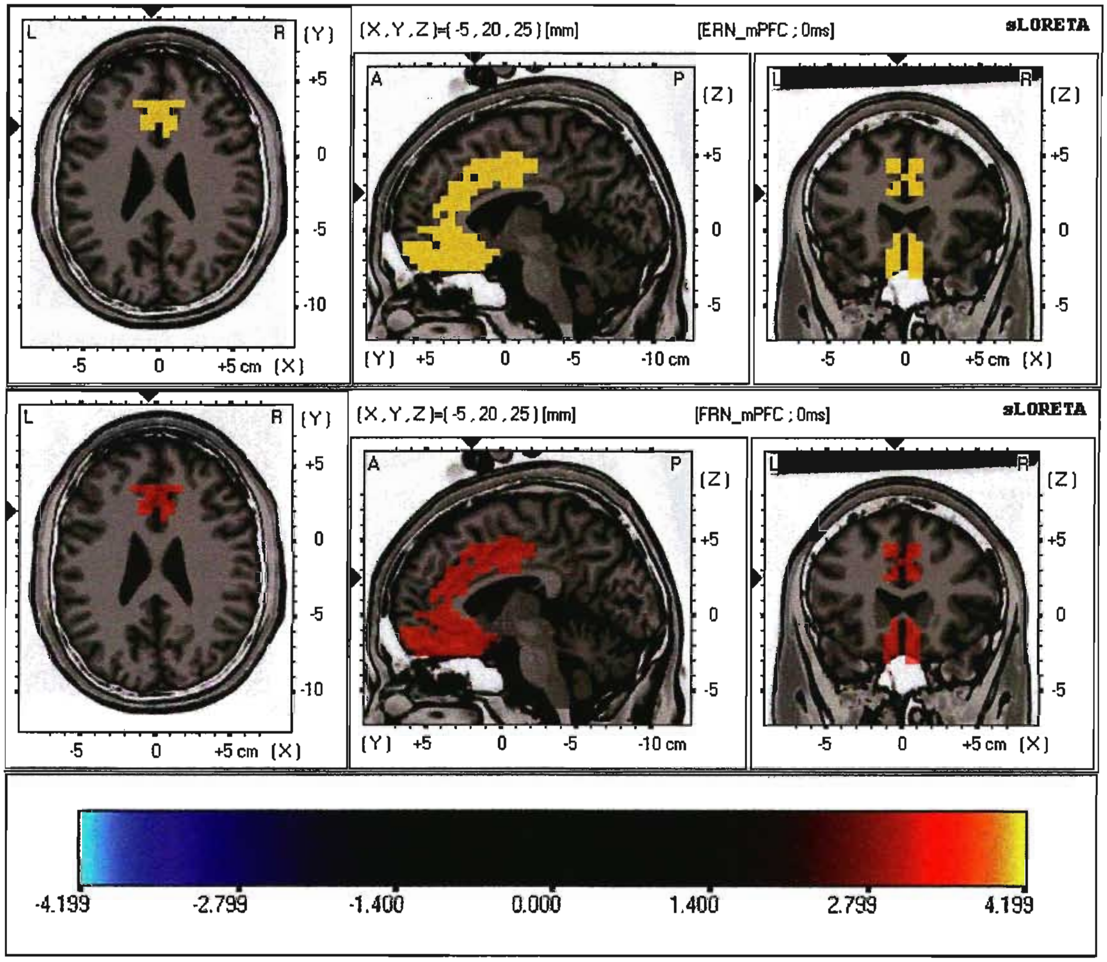

Figure 23. Relative activation in mPFC during self-initiated error detection (ERN) in the Loss condition of the MW Go-Nogo task (top) and during loss feedback (FRN) on the BART (bottom).

As expected, a significant main effect was observed for region, $F(1, 27) = 31.78, p < .001, \eta^2 = .541$, 95% CI [-.22, -.10], indicating that the vmPFC ($M = 3.86, SD = 1.01$) was more active than the dmPFC ($M = 3.68, SD = 1.06$) (see Figure 24). The interaction between ERP and Region was not statistically significant, $F(1, 27) = .99, p = .33, \eta^2 = .035$, suggesting that regional activation during losses is undifferentiated on the basis of self-initiated or externally-initiated error signals.

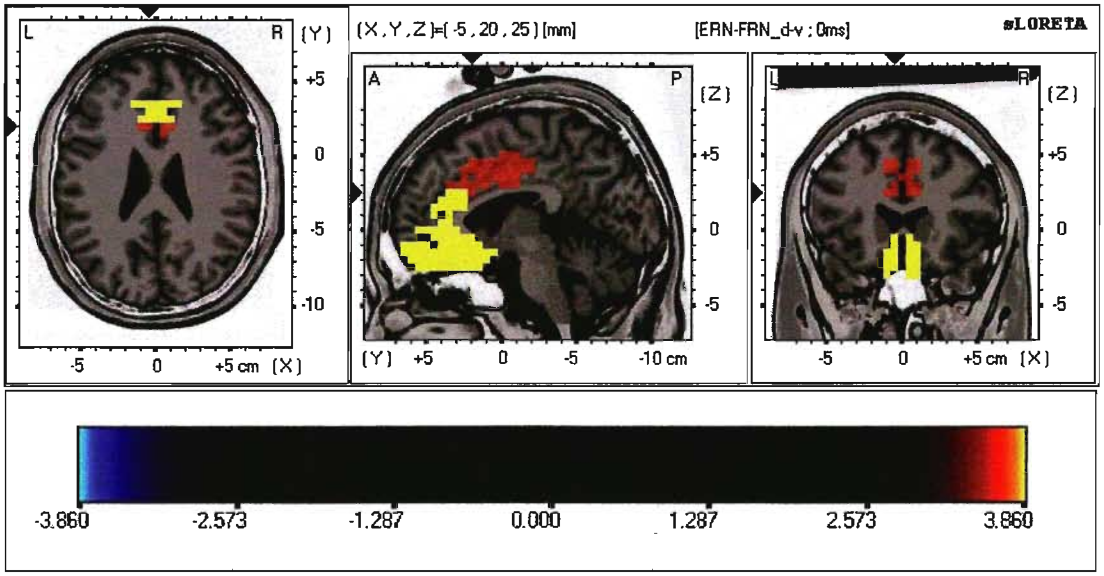

Figure 24. Relative activation in dorsal and ventral mPFC, collapsed across errors from the Loss condition of the MW Go-Nogo task and loss feedback on the BART.

Further analyses

MPFC activation and personality. A series of Pearson r correlations were performed in order to examine the associations between mPFC activation and personality characteristics. The general prediction was that individuals exhibiting greater mPFC responses in the context of making an error would rate themselves lower on measures of approach-related behaviour.

Before focusing on the associations between personality and temperament styles with brain function, correlation analyses were performed between self-reports from our selected questionnaires. This was done to verify that the underlying constructs of approach-related personality converge across similar measures. All subscales of the BAS questionnaire correlated positively with total BAS scores (*r*'s range from .62 to .74, $p <.001$) and these associations which were independent given no association among BAS subscales. Convergent validity was reflected by positive associations between BAS (Fun-seeking subscale) and scores on the SSS-V, including Thrill Sensation ($r = .51, p = .005$), Disinhibition ($r = .39, p = .041$), Boredom ($r = .42, p = .027$), and SSS-V total ($r = .59, p = .001$).

Measures of behavioural inhibition and negative affect also provide evidence supporting the underlying construct of approach-related behaviours characterized by sensation/novelty seeking. Not only were BIS scores positively correlated with Negative Affect ($r = .40, p =.037$) indicating convergence of measures tapping withdrawal tendencies, but showed negative associations with measures of approach-related behaviours, including Thrill Sensation ($r = -.39, p = .04$) and SSS-V total scores ($r = -.42, p = .026$. Similarly, individuals reporting higher levels of Negative Affect also reported significantly lower levels of Thrill Sensation ($r = -.56, p = .002$) and SSS-V total scores ($r = -.45, p = .016$). The positive intercorrelations between approach-related facets of personality, along with negative associations with measures of behavioural inhibition, confirm that the underlying construct is grounded, at least partially, in novelty/sensation-seeking or perhaps risk-taking behaviours.

Measures derived from the BIS/BAS were generally unrelated to measures of mPFC activation, with the exception of a trend indicating that the BAS-Drive Subscale was positively associated with neural activation of the mPFC, $r(28) = .36, p = .056$. Specifically, individuals reporting a higher likelihood to engage in approach-related behaviours exhibit deactivation of mPFC when making an error.

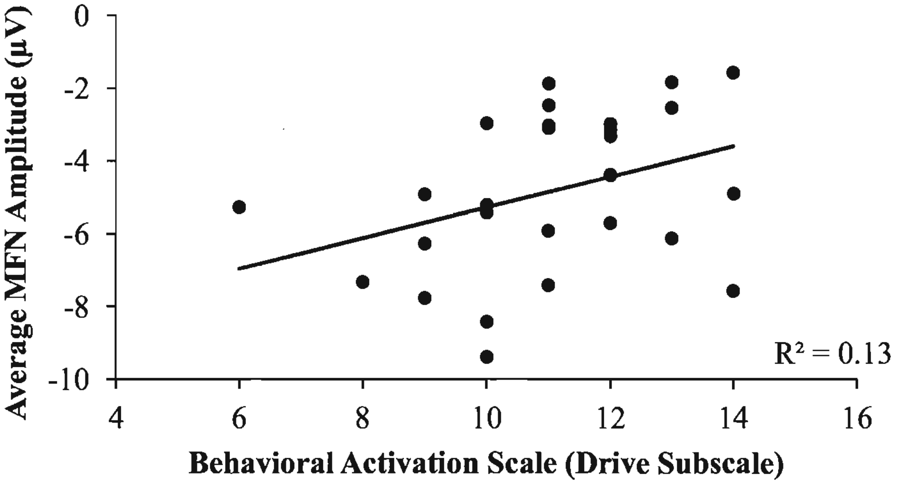

Figure 25. Scatter plot of BAS-Drive scores with average scalp measure of mediofrontal activation.

The Openness to Experience subscale of the HEXACO was found to consistently relate to activation of the mPFC in response to errors such that greater OE was associated with larger (i.e., more negative) MFNs, regardless of whether this activity was associated with errors (ERN), successful behavioural control (N2), or external negative feedback (FRN). Given that all ERPs indexing mediofrontal activation were interrelated, mPFC responses were averaged (i.e., ERN, N2, and FRN) into a composite variable and correlated with Openness to Experience, $r(28) = -.45, p = .008$ (see Figure 26).

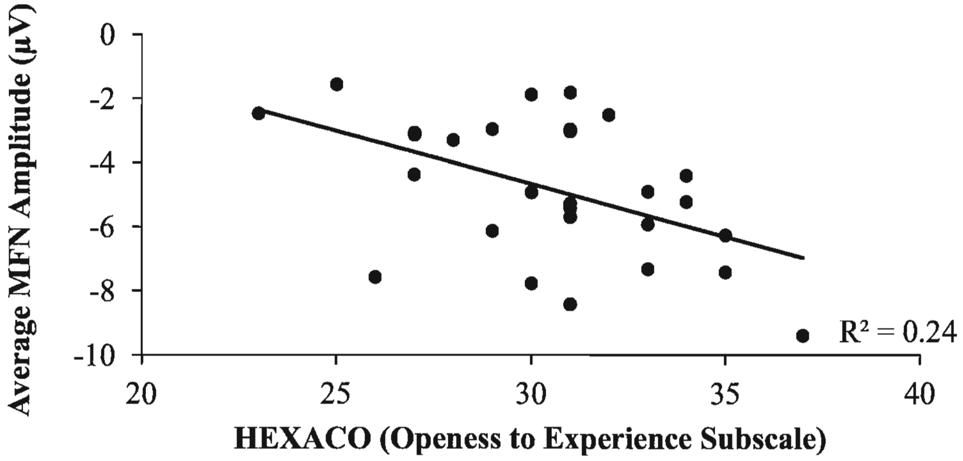

Figure 26. Scatter plot of Openness to Experience scores with average scalp measure of mediofrontal activation.

No other correlations between mPFC activation and personality variables reached statistical significance. It is worth noting that, although the Openness to Experience subscale was not significantly related with any other questionnaire, the association between Openness to Experience and BAS (Drive subscale) approached significance ($r = -.35, p = .07$), suggesting negative relations between the underlying constructs.

Risk-Taking and personality. We examined whether risk-taking on the BART was correlated with self-reports of personality. While several relationships were in the expected direction, the only significant correlation was with Positive Affect, $r(28) = -.45$, $p = .015$, such that higher levels of risk-taking were associated with lower levels of state positive affect.

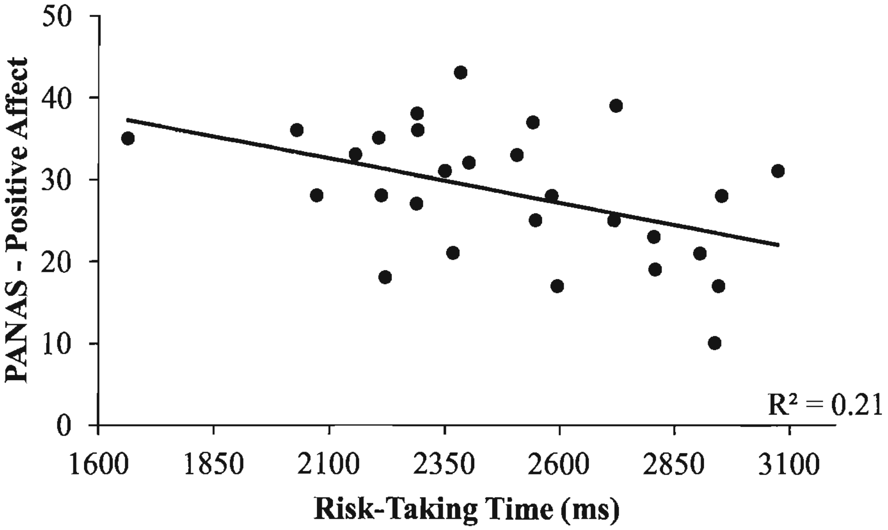

Figure 27. Scatter plot of voluntary risk-taking on the Balloon Analogue Risk Task (BART) with scores of Positive Affect from the Positive and Negative Affect Schedule (PANAS).

Discussion

In the present study, we examined the effects of motivational pressures on indices of medial prefrontal activation, as well as medial prefrontal activity in relation to individual differences in personality and temperament. Our goal was to determine whether or not mPFC activation was sensitive to the arousing nature of the contexts in which behavioural and environmental consequences occur. Additionally, we aimed to test whether or not internally and externally generated error responses recruit different medial prefrontal regions. We found that, during the time of the N2 and ERN on the MW Go-Nogo task and the FRN on the BART, the vmPFC was more active compared to the dmPFC. These data indicate that, compared to dorsal regions, the vmPFC is relatively more active in contexts involving performance-related incentives, independent of the event eliciting the electrocortical response (i.e., errors, Nogo stimulus, negative feedback stimulus). The regional recruitment in the mPFC was found to be similar across internally and externally generated errors signals such that, during the time of the ERN and FRN associated with loss, the vmPFC was more active relative to the dmPFC.

We also found associations between functioning of the mPFC and self-regulation. Generally, greater levels of mPFC activity were associated with increased accuracy (i.e., better inhibitory control) in the MW Go-Nogo task. Similarly, deactivation of the sgACC during negative external feedback was related to greater levels of voluntary risk-taking on the BART. Moreover, our data are in line with previous studies showing that affect/motivation is central to how personality and medial prefrontal function are related. Persons reporting higher levels of approach-related behaviour or cognitive rigidity showed reduced activity of the mPFC when engaging self-regulatory processes.

Cortical generators of MFNs: The medial prefrontal cortex and hot cognition

The results from the present study also suggest that mediofrontal activation, in the context of action monitoring, is tied to affective evaluations. In our data, a consistent main effect of ROI was revealed by similar regional intracerebral CSD for all MFNs. During the time of the ERN, N2, and FRN, activation in the vmPFC was found to be greater than that of the dmPFC. Given that all task conditions featured a performance-related incentive (rewards, punishments, losses), the consistent effect of greater vmPFC activity during these MFNs could reflect the sensitivity of this region to arousing/emotional contexts. Considerable functional neuroimaging and lesion data highlight the importance of the structural and functional integrity of ventromedial regions in affective processes. Injury to the ventromedial frontal regions is associated with impaired modulation of visceral functions and arousal (Bechara & Naqvi, 2009; Pardini et al., 2009), especially when evaluating behavioural and environmental consequences in social and emotional contexts (Bechara, 2004; Damasio, 1996). In addition to studies showing that activity in the vmPFC correlates with indices of peripheral nervous system activation, such as skin conductance (Critchley, Elliot, Mathias, & Dolan, 2000; Patterson, Ungerleider, & Bandettini, 2002), cognitive and behavioural tasks involving emotional content, such as verbal congruency tasks, have been shown to distinctly recruit ventromedial regions of the PFC (Bush et al., 2000; Kanske & Kotz, 2011).

A large body of converging evidence indicates that activity in the mPFC is sensitive to emotional information (Bush et al., 2000), and is involved in the modulation of the autonomic nervous system in response to contextual demands (Critchley, 2005). Not only do axonal projections from the ventromedial frontal lobes synapse onto subcortical limbic structures innervating autonomic nuclei in the brainstem and spinal cord (Barbas et al., 2003), previous research has also shown that, functionally, areas of the mPFC are sensitive to affective information and are linked to physical changes in the autonomic nervous system. Stimulation of the ACC results in viscero-motor changes, including alterations in blood pressure and respiration (Pool & Ransohoff, 1949; Smith, 1945). Activation patterns in the ACC correlate with pupil dilation and heart rate (Critchley et al., 2003; Critchley et al., 2005), blood pressure changes during stress (Gianaros et al., 2005), and predict the suppression of behavioural and limbic responses to emotional stimuli (Chiu et al., 2008; Etkin et al., 2006; Kanske & Kotz, 2011; van Reekum et al., 2009). Moreover, source analysis of EEG/ERP data reveal ventromedial prefrontal sources when electrocortical responses occur in contexts involving negative affect and/or motivational pressures (Luu et al., 2003; Lewis et al., 2006; Ogawa et al., 2011; Segalowitz et al., 2010).

The consistency of greater activity in the vmPFC than the dmPFC also suggests that, to some degree, there is overlap in the cortical generators of these ERPs. This interpretation is supported by previous reports of overlapping cortical sources that are active during action monitoring and self-regulation (Gehring & Willoughby, 2002; Gründler et al., 2009; Luu & Tucker, 2003). For example, in an fMRI study, Menon et al. (2001) found that several mPFC regions, which were engaged during error processing, were similarly engaged during inhibitory control on a Go-Nogo task. sLORETA has been shown to localize activity associated with the ERN, N2, and FRN collected in the same task to overlapping medial prefrontal regions (Gründler et al., 2009), and Independent Components Analysis suggests that the ERN and FRN share a cortical network (Genstch et al., 2009). In the current study, independent of what event elicited mediofrontal activity (i.e., errors, negative feedback, inhibitory control), the vmPFC was similarly sensitive to contexts of motivational pressure.

The ERN and FRN reflecting frontally-mediated evaluation of behavioural and environmental consequences

Functional differences between dorsal and ventral regions of the mPFC have been well established. However, here has been limited consideration of functional differences in the mPFC in relation to MFNs associated with error responses. Our data are consistent with previous research which emphasizes the influence of affect/motivation on the processes reflected by the ERN and FRN.

The monitoring and evaluating of behavioural and environmental consequences is central to self-regulation, a process which is supported by the structural and functional integrity of the mPFC, particularly the ACC (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). An extensive literature indicates that the ERN and FRN reflect medial frontal activation to behavioural and environmental events, respectively, which indicate that goal-directed behaviour needs to be adjusted (Holroyd et al., 2004; Luu

& Tucker, 2003; Segalowitz & Dywan, 2009). If the ERN and FRN reflect the activation of a frontally-mediated evaluative process, spanning internal (i.e., erroneous behavioural responses) and external (i.e., loss feedback stimulus) systems, one would expect to find, during the time of these ERPs, similar regional activation in contexts of motivational pressure. Indeed, our results confirm previous findings which suggest that these ERPs reflect the engagement of frontally-mediated evaluative processes which are central to performance monitoring and action regulation.

Specifically, the role of affect/motivation is reflected in our data showing the preferential recruitment of the vmPFC relative to dmPFC. Examining the ERN and FRN indicated that, compared to the dmPFC, internally (ERN) and externally (FRN) generated error responses both involved relatively greater engagement of ventromedial regions with respect to loss and punishment feedback. Erroneous responses and loss-related external feedback both convey that goal-directed behaviour has been unsuccessful, and that future adjustments need to be made in pursuit of optimal outcomes. The similar effect of relatively greater vmPFC activity suggests that, during the time of these ERPs, evaluative processes are engaged, independent of whether the activation was associated failed action (ERN) or inaction (FRN).

Previous studies by Luu, Tucker, and colleagues emphasize the evaluative processes reflected by the oscillatory patterns of mediofrontal neurons (Luu et al., 2000a; 2000b), particularly with respect to monitoring actions in context. Mediofrontal responses reflect the degree of failed self-control (Luu et al., 2000a), the affective significance of outcomes (Luu et al., 2003), as well as predict future behavioural adaptations (Cohen & Ranganath, 2007; Frank, Woroch, & Curran, 2005; Genstch et al., 2009; Luu et al., 2003; van der Helden, 2010). Other studies indicate that that ERN and FRN are sensitive to evaluations regarding the motivational significance of errors/feedback (Luu & Tucker, 2003), where larger amplitudes in these components are typically found following errors, loss, or negative feedback (Bellebaum, Polezzi, & Daum, 2010; Miltner et al., 1997; Gehring & Willoughby, 2002; Pfabigan et al., 2011; Sato et al., 2005), especially when relevant to goal-directed behaviour and/or learning (Bellebaum et al., 2010; Genstch et al., 2009; Holryod et al., 2009; Yeung et al., 2005). For example, Li, Han, Lei, Holroyd, and Li (2011) found that FRN amplitude correlated with participant ratings regarding their subjectively felt responsibility about task outcomes. Similarly, Bellebaum et al. (2010) observed larger FRNs during an active as compared to a passive choice task. These findings were reported previously by Yeung et al. (2005), who showed that FRNs to gambling outcomes which involved no active choice were reduced as compared to outcomes which were not tied to a response, and that the differences in amplitudes between conditions correlated with subjective reports of task involvement.

A model of mPFC functioning in which the ERN and FRN reflect evaluative processes regarding behavioural and environmental consequences would have been further supported by a significant interaction between region and condition on the MW Go-Nogo task. However, in the current study, greater activity to errors in the Loss condition (i.e., explicit reduction of points), as compared to the Win condition, was revealed as a statistical trend favouring the dmPFC. Additional research is certainly needed, given other researchers have found that ventromedial regions are particularly sensitive to behavioural and environmental consequences which result in explicit punishments.

Several researchers have found additional recruitment of ventromedial regions, particularly in contexts involving negative affect and/or punishments. Additional recruitment of ventral regions occurs when individuals try to resolve conflicting stimulus-response mappings which involve emotional content (Kanske & Kotz, 2011). Also, when mistakes are penalized by monetary losses, as compared to no losses, researchers have found increased activity in rostro-ventral medial prefrontal regions (Taylor et al., 2006) which, compared to baseline, is greater than activity in the dmPFC (Simões-Franklin et al., 2010). Using EEG data, Ogawa et al. (2011) found that the neural sources of error-related activity included an additional ventromedial prefrontal region when participants were given verbal admonishment following errors compared to encouragement or neutral feedback. Other researchers have found ventral sources when localization MFNs recorded in contexts involving distress (Lewis et al., 2006) and reward/punishment feedback (Polezzi et al., 2010; Segalowitz et al., 2010).

There is evidence to suggest that the activation of ventral regions reflects affective evaluations tied specifically to actions, whereas dorsal regions provide additional monitoring of the context in which outcomes occur (see Luu & Tucker, 2003). Using a delayed feedback paradigm to separate response and affective value of performance feedback, Luu et al. (2003) found that the neural sources of response and feedback-locked MFNs could be modeled by ventral and dorsomedial regions, respectively. Cellular recordings by Isomura, Ito, Akazawa, Nambu, and Takada (2003) suggest that neurons in the rostral mPFC participate in cognitive and motor functions focused on action selection, particularly with respect to intended behaviour. An fMRI study on decision-making found that, whereas the dACC was most active when participants surmised an appropriate action, the vACC was engaged when individuals actually committed a motor response (Elliot & Dolan, 1998). Further support comes from neuroimaging studies which have found selective activation of rostro-ventral ACC during the commission of errors on Go-Nogo task (Kiehl et al., 2000; Menon et al., 2001).

These results from previous studies are also in accordance with neuroanatomical and cellular data which define the ventromedial prefrontal cortex as a neural substrate mediating visceromotor responses (Nauta, 1971; Neafsey, 1990). At a cellular level, activity in medial prefrontal neurons has been shown to be sensitive to volitional action selection (Isomura et al., 2003), as well as monitoring and evaluating behavioural and environmental outcomes (Ito, Stuphorn, Brown, & Schall, 2003), particularly with respect to expectation-outcome differences (Ito et al., 2003; Oya, Adolphs, Kawasaki, Bechara, Damasio, & Howard III, 2005). Together, these studies illustrate that the affective/motivational evaluation of behavioural and environmental consequences is closely tied to medial prefrontal function.

Brain-behaviour relationships and self-regulation

Several brain-behaviour relationships were reflected by associations among indices of medial frontal activation and performance. Specifically, we found that intracerebral CSD of dorso- and ventromedial prefrontal regions during the time of the ERN and FRN were strongly correlated with their respective scalp measures, such that greater CSD was associated with larger scalp negativities. Similar findings by Mathalon et al. (2003) were found, such that fMRI measures of activation in dorsal and ventral regions of the mPFC during error commission correlated with ERN amplitudes at the scalp.

It is well established that the mPFC is involved in the control of goal-directed behaviour, with roles in the execution (Forster & Brown, 2011), evaluation (Holroyd & Coles, 2008; Luu et al., 2003; 2004), and adjustment of actions (Amiez et al., 2005; Forstmann et al., 2008; Rubia et al., 2001). Results from the presents study support the broad role the mPFC in self-regulation, where greater mPFC relates to better performance and behavioural control (Miltner et al., 2003; van der Helden et al., 2010). Performance in the loss condition of the MW Go-Nogo task correlated with ERN amplitude, whereas trends were observed between performance and ERN and N2 amplitudes in other task conditions. Also, performance on the Go-Nogo task was positively associated with intracerebral CSD, indicating that greater engagement of both dorsal and ventral medial prefrontal regions during errors was associated with better inhibitory control. Previous studies have found that MFN amplitudes relate to post-error slowing (Ghering et al., 1993), efficiency of response switching (Genstch et al., 2009; Yasuda et al., 2004), as well successful remedial behaviour (Cohen & Ranganath, 2007; van der Helden et al., 2010), such as the extent to which individuals are inclined to learn from previous mistakes (Frank et al., 2005).

Also, we found that larger ERN amplitudes were associated with better performance in the loss condition only, which could indicate a stronger coupling between brain-behaviour mechanisms when the punishment for failed self-regulation is relatively more severe. In an ERP study, Frank et al. (2005) found that ERN amplitude predicted participants' learning about negative outcomes associated with their actions, but not positive outcomes. Other studies have also found that the association between activity in ventromedial regions and performance (e.g., reaction times) are only present in task contexts involving emotional context/stimuli (Kanske & Kotz, 2011; Mohanty et al., 2007).

In the present study, greater average mediofrontal scalp activity was related to lower levels of risk-taking in the BART, an association that was similarly observed for activity in the sgACC. This could be a reflection of the self-regulatory functions mediated by medial prefrontal systems, given that scalp measures, as well as CSD measures of the vmPFC, indicate that deactivation of the mPFC in arousing contexts related to a greater willingness to exhibit behaviours which ultimately become disadvantageous. Finally, strong linear relationships between mediofrontal activation occurring during errors, successful inhibition, and negative feedback can be taken as evidence for the role of the mPFC in supporting self-control.

Personality, temperament, and MFNs

In the present study, there was no effect of context on scalp or intracerebral CSD measures. Whereas previous studies have found that contexts involving emotional content (Lewis et al., 2006; Wiswede et al., 2009), or reward-punishment incentives (Boksem et al., 2008; Santesso et al., 2011) increase MFN amplitude, we found no support for such context effects. This null finding could mean that our context manipulation was ineffective in directly influencing scalp measures of mediofrontal activation. Differences between reward and punishment contexts could have also been clarified by comparing mediofrontal activation in a neutral condition in the absence of performance-related incentives. Results from previous studies show an interaction between context and personality, which leads to an alternative interpretation suggesting that the direct context effects on mediofrontal activity are masked by individual differences in sensitivity to reward-punishment. For example, researchers have found that individuals scoring higher on sensitivity to punishment and behavioural inhibition generate larger MFNs, especially when errors (Boksem et al., 2008) or feedback (Santesso et al., 2011) are associated with large monetary losses.

Consistent with other studies investigating personality and temperament in relation to medial frontal activation, we found that reduced medial frontal activity was associated with a greater self-reported propensity to engage in approach-related behaviours. It is worth noting that our effects between behavioural approach and medial frontal activity were not particularly strong, and were isolated to the Drive subscale of the BAS. Nevertheless, other researchers have found that persons scoring higher on measures of behavioural inhibition/withdrawal related behaviour elicit larger MFNs (Boksem et al., 2006; 2008), whereas those who report a greater tendency for approach-related behaviours show hypoactivation of the medial frontal cortex (Santesso & Segalowitz, 2009; Santesso et al., 2011; Segalowitz et al., 2011). Individual differences in sensitivity to punishment have also been shown to relate feedback processing, such that persons who are more sensitive to punishment elicit larger FRNs and show greater recruitment of ventromedial prefrontal regions (Santesso et al., 2011).

We also found that greater average MFN amplitude was associated with higher self-reported levels of Openness to Experience. These results between Openness to Experience and MFN amplitude may seem counterintuitive given the previous discussion suggesting that greater tendencies to engage in approach-related behaviours relate to lower levels of activity in the mPFC. Although Openness to Experience and BAS (Drive) both reflect approach-related behaviours, this does not mean that the underlying constructs overlap completely. The BAS measure taps approach-related behaviours which are typically characterized as sensation or novelty seeking and risk-taking. Conversely, the Openness to Experience measure more accurately reflects a motivated willingness to engage, approach, and critically assess the environment (DeYoung, 2010). In this sense, finding that individuals who score lower on Openness to Experience present with reduced activation of the mPFC is in line with previous studies illustrating that cognitive styles characterized by rigidity (e.g., closed-mindedness) tend to be associated with lower levels of medial frontal activity during performance monitoring. For example, researchers have found that greater absentmindedness (Hester et al., 2004), greater religious zeal (Inzlicht, McGregor, Hirsh, & Nash, 2009), and conservative political orientations (Amodio et al., 2007; Weissflog et al., 2009) relate to reduced activation of the mPFC. Our results not only confirm previous research indicating that a greater willingness to assess behavioural and environmental consequences is tied to ERN and N2 responses, but are also in line with studies illustrating that internal and external cues are more salient to persons higher in Openness to Experience (Wise, Mann, & Shay, 1992) and that these individuals have larger ERP amplitudes (Gurrera, O'Donnell, Nestor, Gainski, & McCarley, 2001).

Additionally, persons with greater CSD in the sgACC during the time of negative feedback were found to exhibit less risk-taking behaviour on the BART. A recent study by Segalowitz et al. (2011) found that medial prefrontal activation was similarly correlated with personality and temperament, across measures of both scalp activity and CSD. Taken together, these findings not only align with previous literature examining mPFC activation and personality and temperament styles, but emphasize further the role of affective/motivational processes with respect to self-regulation.

Emotional control is central to self-regulation (Allman et al., 2001) and, as previously described, MFNs to some extent reflect affective responses associated with the evaluation of errors and negative feedback. Consistent with this is the evidence that mediofrontal activation is related to mood/affective dimensions of anxiety. For example, higher scores of negative affect and/or emotionality have been shown to relate to increased mediofrontal activation (Luu et al., 2000b; Sato et al., 2005; Yatsuda et al., 2004). Also, persons with clinical depression have been found to elicit larger FRNs to negative feedback than non-depressed controls (Tucker, Luu, Frishkoff, Quiring, & Poulsen, 2003). Across clinical and non-clinical samples, individuals scoring higher on measures of anxiety (Hajcak, McDonald, & Simons, 2003) and obsessive-compulsive disorder (Fitzgerald et al., 2005; Hajcak & Simons, 2002; Hajcak, Franklin, Foa, & Simons, 2008; Ruchsow, Grön, Reuter, Spitzer, & Hermle, 2005) have also been shown to elicit exaggerated mediofrontal responses. In a recent functional neuroimaging study, Yoshimura et al. (2010) found that activity near the sgACC mediated the relationship between depressive symptoms and activation of other medial prefrontal regions involved in self-regulation. If activity in sgACC (i.e., BA25) is associated with states of anxiety, the negative association between sgACC activity at the time of negative feedback and risk-taking could be interpreted as support for the association between mood/anxiety and self-control, with those individuals showing less of an anxiety response also being those demonstrating more risk-taking and less self-control in their everyday lives.

Indeed, there is an extensive literature focused directly on the relationships between the structural and functional integrity of the vmPFC, particularly sgACC, and self-regulation of mood and affect. Structurally, reduced gray matter volume in or near the sgACC has been found in persons with depression (Boes, McCormick, Coryell, & Nopoulos, 2008), in cases of early-onset depression (Botteron, Raichle, Drevets, Heath, & Todd, 2002), as well as other symptoms reflecting mood dysregulation (Drevets, Savitz, & Trimble, 2008).

Functionally, the role of the sgACC in mood regulation is reflected by atypical activation patterns. For example, individuals with family history of mood disorders have been found to exhibit reduced glucose metabolism in sgACC (Drevets et al., 1997), a finding which has been reported in persons with depression characterized by anhedonia (Pizzagalli et al., 2004). On the other hand, other studies have found hyperactivation of the sgACC in persons with bipolar depression, which was successfully reduced with pharmacological treatment (Bauer et al., 2005). Thus, functioning of the sgACC, and the vmPFC more generally, supports affective/evaluative processes and is associated with temperament, personality, and mood, especially in relation to negative affect and anxiety.

Limitations

The results of the current study need to be considered in the context of certain limitations. We did not have any participation restrictions with respect to sex and the sample in the present study was comprised mostly of females. Sex differences are well established, in terms of brain structure and function, as well as in terms of behaviour and therefore the current results may not generalize to males. For example, women have been shown to score higher on measures of anxiety and harm avoidance, differences which can be accounted for, to a large extent, by volumetric sex differences in the ACC (Pujol et al., 2002). Additionally, in a sample of 15-year-old males, Segalowitz et al. (2011), using similar measures as we have used here, found that greater approach-related behaviour related to reduced mPFC activity as measured by both at the scalp and CSD activity. Thus, acquiring more equal sex representations could reveal more relationships between medial frontal activation, self-reported personality, and risk-taking on the BART.

In terms of task limitations, risk-taking on our version of the BART might benefit from having a larger number of possible inflations on a given trial. The risk-taking measures on the BART has shown good reliability (White et al., 2008), and predict real-world risk-taking behaviours including smoking status (Lejuez et al., 2003), substance use (Lejuez et al., 2002; Hopko et al., 2006), and unprotected sexual intercourse (Lejuez et al., 2004). Moreover, risk-taking behaviour on the BART has been shown to recruit medial prefrontal regions involved in self-regulation (Rao et al., 2008). In the present study a maximum of 10 inflations could occur which, although increasing the chances of acquiring enough FRNs to balloon pops to form a stable ERP average, could constrain voluntary risk-taking. In the traditional BART, researchers typically use the adjusted number of pumps as a measure of risk-taking, which is an average of the number of pumps from trials on which no balloon pop occurred. By using our paradigm, we cannot know how many more pumps participants would have allowed on trials where a pop occurred. Researchers could attempt to circumvent this by having individuals choose, prior to starting the inflation, how far they are willing to inflate in the event that a pop does not occur. Whereas the BART has been shown to relate to risk-taking propensity, other tasks modeled from the BART, such as the Balloon Analogue Insurance Task, have been shown differentially relate to personality characteristics, such as protective risk management (Essex, Lejuez, Qian, Bernstein, & Zald, 2011). Furthermore, when balloon pumps on the BART were executed to avoid monetary loss, participants exhibited riskier behaviour as compared to the original version (Benjamin & Robbins, 2007). Thus, altering task presentation could be a way to disentangle which personality characteristics are core to which types of voluntary risk-taking.

With respect to the MW Go-Nogo task, assessing differences in regional activation across contexts involving motivational pressure could benefit from including a neutral condition where all that is at stake is the individual's concern over their performance. Due to time constraints, we chose to exclude a no-point condition on the MW Go-Nogo task. Nevertheless, comparing error and inhibitory-related brain responses resulting in various consequences (gains, losses, missed gains, averted losses) to those having no motivational consequences might clarify the relative sensitivity of vmPFC regions to motivational contexts, and potentially reveal differences in ERP peak amplitudes at the scalp.

Finally, given that several studies have found associations between self-reported affect, task engagement, and mediofrontal activation (Hajcak et al., 2004; Luu et al., 2000b; Pailing & Segalowitz, 2004; Sato et al., 2005; Yeung et al., 2005), assessing participant's general mood across conditions could have been included to corroborate the effects context on brain function.

Future Directions

Given the limited research considering the effects of context on regional activation in the mPFC during the time of MFNs, we first wanted to examine these relationships in isolation. Nonetheless, given that previous research provides evidence for such associations, future investigations should consider the interactions between context and personality on medial prefrontal function. For example, Segalowitz et al. (2011) found that FRNs were modulated as a function of peer presence, and Boksem et al. (2011) reported larger FRNs when the individual's outcomes were relatively worse than those of another participant. A study by Boksem et al. (2008) found that persons high in behavioural inhibition elicited larger ERNs, specifically when errors resulted in an explicit punishment. Taken together, these studies illustrate that contexts of motivational pressure influence mediofrontal activation, and that the nature of this relationships varies across persons.

Another possible avenue of research would be to consider the differences in the relative activation of dorsal and ventral prefrontal regions, in relation to reward-punishment contexts. Examining the degree to which ventral regions are recruited over dorsal regions, in particular contexts (e.g., reward versus punishment), as a function of personality and temperament could have theoretical and clinical implications. Given the role of the vmPFC in emotional processing, these studies could be employed in persons known to have atypical functioning in motivational circuitry relative to other groups, such adolescents and populations with affective/mood disorders.

Acquiring the ERN, N2, and FRN in the same task would allow for more direct comparison of the issues investigated in the current study. Gründler et al. (2009) found overlapping neural generators for these MFNs, all of which were collected from the same task, but these electrocortical responses were not examined with respect to motivational pressure. Experimentally, it may not always be feasible to administer tasks which elicit all three MFNs. This could help clarify the effects motivational pressures on mediofrontal activity associated with errors, response inhibition, and processing negative feedback stimuli.

Using more sophisticated EEG decomposition tools could shed light on the brain dynamics associated with self-regulation. ERPs are typically characterized by distinct voltage fluctuations, varying in space and over time (Fabiani, Gratton, & Federmeier, 2000). However, the fact that ERPs emerge at least partially as a function of transient phase shifts in relation to experimental events (Başar, Başar-Eroglu, & Schürmann, 1992), even in the absence of increases in spectral power (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Makeig, Westerfield, Jung, Enghoff, Townsend, Courchesne, & Sejnowski, 2002), indicates that time-frequency decomposition of ERP signals would retain a purer representation of the changes in on-going EEG oscillations (Makeig, Debner, Onton, & Delorme, 2004).

There is good evidence to suggest that the ERN and FRN result from partial phase-locking of theta oscillations (Luu & Tucker, 2001; Luu & Pederson, 2004; Luu et al., 2004;), with the neural generators of these rhythms in the mPFC (Asada et al., 1999; Christie & Tata, 2009; Luu et al., 2003; 2004; Luu & Tucker, 2001). Given the evidence implicating theta-rhythms in learning and action monitoring, it is likely that the ERN and FRN reflect the entrainment of corticolimbic circuits which support the evaluation of behavioural and environmental consequences (Luu & Pederson, 2004; Luu & Tucker, 2003; 2004).

Conclusions

The results from the present study suggest that affective evaluations of behavioural and environmental consequences are central to self-regulation. The emphasis of affective responses to evaluating outcomes is based on patterns of brain activity across contexts, as well as their association with personality/temperament and performance.

Neither scalp measures nor intracerebral regional CSD differed across reward and punishment contexts. However, we found consistent main effects of regional activation as revealed by measures of intracerebral regional CSD. Whether individuals were making errors, successfully inhibiting responses, or being presented with negative (error) feedback, the vmPFC was relatively more active than the dmPFC. All task conditions involved an incentive that extended beyond the individual's own desire for good performance. Thus, the relatively greater engagement of the vmPFC could reflect the sensitivity of this region to contexts involving motivational pressures. While more research needs to be done to address this possibility, the interpretation is consistent with evidence showing increased activity in ventromedial prefrontal regions in contexts that involve motivational pressures, arousal/stress, and emotional content/stimuli. It is also consistent with the extensive neuroanatomical and neurophysiological data which suggest that the mPFC, particularly rostro-ventral regions, have reciprocal connections with subcortical and brainstem structures which modulate changes in visceromotor and homeostatic systems.

We found general support for the role of the mPFC in self-regulation as evidenced by associations among mediofrontal activation and behaviour. In addition to ERN amplitude correlating with performance in the loss condition, intracerebral CSD in the both dorsal and ventral mPFC correlated with performance across conditions. The association between greater mPFC activity and better self-regulation has been confirmed by previous studies employing a range of functional measures. Also, we found that larger average MFN amplitude and greater activity in sgACC were both associated with lower levels of voluntary risk-taking on the BART, possibly reflecting the self-regulatory functions carried out by the mPFC, particular ventral regions. Strong relationships among MFN amplitudes, as well as those between MFN amplitudes and their respective CSD in the dorsal and ventral mPFC, provide further evidence that activity in the mPFC is tied to self-control.

Associations among mediofrontal activation and personality/temperament also emphasize the role of affect in self-regulation. Individuals reporting a greater propensity to display rigid cognitive styles and engage in approach-related behaviours were found to elicit reduced mPFC activity when exercising self-control. These results are in line with a growing body of literature showing that personality and temperament styles characterized by higher levels of withdrawal-behaviours, inhibition, and/or anxiety are associated with enhanced mediofrontal activity in the context of self-monitoring and self-regulation.

Whereas our effects for an interaction between mPFC region and task condition were weak, similar associations have been previously reported, where the engagement of the vmPFC is particularly enhanced in punishment contexts. We did find that larger ERN amplitudes to be significantly associated with performance only on the loss condition of the MW Go-Nogo task, which could also reflect a stronger coupling between self-regulatory processes when the failed on-line control of behaviour amounts to explicit punishments. Although more research is needed to tease apart the specificity of regional recruitment across contexts, our data also suggest that the ERN and FRN reflect the engagement of a frontally-mediated evaluative process, spanning internal and external monitoring systems, respectively.

This interpretation is based on our finding that errors in the loss condition (ERN) and negative feedback on the BART (FRN) were both associated with relatively greater activity in the vmPFC than the dmPFC and is supported by previous research which has shown that the ERN and FRN share a cortical network, and are often localized to similar regions of the mPFC.

The influence of arousing task contexts on the relative activation of medial prefrontal regions has been somewhat overlooked in the current EEG/ERP literature. Overall, our results are in line with previous research emphasizing that affect/motivation are central to the processes reflected by MFNs, that the vmPFC is involved in regulating motivational/affective systems, and that the underlying mechanisms driving these functions vary across both individuals and contexts. The centrality of affective/motivational processes to behavioural and environmental consequences in self-regulation, along with our findings which emphasize the role of vmPFC activity in arousing contexts, could inform theoretical models focusing on self-regulation medial prefrontal functioning. Moreover, these models could be applied in clinical settings in order to better understand how patterns of neural activation relate to self-regulation and, consequently, how these associations could underlie maladaptive presentations in affective, behavioural, and cognitive systems.

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APPENDICES

Appendix A

General Screening Questionnaire

Name:

Contact Information:

Booking Date:

1. What is your birth date? Approx years of education [High school = 13 (if you graduated in 2003 or later); = 14 (if you graduated in 2002 or earlier)]?

2. Do you use non-permanent hair dyes? The reason I ask is that they could run when wet (and thus stain the equipment).
Yes No

3. Do you have dreadlocks, braids or hair extensions, or anything else about your hair that might make it difficult for us to place the sensor cap on your head? Basically, we have to place sensors on your head to record your naturally occurring brain activity, and braids, etc., make that difficult.
Yes No

4. Do you have any visual impairment that would make it difficult for you to see a standard computer screen?
Yes No

5. Do you have any condition that might affect the nervous system (e.g., multiple sclerosis, epilepsy)?
Yes No

6. Do you have hypoglycaemia, lupus, chronic fatigue syndrome?
Yes No

7. Have you ever had any serious psychiatric difficulties (e.g., schizophrenia, clinical levels of depression or anxiety, etc.)?
Yes No
***If yes, have you ever been under treatment for it?*

8. Have you ever had a head injury or concussion?
Yes No
***If yes, please provide details about (i) nature of the event, (ii) age of injury, (iii) if consciousness was altered and/or lost, (iv)if medical treatment was sought and/or received.*

Appendix B

Demographic and Health Screening Questionnaire

Health and Medical History Questionnaire (Check all that apply)

Subject ID code: ______________ Age: _____ Gender: ____ Date:__________

Item	*Past*	*Continuing problem/relevant details*
Special Problems with Reading		
Special Problems with Arithmetic or Number Skills		
Major Surgery (recent, last few years)		
Recent Major Stress (e.g., death in family/health concerns, in last year)		
Problems with appetite/eating (eating more or less than required)		
Problems with attention or concentration (e.g., ADD)		
Problems with activity level (hyperactivity)		
Problems with mood (Depression/Anxiety)		
Other Psychiatric problems		
Problems with sleep (e.g., falling asleep, frequent or early waking)		
Other serious disease/health concerns (e.g., cancer; chronic pain)		

Medications

Are you taking any prescribed or over-the-counter medications?

Medication	*Purpose*

Use of Stimulants/Suppressants

(0 = none; 1= v. light; 2 = light to moderate; 3 = moderate; 4 = moderate to high; 5 = high)

caffeine (coffee, tea, chocolate, soft drinks)	
alcohol (beer, wine, liquor)	
Nicotine	
Other	

General Health Practices:

	0 1 2 3 4 5 6 7 8 9 10 *Never* *Moderate* *Heavy*
Exercise (how often?)	0 1 2 3 4 5 6 7 8 9 10 *Never* *Moderate* *Heavy*
Diet (healthy choices?)	0 1 2 3 4 5 6 7 8 9 10 Rarely *Occasionally* *Consistently*

Self-reported Height = ________

Self-reported Weight = ________

Appendix C

HEXACO Personality Inventory

DIRECTIONS

On the following pages you will find a series of statements about you. Please read each statement and decide how much you agree or disagree with that statement. Then write your response in the space next to the statement using the following scale:

5 = strongly agree
4 = agree
3 = neutral (neither agree nor disagree)
2 = disagree
1 = strongly disagree

Please answer every statement, even if you are not completely sure of your response.

Please provide the following information about yourself.

1 ____ I would be quite bored by a visit to an art gallery.

2 ____ I plan ahead and organize things, to avoid scrambling at the last minute.

3 ____ I rarely hold a grudge, even against people who have badly wronged me.

4 ____ I feel reasonably satisfied with myself overall.

5 ____ I would feel afraid if I had to travel in bad weather conditions.

6 ____ I wouldn't use flattery to get a raise or promotion at work, even if I thought it would succeed.

7 ____ I'm interested in learning about the history and politics of other countries.

8 ____ I often push myself very hard when trying to achieve a goal.

9 ____ People sometimes tell me that I am too critical of others.

10 ____ I rarely express my opinions in group meetings.

11 ____ I sometimes can't help worrying about little things.

12 ____ If I knew that I could never get caught, I would be willing to steal a million dollars.

13 ____ I would enjoy creating a work of art, such as a novel, a song, or a painting.

14 ____ When working on something, I don't pay much attention to small details.

15 ____ People sometimes tell me that I'm too stubborn.

16 ____ I prefer jobs that involve active social interaction to those that involve working alone.

17 ____ When I suffer from a painful experience, I need someone to make me feel comfortable.

18 ____ Having a lot of money is not especially important to me.

19 ____ I think that paying attention to radical ideas is a waste of time.

20 ____ I make decisions based on the feeling of the moment rather than on careful thought.

21 ____ People think of me as someone who has a quick temper.

22 ____ On most days, I feel cheerful and optimistic.

23 ____ I feel like crying when I see other people crying.

24 ____ I think that I am entitled to more respect than the average person is.

25 ____ If I had the opportunity, I would like to attend a classical music concert.

26 ____ When working, I sometimes have difficulties due to being disorganized.

27 ____ My attitude toward people who have treated me badly is “forgive and forget”.

28 ____ I feel that I am an unpopular person.

29 ____ When it comes to physical danger, I am very fearful.

30 ____ If I want something from someone, I will laugh at that person's worst jokes.

31 ____ I’ve never really enjoyed looking through an encyclopedia.

32 ____ I do only the minimum amount of work needed to get by.

33 ____ I tend to be lenient in judging other people.

34 ______ In social situations, I'm usually the one who makes the first move.
35 ______ I worry a lot less than most people do.
36 ______ I would never accept a bribe, even if it were very large.
37 ______ People have often told me that I have a good imagination.
38 ______ I always try to be accurate in my work, even at the expense of time.
39 ______ I am usually quite flexible in my opinions when people disagree with me.
40 ______ The first thing that I always do in a new place is to make friends.
41 ______ I can handle difficult situations without needing emotional support from anyone else.
42 ______ I would get a lot of pleasure from owning expensive luxury goods.
43 ______ I like people who have unconventional views.
44 ______ I make a lot of mistakes because I don't think before I act.
45 ______ Most people tend to get angry more quickly than I do.
46 ______ Most people are more upbeat and dynamic than I generally am.
47 ______ I feel strong emotions when someone close to me is going away for a long time.
48 ______ I want people to know that I am an important person of high status.
49 ______ I don't think of myself as the artistic or creative type.
50 ______ People often call me a perfectionist.
51 ______ Even when people make a lot of mistakes, I rarely say anything negative.
52 ______ I sometimes feel that I am a worthless person.
53 ______ Even in an emergency I wouldn't feel like panicking.
54 ______ I wouldn't pretend to like someone just to get that person to do favors for me.
55 ______ I find it boring to discuss philosophy.
56 ______ I prefer to do whatever comes to mind, rather than stick to a plan.
57 ______ When people tell me that I'm wrong, my first reaction is to argue with them.
58 ______ When I'm in a group of people, I'm often the one who speaks on behalf of the group.
59 ______ I remain unemotional even in situations where most people get very sentimental.
60 ______ I'd be tempted to use counterfeit money, if I were sure I could get away with it.

Appendix D

Behavioral Inhibition System and Behavioral Activation System

Using the scale below, please circle the appropriate number in the column beside each item.

1 **Strongly Disagree**	**2** **Disagree**	**3** **Agree**	**4** **Strongly Agree**

1. If I think something unpleasant is going to happen I usually get pretty "worked up."	1	2	3	4
2. When I get something I want, I feel excited and energized.	1	2	3	4
3. When I want something, I usually go all-out to get it.	1	2	3	4
4. I will often do things for no other reason than that they might be fun.	1	2	3	4
5. I worry about making mistakes.	1	2	3	4
6. I go out of my way to get things I want.	1	2	3	4
7. I crave excitement and new sensations.	1	2	3	4
8. When I'm doing well at something, I love to keep at it.	1	2	3	4
9. If I see a chance to get something I want, I move on it right away.	1	2	3	4

10. When good things happen to me, it affects me strongly.	1	2	3	4
11. Criticism or scolding hurts me quite a bit.	1	2	3	4
12. I feel pretty worried or upset when I think or know somebody is angry at me.	1	2	3	4
13. I'm always willing to try something new if I think it will be fun.	1	2	3	4
14. It would excite me to win a contest.	1	2	3	4
15. Even if something bad is about to happen to me, I rarely experience fear or nervousness.	1	2	3	4
16. When I see an opportunity for something I like, I get excited right away.	1	2	3	4
17. When I go after something I use a "no holds barred" approach.	1	2	3	4
18. I feel worried when I think I have done poorly at something.	1	2	3	4
19. I often act on the spur of the moment.	1	2	3	4
20. I have very few fears compared to my friends.	1	2	3	4

Appendix E

Positive and Negative Affect Schedule

Read each item and then mark the appropriate answer in the space next to that word. Indicate to what extent you have felt this way today.

1	2	3	4	5
very slightly or not at all	a little	moderately	quite a bit	extremely

_____interested

_____distressed

_____excited

_____upset

_____strong

_____guilty

_____scared

_____hostile

_____enthusiastic

_____proud

_____irritable

_____alert

_____ashamed

_____inspired

_____nervous

_____determined

_____attentive

_____jittery

_____active

_____afraid

Appendix F

Zuckerman Sensation Seeking Scale Form V

Please indicate which is more like you by circling either A or B for the following questions.

A. I like "wild" uninhibited parties
B. I prefer quiet parties with good conversation

A. There are some movies I enjoy seeing a second or third time
B. I can't stand watching a movie that I've seen before

A. I often wish I could be a mountain climber
B. I can't understand people who risk their necks to climb mountains

A. I dislike all body odors
B. I like some of the earthy body smells

A. I get bored seeing the same old faces
B. I like the familiarity of everyday friends

A. I like to explore a strange city or section of town by myself, even if it means getting lost
B. I prefer a guide when I am in a place I don't know well

A. I dislike people who do or say things just to shock or upset others
B. When you can predict almost everything a person will do and say, he or she must be a bore

A. I usually don't enjoy a movie or play where I can predict what will happen in advance
B. I don't mind watching a movie or play that I can predict what will happen in advance

A. I have tried marijuana or would like to
B. I would never smoke marijuana

A. I would not like to try any drug, which might produce strange and/or dangerous effects on me
B. I would like to try some of the drugs that produce hallucinations

A. A sensible person avoids dangerous activities
B. I sometimes like to do things that are a bit frightening

A. I dislike people who are uninhibited and free about sex
B. I enjoy the company of people who are uninhibited and free about sex

A. I find that stimulants make me uncomfortable
B. I often like to get high (drinking liquor or smoking marijuana)

A. I like to try new foods that I have never tasted before

B. I order the dishes that I am familiar with, to avoid disappointment and unpleasantness

A. I enjoy viewing home movies, videos, or travel slides
B. Viewing someone's home movies, videos, or travel slides bore me tremendously

A. I would like to take up the sport of water skiing
B. I would not like to take up the sport of water skiing

A. I would like to try surfboard riding
B. I would not like to try surfboard riding

A. I would like to take off on a trip with no preplanned or definite routes, or timetable
B. When I go on a trip I like to plan my route and timetable fairly carefully

A. I prefer the `down to earth' kinds of people as friends
B. I would like to make friends in some of the `far-out' nonconformist groups

A. I would not like to learn to fly an airplane
B. I would like to fly an airplane

A. I prefer the surface of the water than to the depths
B. I would like to go scuba diving

A. I would like to meet some persons who are homosexual (men or women)
B. I would stay away from anyone I suspect of being gay or lesbian

A. I would like to try parachute jumping
B. I would never want to try jumping out of a plane, with or without a parachute

A. I prefer friends who are excitingly unpredictable
B. I prefer friends who are reliable and predictable

A. I am not interested in experience for its own sake
B. I like to have new and exciting experiences and sensations even if they are a little frightening, unconventional or illegal

A. The essence of good art is in its clarity, symmetry of form, and harmony of colors
B. I often find beauty in the `clashing' colors and irregular forms of modern paintings

A. I enjoy spending time in the familiar surroundings of home
B. I get very restless if I have to stay around home for any length of time

A. I like to dive off the high board
B. I don't like the feeling I get standing on the high board (or I don't go near it at all)

A. Heavy drinking usually ruins a party because some people get loud and boisterous
B. Keeping the drinks full is the key to a good party

A. The worst social sin is to be rude
B. The worst social sin is to be a bore

A. A person should have considerable sexual experience before marriage
B. It's better if you begin your sexual experience for the first time after you get married

A. Even if I had the money, I would not care to associate with flighty rich persons
B. I could conceive of myself seeking pleasures around the world with flighty rich persons

A. I like people who are sharp and witty, even if they do sometimes insult others
B. I dislike people who have their fun at the expense of hurting the feelings of others

A. There is altogether too much portrayal of sex in movies
B. I enjoy watching many of the `sexy' scenes in the movies

A. I feel best after taking a couple of drinks
B. Something is wrong with people who need liquor to feel good

A. People should dress according to some standard of taste, neatness
B. People should dress in individual ways even if the effects are sometimes strange

A. Sailing long distances in small sailing crafts is foolhardy
B. I would like to sail a long distance in a small, but seaworthy sailing craft

A. I have no patience with dull or boring persons
B. I find something interesting in almost every person I talk to

A. Skiing down a mountain slope is a good way to end up on crutches
B. I think I would enjoy the sensations of skiing very fast down a high mountain slope

Appendix G

Consent Form

Project Title: Neural Responses and Performance Monitoring Nov 2010

Principal Student Investigator :	Faculty Supervisor:
Stefon van Noordt (MA Candidate)	Dr. Sid Segalowitz (Professor)
BrockUniversity, Psychology Dept.	Brock University, Psychology Dept.
sv05lz@brocku.ca	sid.segalowitz@brocku.ca
905-688-5550, Ext. 5511	905-688-5550, Ext. 3465

PURPOSE/INFORMATION: In this study, we explore the relationship between brain functioning, general physiological arousal, and cognitive task performance. You will be asked to perform a series of computer tasks by making key-press responses to stimuli that come up on the computer screen. Each task will be described to you, in detail, before starting. In order to monitor your physiological responses, the following measures will be taken with the equipment listed below:

EEG/ERPs: *soft mesh-like cap with 128 sensors, interconnected with elastomers*

Heart rate: *two small sensors, one below collar bone, one on lower rib*

Respiration: *belt fitted, over clothing, around the chest*

Additionally, you will be asked to complete brief demographic and self-report personality questionnaires. The entire session should take approximately 2 hours. Please feel free to ask questions about the study at any time.

RISKS/BENEFITS: There are no known risks associated with participating in this study. The benefits are that the information from this study will contribute to our understanding of how the human brain responds to different outcomes.

CONFIDENTIALITY: All information is kept strictly confidential. You will never be identified in any way in presentations of the results. Your name will not be associated with the data we collect but rather a code number will be used. All data, including questionnaires, behavioural responses, and physiological responses will be kept in a lab with restricted entry and be available only to our researchers. Data will be kept for the purpose of future analyses on related research questions about brain functions and their correlates. However, when data analyses are complete, all computer data will be deleted and paper files shredded.

PARTICIPATION: We want to remind you, that your participation in this study is entirely voluntary. You may decline to participate at any time or you have the right to omit answers to any question(s) you choose. Some of the tasks you will perform involve the opportunity to win/gain points, and these will translate into a monetary payout upon study completion. Therefore, in addition to receiving a maximum of two hours participation credit, you will additionally be eligible for monetary compensation.

POTENTIAL PUBLICATION: The results from this study may be reported in journal articles, presentations, or books. However, I would like to emphasize again that you will not be identified in any way. Should you be interested about the results of this study, we encourage you to contact either of the researchers after June 2011.

Please read and fill out the consent block to indicate whether you will receive monetary compensation or course participation hours for taking part in this study.

CONSENT: I have read and understand the above information. I have received a copy of this form. I understand that I may ask questions now or in the future. I agree to participate in this study.

Please check appropriate box:

[ ] I have read and understand the above information regarding this study.

[ ] I have received a copy of this form.

[ ] I understand that I may ask questions in the future.

☐ **I am participating in this research project for 2 hours of research participation in a psychology course and understand that, should I choose to withdraw, I may lose some of the participation credit accordingly.**

☐ **I understand that some of the tasks in this study involve the opportunity to win/accumulate points, and that my points will be converted to a monetary payout upon completion of the session.**

Date: ____________________

____________________________ ____________________________

Participant name (please print) **Signature of participant**

____________________________ ____________________________

Course for participation **Signature of researcher**

CONTACT: If you have questions at any time about the study or the procedures you may contact the researchers. This project has been reviewed and received ethics clearance through the Office of Research Ethics Board (File # 10-101). If you have any pertinent questions regarding your rights as a participant, please contact the Research Ethics Officer at reb@brocku.ca, 905-688-5550 ext 3035.

If you may be interested in being contacted for future research projects, please sign below and indicate some contact information (such as an email address). At the future time, you can of course decide whether or not to participate in the study. If research participation credit is not needed at that time, you can choose the cash payment option for your participation.

____________________________ ____________________________

Participant name (please print) **Signature of participant**

Contact information (e.g., email address, tel number): ____________________________

***** THANK YOU FOR YOUR PARTICIPATION*****

Appendix H

Debriefing Form

Project Title: Neural Responses and Performance Monitoring

Principal Student Investigator:	Faculty Supervisor:
Stefon van Noordt (MA Candidate)	Dr. Sid Segalowitz (Professor)
BrockUniversity, Psychology Dept.	Brock University, Psychology Dept.
sv05lz@brocku.ca	ssegalowitz@brocku.ca
905-688-5550, Ext. 5511	905-688-5550, Ext. 3465

PURPOSE/PROCEDURE: The study you participated in today assessed your physiological responses to a variety of outcomes. In some cases, your neural and sympathetic responses were measured when you made a correct or an incorrect response. For these tasks, the chances of making an error were manipulated by adjusting the time window within which you could deliver a correct response. Thus, making errors on these tasks was an expected part of normal performance and provided an opportunity to see your physiological response whenever an error occurred. In other cases, responses associated with different feedback information were measured.

The anterior cingulate cortex is a region in the brain which is active when someone is monitoring their performance on a task, checking for correct versus incorrect responses. Activity in this brain region can be observed by using brainwave patterns (called event-related potentials, or ERPs), including in the current study, the error-related negativity (ERN) and the feedback-related negativity (FRN). The ERN and FRN are specific brainwave patterns which are elicited when an individual realizes they have made an error (ERN), or is presented with feedback indicating that an undesirable outcome has occurred (FRN). Currently, there is debate about whether or not the ERN and FRN reflect the same process in the brain or if they are associated with activity in the same portions brain tissue. In addition, researchers have not adequately investigated whether the ERN and FRN are sensitive to the extent of the person's personal investment in the task. This is what we are doing with this study.

In addition to investigating the relationships between brainwave patterns, specific activation patterns in the brain, and the context of the task, we collected personality information. These questionnaires will allow us to determine whether differences in personality, as measured by these self-reports, are associated with variation in brain activity.

We would ask that if any future potential participants ask you about today's study, you say that you had to do computer tasks while physiological measures were taken. Also, please do not show this form to other potential participants, this is just for your viewing. The reason we do not want other participants to see this form is so they do not find out about the specific purpose of the computer task, and questionnaires beforehand as this could prevent them from responding naturally to the questions. Your co-operation on this is much appreciated.

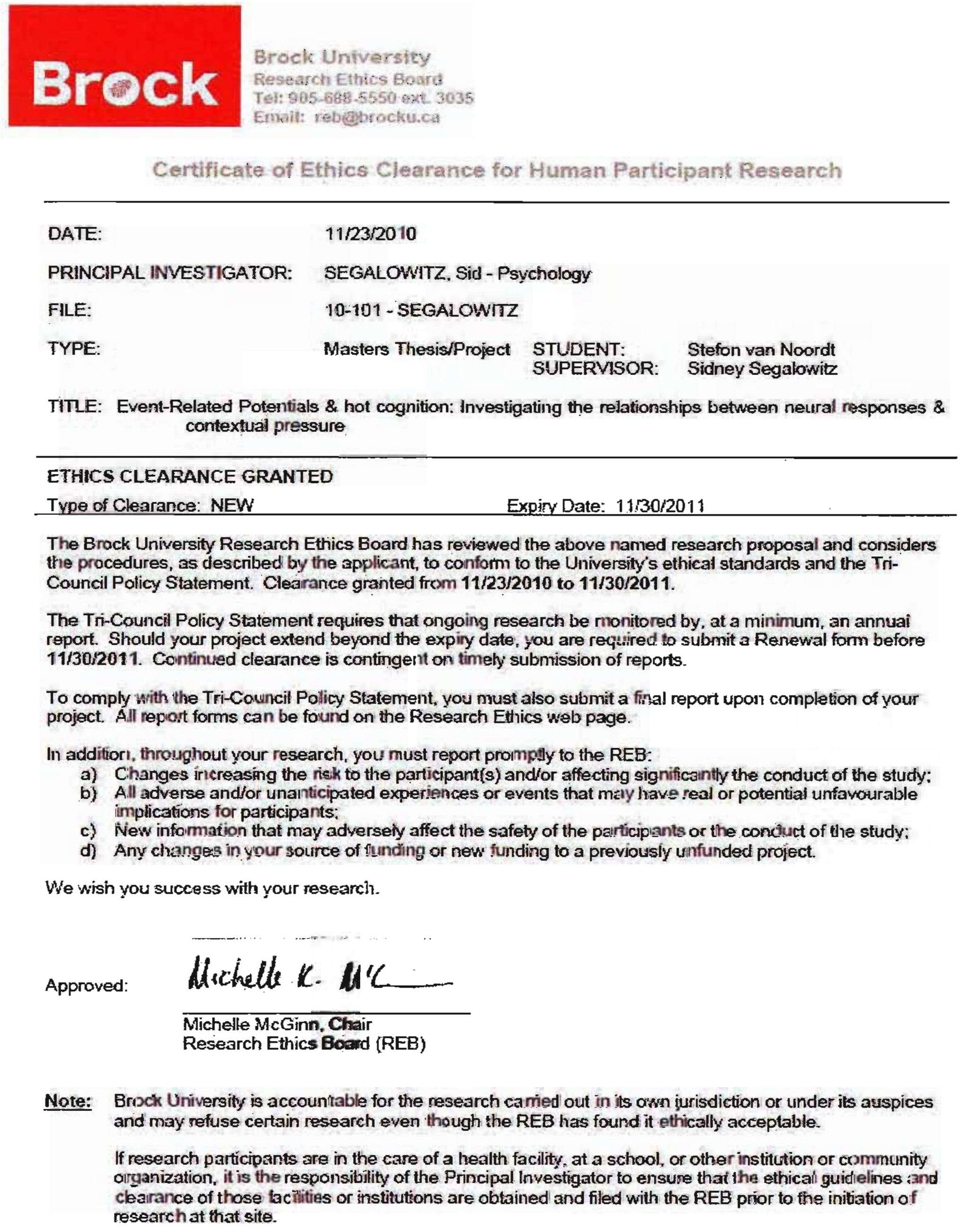
CONTACT: If you have questions at any time about the study or the procedures you may contact the researchers. This project has been reviewed and received ethics clearance through the Office of Research Ethics Board (File # 10-101). If you have any pertinent questions regarding your rights as a participant, please contact the Research Ethics Officer at reb@brocku.ca, 905-688-5550 ext 3035.

FEEDBACK AND PUBLICATION: The results from this study may be used in journal articles, presentations, or books published. The results of this research study will be available approximately one year from now. If you would like a copy of the results, please contact the researcher at that time.

Thank you for your time and support in participating in this study!

Appendix I

Research Ethics Board – Study Approval



Brock
Brock University
Research Ethics Board
Tel: 905-688-5550 ext. 3035
Email: reb@brocku.ca

Certificate of Ethics Clearance for Human Participant Research

DATE: 11/23/2010

PRINCIPAL INVESTIGATOR: SEGALOWITZ, Sid - Psychology

FILE: 10-101 - SEGALOWITZ

TYPE: Masters Thesis/Project STUDENT: Stefon van Noordt
SUPERVISOR: Sidney Segalowitz

TITLE: Event-Related Potentials & hot cognition: Investigating the relationships between neural responses & contextual pressure

ETHICS CLEARANCE GRANTED

Type of Clearance: NEW Expiry Date: 11/30/2011

The Brock University Research Ethics Board has reviewed the above named research proposal and considers the procedures, as described by the applicant, to conform to the University's ethical standards and the Tri-Council Policy Statement. Clearance granted from **11/23/2010 to 11/30/2011.**

The Tri-Council Policy Statement requires that ongoing research be monitored by, at a minimum, an annual report. Should your project extend beyond the expiry date, you are required to submit a Renewal form before **11/30/2011.** Continued clearance is contingent on timely submission of reports.

To comply with the Tri-Council Policy Statement, you must also submit a final report upon completion of your project. All report forms can be found on the Research Ethics web page.

In addition, throughout your research, you must report promptly to the REB:

a) Changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) All adverse and/or unanticipated experiences or events that may have real or potential unfavourable implications for participants;
c) New information that may adversely affect the safety of the participants or the conduct of the study;
d) Any changes in your source of funding or new funding to a previously unfunded project.

We wish you success with your research.

Approved: Michelle K. Mc

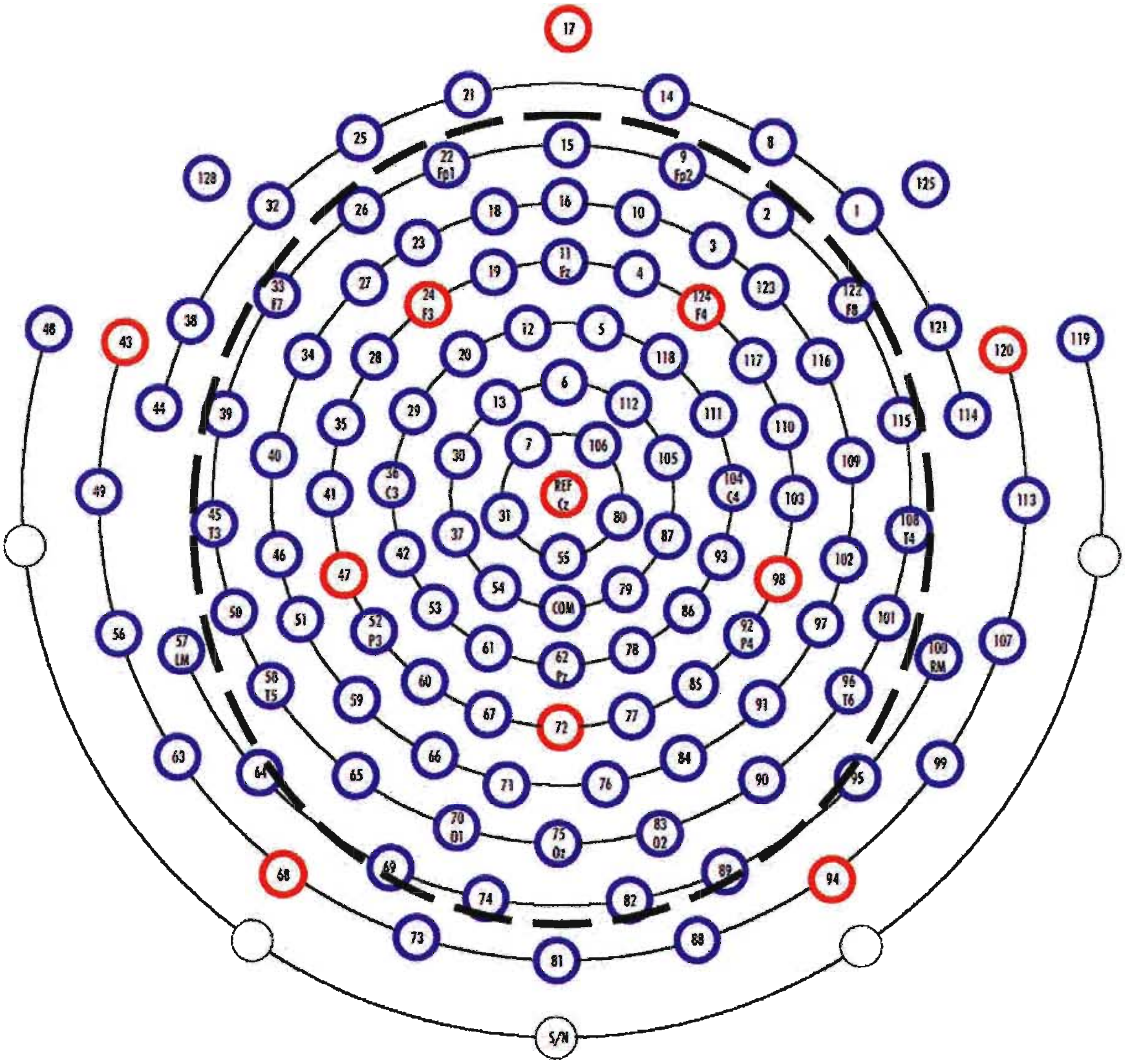
Michelle McGinn, Chair
Research Ethics Board (REB)

Note: Brock University is accountable for the research carried out in its own jurisdiction or under its auspices and may refuse certain research even though the REB has found it ethically acceptable.

If research participants are in the care of a health facility, at a school, or other institution or community organization, it is the responsibility of the Principal Investigator to ensure that the ethical guidelines and clearance of those facilities or institutions are obtained and filed with the REB prior to the initiation of research at that site.

Appendix J

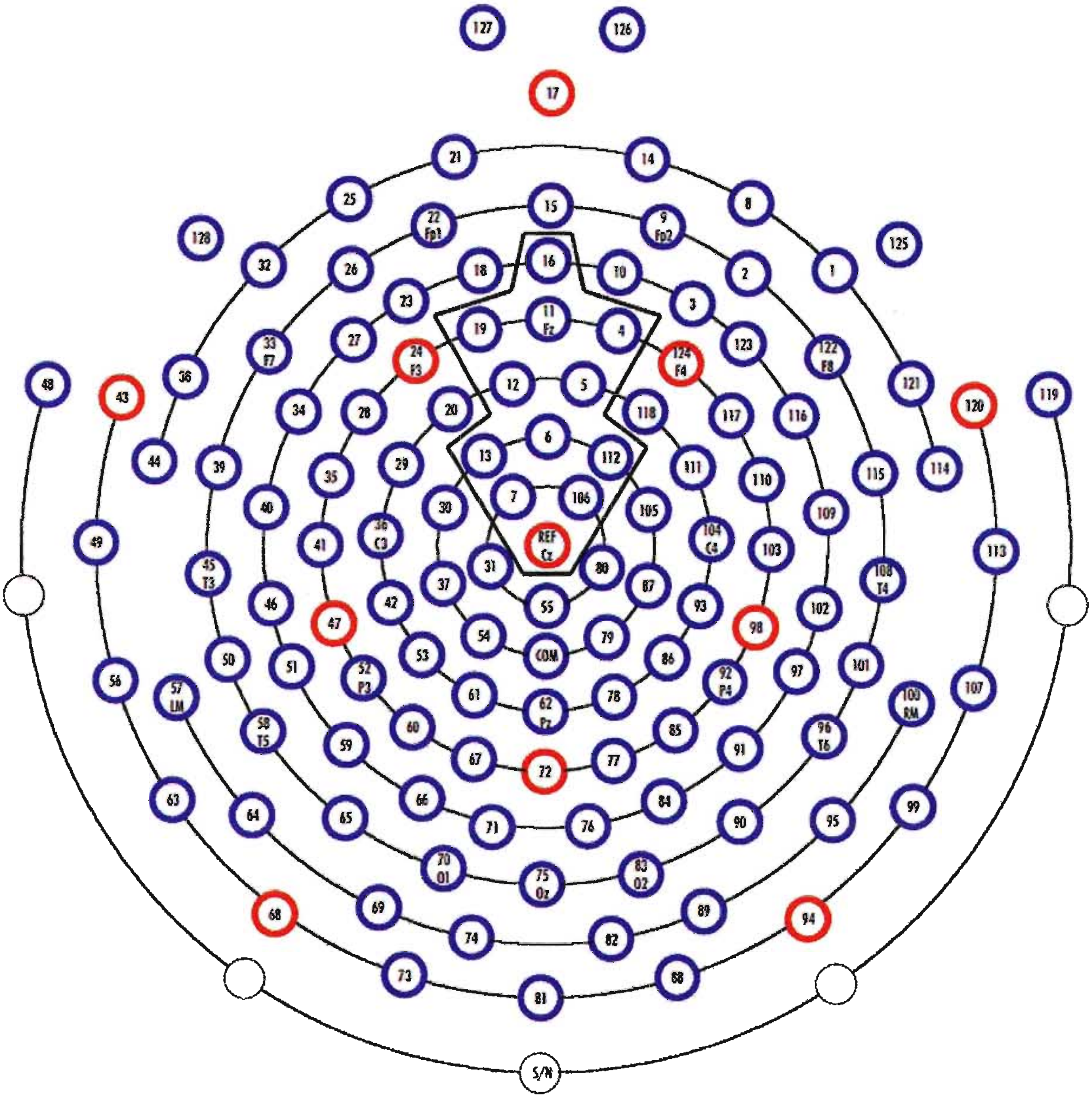
Standard 98 Channel Montage for Creating Average Reference



All cannels falling on or inside the dashed black lines were included in the standard average referencing montage.

Appendix K

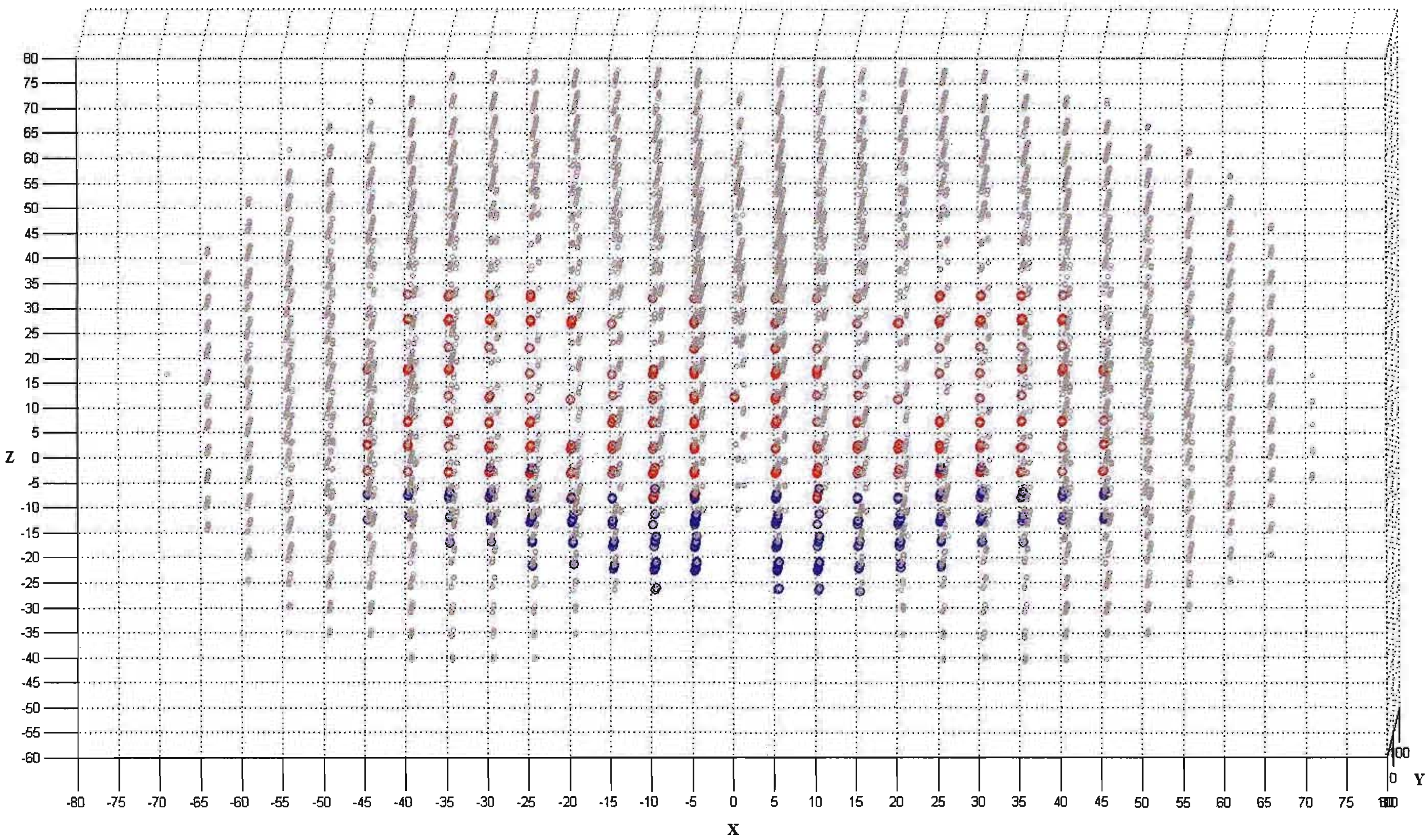
Frontal Midline Channels Selected for Scoring Mediofrontal Negativities



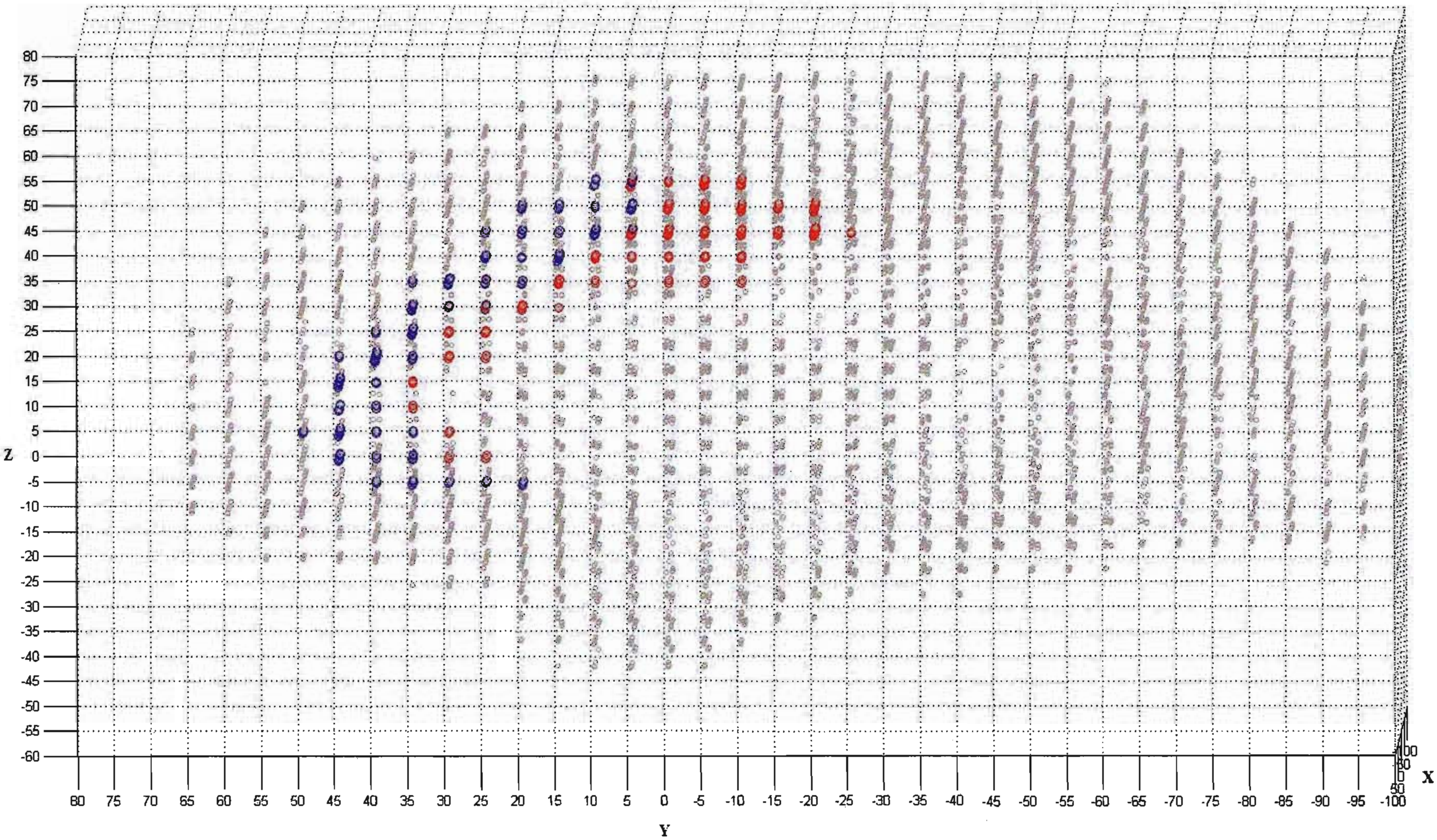
All cannels falling inside the solid black lines were used as the frontal midline sites for scoring mediofrontal negativity MFN amplitudes.

Appendix L

3-D Voxel Plots for Dividing Brodmann Areas on Cartesian Coordinates



All 6,239 voxels corresponding to cortical matter plotted in 3-D space. Brodmann Areas 10 (red voxels) and 11 (blue voxels) were divided into medial (x-coordinate = <20, >-20) and lateral (x-coordinate = >+/-20) regions.



All 6,239 voxels corresponding to cortical matter plotted in 3-D space. Brodmann Areas 24 (red voxels) and 32 (blue voxels) were divided into dorsal (y-coordinate = <20, x-coordinate = >24) and ventral (y-coordinate = >20, x-coordinate = <24) regions.

Appendix M

Normality Data for Measures of Behavioural Performance

	Normality	
	Skewness	Kurtosis
Win Condition		
Correct Response Time	<0.001	-0.36
Error Response Time	0.28	-0.26
Nogo Accuracy	-0.24	-0.56
Loss Condition		
Correct Response Time	-0.37	-1.02
Error Response Time	-0.27	-0.80
Nogo Accuracy	0.13	-0.28
BART Risk-Time	-0.18	-0.20

Note: Skewness SE=0.44; kurtosis SE = 0.86

Descriptive and normality statistics for behavioural measures.

Appendix N

Normality Data for Measures of Neural Activity

Descriptive and normality statistics for measures of neural activation.

	Normality	
	Skewness	Kurtosis
Win Condition		
ERN		
Amplitude	-0.11	-0.44
dmPFC CSD	-0.02	-0.39
vmPFC CSD	-0.13	-0.54
N2		
Amplitude	-0.81	0.91
dmPFC CSD	0.22	0.84
vmPFC CSD		
Loss Condition		
ERN		
Amplitude	-0.88	0.14
dmPFC CSD	0.79	0.80
vmPFC CSD	0.77	0.77
N2		
Amplitude	0.02	-0.87
dmPFC CSD	0.23	-0.38
vmPFC CSD	0.60	-0.06
FRN		
Amplitude	-0.58	-0.37
dmPFC CSD	-0.60	2.19
vmPFC CSD	-0.36	1.33

Note: Skewness SE=0.44; kurtosis SE = 0.86

Appendix O

Normality Data for Measures of Personality

Descriptive and normality statistics for personality and temperament questionnaires.

			Normality	
	M	*SD*	Skewness	Kurtosis
HEXACO				
Honesty-Humility	32.50	4.25	0.15	0.18
Emotionality	31.46	2.59	0.53	0.13
Extraversion	30.57	2.67	-0.36	-0.31
Agreeableness	30.14	4.16	0.55	-0.32
Conscientiousness	29.35	3.03	1.71	4.50
Openness to Experience	30.50	3.25	-0.28	-0.04
BIS-BAS				
Drive	11.07	1.88	-0.54	0.60
Reward Responsiveness	17.36	1.79	-0.54	-0.64
Fun Seeking	11.18	2.33	0.24	-0.51
BIS	16.68	3.03	-0.25	-0.54
PANAS				
Positive Affect	28.36	7.99	-0.35	-0.43
Negative Affect	16.32	6.41	2.07	5.83
SSS-V				
Thrill and Adventure Seeking	6.71	2.75	-0.16	-0.94
Experience Seeking	5.21	1.57	-0.44	-0.80
Disinhibition	5.07	2.28	-0.16	-0.73
Boredom Susceptibility	1.96	1.43	1.16	1.10

Note: Skewness SE=0.44; kurtosis SE = 0.86