Theta activations associated with goal-conflict processing: Evidence for the revised "Behavioral Inhibition System"

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Abstract

In the theory of the Behavioral Inhibition System (BIS), Gray and McNaughton (2000) classified events that produce or inhibit goal-directed behaviour into two affective categories: approach versus avoidance. We experience goal-conflict when approximately equal but incompatible approach and avoidance tendencies are concurrently activated. Gray and McNaughton (2000) proposed goal-conflict as a class of mechanisms separable from "simple" mechanisms: Goal-conflict effects are maximal when incompatible approach and avoidance tendencies are balanced. simple effects are maximal when either approach or avoidance tendencies predominate.

Gray and McNaughton (2000) saw the hippocampus as a key nexus for resolving goal-conflict by recursive amplification of the subjective value of punishment, thereby increasing avoidance tendencies. Rodent hippocampal theta (4-12 Hz) is necessary (but not sufficient) for correct and efficient transmission of hipppocampal outputs. The BIS theory is fundamentally an animal model. It is not clear if a human BIS exists in the same form. Record human hippocampal (4-12 Hz) activity from the scalp is unlikely. However, during goal-conflict resolution, cortically generated theta recorded from the scalp could be modulated by human hippocampal theta. Therefore, superficially recorded 4-12 Hz theta spectra power was used to assess if specific goal-conflict processing activity could be detected in humans.

Human goal-conflict processing was assessed in four experiments: the Stop-Signal Task (**SST**), an existing experimental task, and three variations of a task termed "**Choice**", created for this thesis. Across experiments, three key conditions were created. Approach and avoidance were balanced in the intermediate condition (maximal goal-conflict). Net approach and avoidance predominated in the adjacent conditions respectively (minimal goal-conflict). Goal-conflict was assessed as the difference between activity in the intermediate condition and the average activity across the adjacent conditions (via extraction of the orthogonal quadratic trend for significance testing).

Goal-conflict increased activations consistently at F8, above the right frontal cortex. Increase in task dependent goal-conflict activations were also observed at F7, Fz and F4 above the frontal cortex, and T3, T4, T5 and T6 above the temporal cortex. Activations within the human theta frequency range (4-7 Hz) were consistently detected in the **Choice** tasks. In the **SST**, activations spanned the conventional human theta (4-7 Hz) and alpha (8-12 Hz) frequencies. In the **Choice** tasks, higher conflict theta at T3, T5 and F8 predicted increased avoidance.

Taken together, the findings support Gray and McNaugthon's (2000) views that a) goal-conflict is a class of mechanism separable from simple approach and avoidance; b) goal-conflict processing recruits and increases cortical rhythmic activity within the same frequency range as rodent hippocampal theta (4-12 Hz); and goal-conflict is resolved by increasing the subjective value of punishment, thereby increasing avoidance tendencies. Although speculative, the current work identified a right inferior frontal gyrus neural circuit for slower, and a presupplementary motor area circuit for faster behavioral inhibition during goal-conflict resolution. These circuits are not explicit in the current BIS model.

Preface

"Ignorance gave me courage to seek truth. The search brought fear of never finding it. But I shall not despair for where there is passion, there is hope. Each endeavor brings me closer to the truth."

Thoughts on my thesis

I am grateful for Professor Neil McNaughton's supervision on this thesis. He made himself available whenever I needed assistance. Members of the McNaughton lab also contributed to the thesis's conception and completion. To Damon, I am thankful for him developing the data processing tools. Phillip's fourth year thesis inspired the **Choice** paradigm and Jane collected data for replication 1 of the Stop-Signal Task. Thanks also to the technicians, the programmers and the administrative staff of the Psychology Department at the University of Otago. They are a great team! The experiments ran smoothly with their assistance.

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This thesis is dedicated to my husband Peter. He did the laundry, the cooking, the nappies change, the waking up in the nights etc whenever I needed to focus on the thesis. His support has been stoic. This is also for Sophie, my daughter. She is my inspiration.

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List of Abbreviations

ANOVA	Analysis of variance
BIS:	Behavioral Inhibition System
EEG:	Electroencephalogram
EOG:	Electro-oculogram
EPQ-R:	Eysenck Personality Questionnaire-Revised
***f*MRI**:	Functional Magnetic Resonance Imaging
Gpi:	Globus pallidus pars interna
iEEG:	Intracranial electroencephalogram
IFG:	Inferior Frontal Gyrus
MB:	Mamillary bodies
MS/DB:	Medial septum/diagonal Band of Broca
$P_{inhibit}$	Probability of inhibition
PreSMA:	Presupplementary motor area
SSD:	Stop-Signal Delays
SSRT:	Stop-Signal Reaction Times
SST:	Stop-Signal Task
STAI:	Spielberger State-Trait Inventory

1 Introduction

1.1 Human goal-directed behavior – more than meets the eye

> "My diving bell becomes less oppressive, and my mind takes flight like a butterfly. There is so much to do. You can wander off in space or in time, set out for Tierra del Fuego or for King Midas's court. You can visit the woman you love, slide down beside her and stroke her still sleeping face. You can build castles in Spain, steal the Golden Fleece, discover Atlantis, realize your childhood dreams and adult ambitions." (Bauby, 1997, prologue)

Sugrue, Corrado and Newsome (2005) illustrated the dissociation between actions and internal brain processes with the above excerpt from a memoir by Jean-Dominique Bauby. After a stroke, Jean-Dominique Bauby wrote his memoir by blinking his left eye, the only voluntary movement he was capable of, to select each letter. His memoir is a powerful reminder that much more than meets the eye goes on in the brain.

Behavior directed by a goal, namely writing a memoir in Jean-Dominique Bauby's case, involves internal brain processes beyond those that simply control motor acts. The relationships between behaviour and the various internal processes is complex (Hinde, 1982) and make it difficult to simply define and describe what a goal is. Hinde (1966) defined the term "goal" in the following way:

> "Some authors have labeled behaviors as 'directive' or 'goal directed" on the sole criterion that variable means are used to achieve a consummatory situation...[but if] each type of behavior is stereotyped, its cessation could be due merely to inhibitory effects consequent upon performances, rather than to error signals...[In contrast] if rats are subjected to spinal or cerebellar operations so as to interfere with their motor coordination, they may nevertheless use quite novel movements to make errorless runs through a maze. The essential point here is that the new movements are not stereotyped, but selected from variable patterns in such as a manner as to bring the animal nearer

the goal. Furthermore, the new patterns are "directly and efficiently substituted without any random activity."(Hinde, 1966, p. 307)

In a later version of his work on animal behavior, Hinde's (1982) explained goal-directed behavior has to meet two criteria. Firstly, the course of action selected to attain the goal is not random, and the most economical course is chosen. Stereotypical behaviors are observed in relation to certain goal situations only because those behaviors are economical in the situation concerned. Secondly, if the stereotyped behavior is not accessible, it is substituted with an alternate means, such as blinking instead of writing to produce a memoir. Critically, the alternate means is not random, and the most economical course of action that is available for the same end result is still chosen.

1.2 Goal-conflict as a class of mechanisms separable from simple approach and simple avoidance

Gray and McNaughton (2000) saw behaviour as goal-directed in Hinde's (1966, 1982) terms. They also viewed events that produce or inhibit goal-directed behaviour as falling into just two affective categories: positive/rewarding and negative/punishing (see also Gray, 1975). Stimuli that elicit the tendencies to direct an overt pre-potent response to it are, by definition, positive/rewarding; stimuli that elicit tendencies to stop the overt pre-potent response are negative/punishing. In retaining a simple two system core for the control of goal-directed behaviour, Gray and McNaughton (2000) also viewed the omission of an expected reward as having the same effects as a punishment and omission of an expected punishment as having the same effects as a reward.

The tendencies to direct an overt pre-potent response to rewarding stimuli represent our tendencies to approach the stimuli, i.e. approach tendencies. A desirable object, a situation, a location, or a person etc. could represent the stimulus. So the stimulus often includes different attributes, for example the smell and distance of a location. Not all of the attributes of the stimulus are desirable. For example, making a left click on a computer mouse could produce either a monetary gain or a monetary loss. The potential gain creates the tendency to make left clicks but the potential loss creates the tendency

to avoid (inhibit) making left clicks. The tendencies to inhibit pre-potent responses to potentially rewarding stimuli due to potential punishment represent a form of avoidance known as "passive avoidance".

When we produced adaptive overt responses to avoid punishment (as opposed to stopping responses to avoid punishment in passive avoidance), we are engaged in another form of avoidance known as "active avoidance". For example, a robber would be caught if he does not *run away* when he spots a policeman. This is in contrast with overt responses produced when there is a desire to approach rewarding stimuli, for example, when a woman *runs towards* a policeman for help after she has just been robbed. Overt responses in the former case are driven by active avoidance tendencies. In the latter, they are driven by approach tendencies.

The dichotomy between reward versus punishment, positive versus negative stimuli, and approach versus avoidance is established as a core concept used to explain human behaviors (Pavlov, 1927; Skinner, 1938; Thorndike, 1911). This dichotomy has a strong influence on neuroscience, leading to a corresponding division of neural systems into two general classes (Carver & White, 1994; Davidson, 1995; Elliot & Covington, 2001; Gable, Reis, & Elliot, 2003; Rolls, 2000). One system processes reward, positive stimuli and approach behaviors (Depue. & Collins, 1999; Kalivas & Nakamura, 1999; Wise, 2002) The other system processes punishment, negative stimuli and avoidance behaviors (Ledoux, 1995).

Our environment is filled with multiple complex stimuli that are often a combination of positive and negative attributes. At any point in time, our behaviors are likely to be influenced by concurrently activated approach, passive-avoidance and active-avoidance tendencies. When these tendencies are incompatible, and just one tendency is highly activated then it will capture behavior. However, when concurrently activated incompatible tendencies are approximately equal, it is difficult for a "winner-take-all" system to direct behavior in a consistent fashion.

Gray and McNaughton (2000) proposed that we experience goal-conflict when approximately equal but incompatible approach and avoidance tendencies are concurrently activated. Goal-conflict explains animals' dithering behavior in the wild i.e. they initially approach the location where the food is but then move away when they are close for fear of a predator (McFarland, 1987). Dithering has also been observed under experimental conditions when animals move back and forth when faced with stimuli that include components of reward and punishment (Gray, 1987; Miller, 1944).

Gray and McNaughton (2000) proposed goal-conflict as a class of neural mechanisms that is separable from "simple" neural mechanisms. "Simple" here refers to processes that could be complex but mediates processing of either relatively pure approach or relatively pure avoidance. Goal-conflict effects occur only when incompatible simple approach and avoidance tendencies are concurrently activated. Hence, when goal-conflict effects occur they are always superimposed on simple effects. But goal-conflict and simple effects are separable. In Gray and McNaughton's (2000) theory, goal-conflict effects are maximal when incompatible approach and avoidance tendencies are balanced. Simple effects are maximal when either approach or avoidance tendencies predominate. Therefore, goal-conflict can be conceptualized as a class of mechanisms, separable from simple approach and simple avoidance processes, *per se*, but resulting from an interaction between them.

1.3 The hippocampus as a goal comparator – a key structure in resolving goal-conflict

Gray and McNaughton (2000) proposed that the hippocampus is a key nexus for resolving goal-conflict. A goal is represented in a brain area as a neural compound of an *overt type of adaptive response* and a particular configuration of stimuli or situation. If either of these attributes is different then the neural representation is of a different goal (e.g. water at the end of a runway is a different goal from food in the same place, and both are different from food in a different place).

According to Gray and McNaughton (2000), information about any activated goal encoded in cortical or sub-cortical regions is transmitted to the hippocampus constantly in the form of efferent copies. Concurrently activated goals will thus produce concurrent distinct activations in the hippocampus. The hippocampus acts as a comparator when it receives information about goals. It compares the level of concurrently activated approach and avoidance tendencies in a goal and the concurrent levels of activation between incompatible goals. Normally, a goal with a very highly activated dominant tendency will emerge as a clear winner in the competition for control within the motor system. In this case, because of the imbalance in level of activations between the different goals, the hippocampus will not detect conflict. It will thus *not produce an output,* and is only in "just checking" mode. The hippocampus only produces an output when it detects concurrently activated, incompatible tendencies, with nearly equal levels of activation either in a goal[1] or between goals. Below, I will present the principles of goal-conflict resolution in the hippocampus between concurrently activated approach and avoidance tendencies in a goal. Note that conflict between two or more goals can arise from concurrently activated approach-approach or avoidance-avoidance tendencies as well as approach-avoidance. This will not be further discussed since the basic principles in resolving approach-avoidance conflict in a goal apply to the other cases.

To resolve approach-avoidance conflict in a goal, the hippocampus first inhibits overt responses. This is achieved by blocking output from the areas defining the goal to the areas responsible for achieving it while leaving the goal representations themselves activated. The hippocampus then amplifies the value of punishment and so increases existing simple avoidance tendencies (this could include both active and passive avoidance in conflict between separate goals). The amplification process is recursive

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[1]It is unclear if Gray and McNaughton (2000) viewed any conflict between concurrently activated avoidance and approach tendencies as conflict between goals. I consider a goal as a neural compound of an *overt type of adaptive response* and a particular configuration of stimuli. Thus, the inhibition of an overt response is not a goal. So it is possible to have conflict between concurrently activated tendencies related to a single goal. Note that this could be a departure from Gray and McNaughton's (2000) view on what is a goal.

and only stops when existing avoidance tendencies are sufficiently more highly activated than the existing approach tendencies to emerge as a clear winner. The weights of existing approach tendencies are left unchanged. In some cases, this is the only critical functional output of the hippocampus and the conflict is resolved solely by changing the weights of existing simple avoidance tendencies.

In Gray and McNaughton's (2000) model, the hippocampus also initiates a parallel process to explore and scan the environment for new information (it also scans memory for similar additional information.) The new information may change the activations of existing simple approach and avoidance tendencies. Again, this allows a clear winner to emerge, thereby resolving the conflict. In this case the resolution can be in the direction of approach or avoidance depending on the valence of the new information.

Goal-conflict resolution also involves increases in attention and arousal. It is not clear if the hippocampus is important for these outputs. The amygdala for example, seems to play a more important role than the hippocampus in arousal during goal-conflict resolution (McNaughton & Corr, 2004).

1.4 Goal-conflict as hippocampal avoidance that recruits anxiolytic sensitive theta activity-an implication of the theory of the BIS

As suggested in the previous section, the hippocampus resolves goal-conflict by first inhibiting overt responses and then increasing existing simple avoidance tendencies. The idea that it has a role in some form of behavioral inhibition is not novel (Douglas, 1967; Kimble, 1969) but the specific mechanisms proposed by Gray (1982) are unique.

Gray (1982) saw the rodent hippocampus as the core of a neural system involved in behavioral inhibition. He named this system the "Behavioral Inhibition System" (BIS). In Functional Magnetic Resonance Studies (*f*MRI), the human hippocampus has been implicated in mechanisms compatible with those assumed to underlie behavioral inhibition in Gray's (1982) theory of the BIS (Anderson, et al., 2004; Caplan, McIntosh, & De Rosa, 2007; Depue, Curran, & Banich, 2007; Kumaran & Maguire, 2006, 2007a, 2007b; Milad, et al., 2007). For example, Caplan, McIntosh and De Rosa

(2007) found recruitment of a network including the medial septum/diagonal Band of Broca (MS/DB) nuclei of the basal forebrain and the right hippocampus in a proactive interference task. Activations in the right hippocampus co-varied with the MS/DB when the task demands required inhibition of a pre-potent response to a non-target that was previously a target. The MS/DB controls hippocampal theta rhythm, 4-12 Hz brain oscillations that are predominant in the rodent hippocampus (Bland, 1986). MS/DB and hippocampus co-activations could reflect the induction of theta rhythm, to facilitate the resolution of the conflict arising from concurrently activated tendencies to respond to and inhibit the non-target.

Gray (1982) also saw the hippocampus as a key target of anxiolytic drugs. He thus assessed the effects of anxiolytics on hippocampal theta in rodents. By the 2000 version of the BIS theory (Gray and McNaughton, 2000), it had been demonstrated that anti-anxiety drugs share common behavioral effects with hippocampal lesions (see discussion in appendix 1 and appendix 8 in Gray and McNaughton, 2000). It had also been shown that all classes of anti-anxiety drugs appear to produce similar changes in hippocampal theta (Coop & McNaughton, 1991; Coop, McNaughton, & Scott, 1992; Coop, McNaughton, Warnock, & Laverty, 1990; McNaughton & Coop, 1991; McNaughton, Kocsis, & Hajos, 2007; Zhu & McNaughton, 1991a, 1991b, 1994a, 1994b, 1994c, 1995a, 1995b, 1995c)

A key characteristic of the BIS was clarified in the 2000 version of the BIS theory, which was implied in Gray's (1982) original version. Gray and McNaughton (2000) now saw hippocampal behavioral inhibition as a form of inhibition specific to goal-conflict (see also McNaughton & Corr, 2004). This is conceptually important. Taken together with the responsiveness of hippocampal theta to anxiolytic actions, this suggests that anxiolytics may target only goal-conflict related avoidance behaviors.

Existing pharmacological and ethological studies on rodents support this idea. Anxiolytic drugs appear to affect only goal-conflict related avoidance behaviors while panicolytic drugs appear to affect simple avoidance related behaviors (Blanchard & Blanchard, 1988; Blanchard, Griebel, & Blanchard, 2003; Blanchard, Griebel, Henrie,

& Blanchard, 1997; McNaughton & Corr, 2004). In humans, the distinction is debatable (Fowles, 2000) but evidence of it has emerged (Perkins, Kemp, & Corr, 2007). Perkins, Kemp and Corr (2007) found evidence of separate personality constructs for anxiety and fear, which are currently viewed as the emotional dimensions of goal-conflict related avoidance and simple active avoidance respectively (Corr & Perkins, 2006; McNaughton & Corr, 2004).

1.5 Implications of the rodent BIS for humans

The theory of the BIS (Gray and McNaughton, 2000) is fundamentally an animal model and it is not yet clear if a human BIS exists in the same form (although it is clear that anxiolytic drugs have similar actions in humans and other animals). The identification of a class of avoidance behaviors that could be the target of anxiolytic actions could have important clinical implications. In particular, for the treatment of deficits in goal-conflict related avoidance. Many disorders such as Attention Deficit Hyperactivity Disorder (ADHD) (Clark, et al., 2007; Liotti, et al., 2007), mood and personality disorders (Craske & Waters, 2005; Gray and McNaughton, 2000; Nigg, Silk, Stavro, & Miller, 2005; Shulman, 1997) are associated with deficits in avoidance behaviors. The causes of these deficits are unclear. Goal-conflict could be used as a diagnostic tool. It can assess the likelihood a patient with avoidance deficits would respond well to anxiolytics. This would help clinicians make more informed decisions in selecting the appropriate drugs for their patients. However, separating goal conflict processing from the simple approach and simple avoidance processing in which it is embedded is not straightforward.

1.6 The role of rodent hippocampal theta in goal-conflict processing

In the theory of the BIS (Gray & McNaughton,(2000), hippocampal theta is crucial for efficient transmission of information during goal-conflict resolution. McNaughton, Ruan and Woodnorth (2006) recently showed that restoration of hippocampal theta-frequency rhythmicity restored learning in rodents even though it did not restore the normal cell firing patterns. This suggests that hippocampal theta may have functional significance crucial to efficient goal-conflict processing. However, its function could be equally important for other processes. In rodents, hippocampal theta has been

implicated in sensorimotor integration, sensory and memory processing (Bland & Oddie, 2001; Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999; O'Keefe & Nadel, 1978; Sainsbury, 1998). So hippocampal theta is not specific to goal-conflict processing and is recruited by multiple neural systems.

1.7 Difficulties in using human hippocampal theta as an index of goal-conflict

In rodent studies, 4-12 Hz rhythm recorded from the hippocampal system is referred to as theta. Theta rhythm in rodents is defined more by its source (the hippocampus) than by its frequency band. This is because it was first discovered in the hippocampus (Arduini, Arduini, & Green, 1953) and has a clear cellular source. Reference to "theta rhythm" in rodent studies is often analogous to "hippocampal theta rhythm" but it has also been recorded in cortical (Bilkey & Heinemann, 1999; Jones & Wilson, 2005) and other sub-cortical regions (Kirk & McNaughton, 1993; Kirk, Oddie, Konopacki, & Bland, 1996). In contrast, we generally refer to rhythmic activity in humans by its frequency bands since the cellular sources cannot be easily identified. In human studies, theta is generally referred to as 4 to 7 Hz, alpha as 8 to12 Hz and beta as 12 to14 Hz rhythmic activities. The frequency limits between bands can vary slightly across studies. On some occasions, it is more appropriate to define them according to their functional response to the experimental tasks (Klimesch, 1999). For the current thesis, the rodent convention of treating 4-12 Hz rhythm as a functional class of activity is adopted. Theta is taken to potentially refer to 4-12 Hz rhythmic activity unless specified. Whenever possible, frequencies will be clearly specified.

It has been difficult to record 4-12 Hz rhythmic activity from the human hippocampus. Recently, Ekstrom et al. (2005) were the first to demonstrate 3-12 Hz task-related rhythmic activity in the human hippocampus. The activity was observed during virtual navigation. Previously, rhythmic activity recorded from the human hippocampus within this frequency range was not related to behavioral changes. For example, 4-7 Hz rhythm was recorded during sleep (Cantero, et al., 2003) and 7 Hz activity was elicited by hypothalamic stimulation (Sano, 1970).

The conclusive demonstration of task-related human hippocampal rhythm was only possible with intra-cranial electroencephalography (iEEG). Electrode placements in iEEG studies are decided on the needs of the patients and so are not standardised. For clinical purposes, depth electrodes, which provide the most accurate information on the source of EEG, are rarely used. Even when depth electrodes are used, they may not be implanted in the hippocampus for clinical reasons. Experimental studies with iEEG are also costly and time-consuming. Studies are scheduled according to the availability of patients and their surgical needs. Consequently, it is unlikely that iEEG will become a mainstream research technique. *f*MRI is a logical alternative but it does not provide information on brain rhythms, which could be a crucial form of brain processing. The scientific and clinical implications of hippocampal theta rhythm, and brain oscillations in general, have sustained research on their roles despite the recording difficulties in humans and the advent of *f*MRI (Buzsaki & Draguhn, 2004; Kahana, 2006).

1.8 Assessing human goal-conflict activity – superficially recorded theta as a theoretically driven dependent variable

Recording EEG superficially from the human scalp is non-invasive, less expensive and more easily available than iEEG. It is commonly used to assess human rhythmic activity. In the current work, superficial EEG is used to try and assess human goal-conflict activity. Superficially recorded human EEG is unlikely to include electrical components from human hippocampal rhythmic activity as the hippocampus is buried within the cortex. Evidence of human cortical generators of 4-12 Hz activity also suggests that 4-12 Hz activity recorded superficially can be independent of the human hippocampus (Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999; Ishii, et al., 1999; Raghavachari, et al., 2006; Tuladhar, et al., 2007; Tzur & Berger, 2007). Additionally, human cortical theta activity, like rodent hippocampal theta, has been implicated in various processes such as memory, sensory and motor processing (Kahana, 2006; Klimesch, 1999; Mizuhara & Yamaguchi, 2007). In both humans and rodents, theta activity itself is not specific to goal-conflict processing (it is necessary but not sufficient for correct goal-conflict functioning) and appears to be a form of processing recruited by multiple neural systems.

However, theta is important for transmitting hippocampal output during goal-conflict resolution. Hence, the likelihood of detecting coherent theta activity between the human hippocampus and the cortex should increase during goal-conflict resolution. This suggestion is supported by evidence of coherent theta activity between the hippocampus and cortical regions in both humans and rodents. Ekstrom et al. (2005) found correlations between human hippocampal and cortical rhythms in the 4-8 Hz range during virtual navigation (correlations of 9-12 Hz activity were not examined but electrodes in the hippocampus and cortical regions showed significant activations at these frequencies during virtual navigation). So if a rodent-like human hippocampal rhythm exists, it should be possible to detect its modulation of cortical rhythms with superficial EEG. In rodents, Jones and Wilson (2005), Siapas, Lubenov and Wilson (2005), and Young and McNaughton (2008) have also reported coherent 4-12 Hz rhythmic activity between the hippocampus and cortical regions. In particular, Siapas, Lubenov and Wilson (2005) found evidence suggesting prefrontal activity was modulated by hippocampal output (the prefrontal rhythm occurred later than hippocampal rhythm). And critically, Young and McNaughton (2008) showed that the rodent cortex and hippocampus could also show theta oscillations independently of each other.

Although scarce, there is evidence linking human superficial theta activity to goal-conflict. To date, a study by Moore, Gale, Morris and Forrester (2006) appears to be the only systematic attempt to examine goal-conflict processing and human cortical theta activity. Unfortunately, the effects of goal-conflict were confounded with simple inhibition. They observed higher theta activity (averaged 4-7 Hz) across a wide selection of scalp electrodes during inhibition of stronger pre-potent responses. In their paradigm, both goal-conflict specific inhibition and simple inhibition activity increased steadily across experimental conditions. The two effects were therefore not separable. However their findings suggest a possible link between goal-conflict and human cortical theta.

Although not intended as a study on goal-conflict, Cohen, Elger and Ranganath (2007) obtained findings that linked increased superficial theta activity (4-7 Hz) with goal-

conflict. Participants had to choose between a left or right target on the computer screen. The probability of the left versus the right target producing wins and losses (of the same value) differed across three conditions as follows: a) 75:25; b) 50:50 and c) 25:75. In the 50:50 condition, both targets were equally likely to produce wins/losses of the same value. According to Gray and McNaughton's (2000) theory of the BIS, goal-conflict should therefore be maximal in the 50:50 condition. Cortical theta activity showed a relative increase in the 50:50 condition during feedback of a loss but not feedback of a win (see fig 7 in Cohen 2007, only data at scalp electrode Fz was available). This is consistent with Gray and McNaughton's (2000) view that the hippocampus amplifies punishment to resolve goal-conflict, and this view explains why there were no changes in theta for feedback of a win.

1.9 Hypotheses of the current thesis

To see if specific goal-conflict processing activity could be detected in humans, I tested the following three hypotheses.

1.9.1 Hypothesis 1— Goal-conflict represents a class of mechanisms that is distinct from simple approach/avoidance

Processing specific to goal-conflict was assessed by manipulating goal-conflict and simple avoidance/approach across three experimental conditions. Goal-conflict was created with the presentation of stimuli that elicit approach and avoidance tendencies concurrently. Approach and avoidance were balanced in the intermediate condition. Net approach and avoidance predominated in the adjacent conditions respectively. Given that approach and avoidance tendencies scale linearly across the three conditions, i.e., are maximal in the adjacent conditions, activity that peaks in the intermediate condition cannot be attributed to simple approach/avoidance. It can only be explained by the effect of goal-conflict, which increases as concurrently activated tendencies approximate each other and should be maximal in the intermediate condition. Goal-conflict was therefore assessed as the difference between activity in the intermediate condition and the average activity across the adjacent conditions (and was assessed via extraction of the orthogonal quadratic trend for significance testing).

1.9.2 Hypothesis 2— Goal-conflict processing recruits and increases cortical rhythmic activity within the same frequency range as rodent hippocampal theta (4-12 Hz)

Changes in task-related human EEG were recorded from 15 electrode sites. The superficially recorded EEG was Fast Fourier transformed into 0.5 seconds spectra power. Spectral powers for 4-12 Hz activity were extracted. Thus, variations across the three key experimental conditions described above were assessed via theta spectral power.

1.9.3 Hypothesis 3— Goal-conflict increases avoidance tendencies

Gray and McNaughton's (2000) view that goal-conflict is resolved via increasing punishment is tested by correlating goal-conflict specific theta activations with behavioral measures of avoidance. This measure assessed the contribution of goal-conflict (as opposed to simple approach and avoidance) to avoidance behaviors. Two experimental paradigms were used in the current work. The Stop-Signal Task (**SST**) was an existing experimental task. The task termed "**Choice**" was a new paradigm created for this project. Three variations of the **Choice** task were tested. In the **SST**, the time participants took to stop an overt response was estimated from the Stop-Signal Reaction Time (SSRT). Faster SSRTs measured increased avoidance tendencies. In the **Choice** task, the frequency participants avoided the potential monetary reward (due to the presence of potential loss) from a left click measured avoidance tendencies. Fewer left clicks indicated increased avoidance tendencies. These measures were tested for correlation with goal-conflict specific theta activity.

1.10 Organization of the chapters

Four experiments were conducted using the two paradigms described above to test the effects of goal-conflict. The **Choice** experiments were conducted first (this consisted of three experiments that were variations of the same paradigm). Given that they appeared to produce consistent right frontal activation in relation to conflict they were followed by the **SST**. The **SST** was chosen as previous work had implicated the right inferior frontal gyrus specifically (and so right frontal cortex more generally) in behavioural inhibition.

However results on the **SST** are reported first, below. It provides the clearest link between the EEG activation observed in the current thesis and previous work that indicates a likely neural source. It also involves the simplest, and so most easily interpreted, behavioural responding. However, there are caveats as to whether the **SST** effects detected could be interpreted as being specific to goal-conflict. These limitations are addressed by the **Choice** paradigm and so this is presented second as it follows on from the **SST** logically.

In chapter 2, the next chapter, the methods common to all four experiments are presented. Chapter 3 includes a description of the methods specific to the **SST**. It also includes a report of the SST results and a discussion of the limitations. In chapter 4, the methods specific to **Choice** experiment **1**, **2** and **3** are presented. Chapters 5, 6 and 7 include reports of the results and brief discussions for **Choice** experiment **1**, **2** and **3** respectively. Chapter 8 assessed if variations in evoked potentials could have contributed to variations in theta spectral power across the three key experimental conditions in the four experiments. In chapter 9, the concluding chapter, the implications of the current findings are discussed.

1.10.1 A final note

The idea that the BIS mediates a specific form of avoidance behavior, separable from simple avoidance behavior, raises an important question for personality (Corr, 2004). It raises the question if an existing personality dimension or trait reflects proneness to BIS avoidance. Identifying the personality dimension of the BIS is beyond the scope of the current thesis. However, personality measures most likely to show relations with BIS avoidance activity such as Eysenck's Neuroticism and Trait Anxiety (measured by Spielberger State-Trait Anxiety Inventory) were collected. These scores were correlated to goal-conflict activations observed in the current thesis. The results are reported in the results section for each experiment for readers interested in the neuropsychological basis of personalities, but will not be discussed further.

2 General Methods

The EEG recording and data processing procedure was identical across the four experiments. The methods are detailed below.

2.1 Participants

Participants were recruited from the University of Otago's "Student Job Search" programme and were paid for participating in the experiments except for participants in replication 2 of the Stop-Signal Task (**SST**). In replication 2 of the **SST**, participants participated voluntarily as part of a practical class requirement. These students were enrolled in a Biopsychology course.

2.2 Apparatus/Materials

2.2.1 Stimuli presentation

The presentation of the stimuli and other aspects of the experiments (including EEG recording) were controlled by a purpose-built programme in Visual Basic 6. The experiments were run on an IBM personal computer with a 14 inch cathode-ray tube (CRT) monitor.

2.2.2 Questionnaires

The Eysenck Personality Questionnaire-Revised (EPQ-R) (Eysenck & Eysenck, 1991)and the Spielberger State-Trait Anxiety Inventory (STAI) (Spielberger, 1983) were administered.

2.2.3 EEG recording

Electro-caps (Electro Cap International, USA) mounted with pure tin electrodes were used for recordings. Three caps, large (580-620 mm), medium (540-580 mm) and small (500-540 mm) were used to accommodate different head circumferences. The electrodes on the caps were positioned according to the International 10-20 electrode placement system. EEG data were recorded from F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6. EEG was also recorded from Fp1, to detect the occurrence of

eye blinks (see section 2.4.1 on eye blink removal procedure). The electrodes were referenced to activity averaged across the two earlobes, recorded with clip-on pure tin ear electrodes (A1 and A2). Electrodes on the caps were filled with Electro Cap International Electro-Gel for recording purposes. Impedances were checked with a General Devices impedance meter (EIM 107-37A, USA). Mindset Model MS-1000 hardware (Nolan Computer Systems, USA) was used to capture, amplify and digitize the EEG signals. Bandpass filters were set to capture frequencies between 1.8 Hz-36 Hz. The EEG sampling rate was set to 128 Hz. EEG recording software controlling the MindSet was written in Visual Basic and formed part of the same program that controlled the experiments.

2.2.4 Testing areas

Participants were tested in body-protected areas. All the participants were tested in an 800 x 1800 x 2400 mm (length x width x height) booth except in the **SST**, half the participants in replication 2 were tested in an 1800 x 1800 x 2600 mm (length x width x height) room. In both areas, participants were seated in a dental chair. Adjustable neck supports were provided to minimize head movements.

2.3 Procedure

Participants were given basic information on the experiment via an information sheet (see appendices 1 and 2). They were asked to sign a consent form after any queries they had were clarified. Participants then filled out the STAI-Trait and EPQ-R questionnaires. They were encouraged to complete the questionnaires in about 20 minutes and not to deliberate over their answers. On average, the participants took about 15 to 25 minutes to complete the questionnaires. Next, participants put on the electro-caps. Impedances of the electrodes were checked and contact was improved where necessary. Impedances were lowered to 5 kohms or below. The whole process generally took about half an hour but could take up to 45 minutes if difficulties in lowering impedances were encountered. Participants were directed to the EEG recording area once the impedances were checked.

To ensure that the EEG recording set up was in proper working condition, tests were administered to assess the effects of eye blinks and of production of relaxation-induced alpha rhythm. In the eye-blink test, participants were told to blink at the onset of a symbol on the computer screen – this occurred every one seconds. For the alpha test, participants were told to close their eyes and relax. Each test lasted 10-seconds and one test of each sort was carried out. The resultant EEG was screened immediately for artifacts in the records.

Participants then filled out the STAT-State questionnaire before instructions on the experimental task were given. Participants filled out the STAI-State questionnaire again after the task. Participants also filled out the feedback forms on the task in the **Choice** experiments. Participants were then cleaned up, debriefed and thanked for their participation.

2.4 Data processing

2.4.1 EEG artifacts removal

Post processing was carried out using purpose built software written in Visual Basic. The data were first low-pass filtered (using a simple 3 point running mean) to reduce residual high frequency signals including 50 Hz electrical noise. They were then corrected for EEG artifacts by an automatic eye blink removal procedure developed by (McNaughton & Mitchell, 2006), followed by visual inspection and manual removal of the EEG segments that included uncorrected eye blinks and other artifacts such as eye movements and saccade.

The automatic eye blink removal procedure used an algorithm that detected EEG signals in Fp1 that matched a generic, flexible, eye blink template. The template captured the general ballistic properties of an eye blink. The parameters of the template were flexible, to account for variations between eye blinks and participants. Limits were set to make sure its properties conform to that of an eye blink.

Once the template had been fitted to the specific detected eye blink signal on Fp1, linear regression was used to determine the size and direction of the eye blink

component separately for each channel, in the form of a slope coefficient. The eye blink template was then adjusted in amplitude using the slope coefficient and subtracted from that channel to leave residual EEG for each channel.

More specifically, the procedure stepped through the Fp1 record, in one sample steps, until it detected a 40ms segment for which a linear regression delivered a mean above the average baseline and a slope of greater than 1.4μV/ms. It extrapolated this line back to the baseline. It then used a linear regression procedure to successively locate the next line segment (slope steeper than -1.4 μV/ms) descending to the baseline, descending below the baseline (slope steeper than -0.7 μV/ms) and returning to the baseline (no slope restriction) and, if present, two more line segments representing a final positive wave. Each portion of this straight line model of the eye blink was then smoothed until its fit with the actual eye blink was optimized in terms of maximum variance accounted for. The resultant optimised template was then tested for goodness of fit. If either the fit was less than 50% of the variance or was greater than the fit at the previous step the procedure was repeated for a further step. Provided the 50% variance threshold had been breached, the template with the best fit was then used to remove the eye blink from all channels, including Fp1. The same basic procedure was then repeated (using the processed Fp1 channel) with detection based on a 70ms segment with a slope steeper than -1.4 μV/ms. It is an advantage of this template procedure that it can remove an eye blink leaving clear residual EEG even on FP1, where the blink is detected, and does not remove any rhythmic components present at Fp1 from the EEG. Figure 2.1A shows an EEG record before automatic blink removal procedure. Figure 2.1B shows the residual EEG after the procedure.

After automatic eye blink removal, the original Fp1 record was reinstated to allow the experimenter to check the corrected record during subsequent visual inspection for manual removal of movement and muscle-related artifacts and for eye blinks that were uncorrected by the procedure. Uncorrected eye blinks were usually compounded with another blink or eye movements (see figure 2.1C). The recordings were also inspected for eye movements, saccade and other movement artifacts (see figure 2.1D for example of artifacts that were selected for exclusion). When artifacts were spotted by visual

inspection, although signals in some sites might appear unaffected, the EEG segments across all channels were replaced with missing data markers.

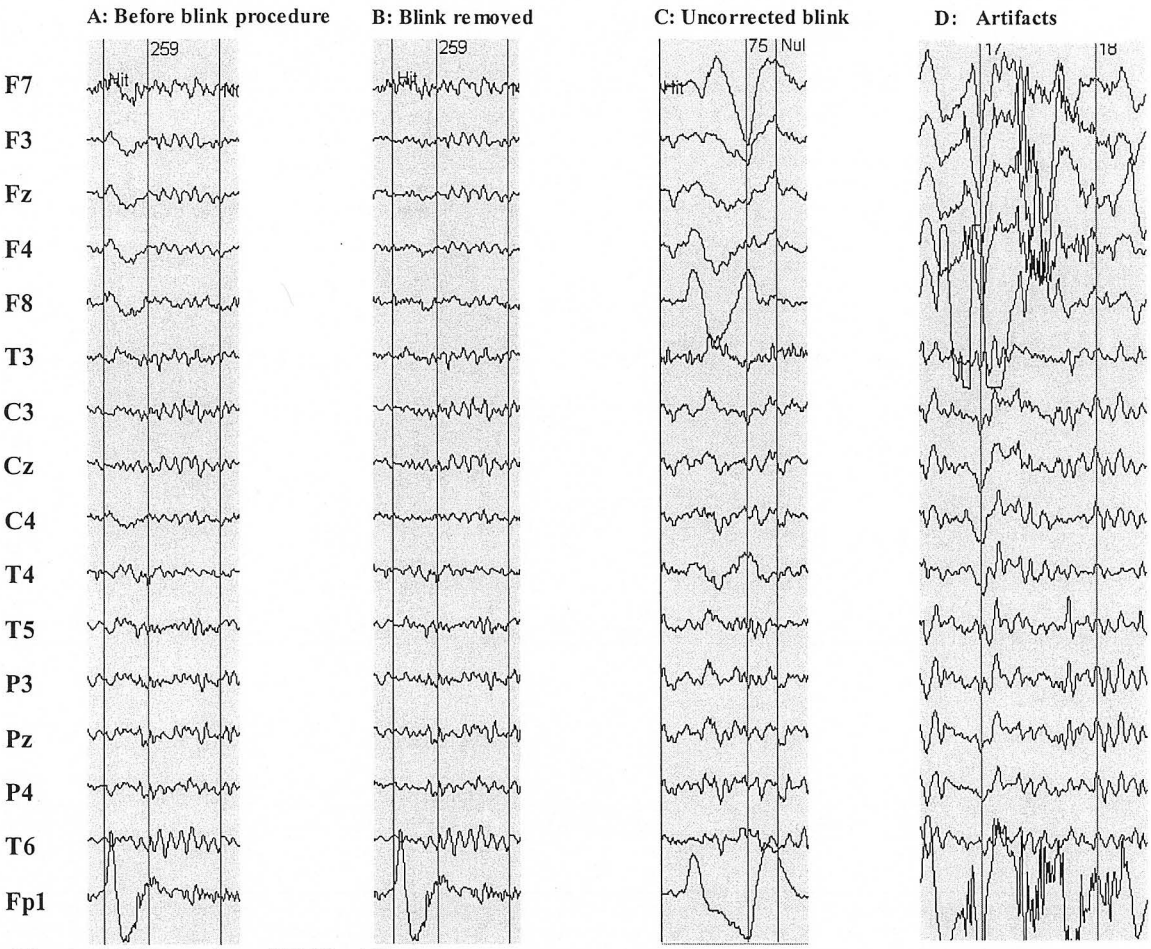

Figure 2.1 Examples of EEG artifacts
A. Original record before automated eye blink procedure. **B.** Record in 2A after blinks were removed. **C**. Eye blinks uncorrected by the automated procedure. **D**. Example of artifacts that were visually marked for exclusion.

In the **SST**, an additional step was included to further reduce the amount of data that had to be discarded due to eye movements and slow waves below 4 Hz. Fp1 (with eye blinks removed) was digitally low pass filtered to eliminate theta frequencies and above. The entire record was then fitted to each channel separately with least squares regression, scaled with the slope coefficient and subtracted from the channel to eliminate remaining low frequency artifacts.

2.4.2 Spectral power post-processing

Data were converted to microvolt values before power spectrum was assigned to the period of interest, which contained 0.5s of EEG. The spectrum was generated from a Fourier Transform of a 1s block of EEG, which had first been subjected to a Hanning window. The 1s contributing to the power spectrum consisted of the 32 samples preceding the start of the assigned 0.5s, the 64 samples during the 0.5s and the 32 samples following the end of the 0.5s. The Hanning window extracts maximum power from the central portion of the EEG analysed, with much less power being derived from the tails. Each power spectrum was then log transformed to normalise error variance before any averaging procedures. Where the EEG to be analyzed contained any missing data, the entire spectrum for that 0.5s period was set to missing data markers. With 128 EEG samples in each 1s block analyzed, the frequency resolution of the power spectrum was 1 Hz. Participants' individual trials containing spectral power were then averaged. When more than 30 % of the trials contributing to the average for any 0.5s power spectrum contained missing values, that average spectrum was replaced with missing data markers. Participants with more than 10% of their overall data replaced with missing data markers were excluded from the analyses.

2.5 Use of EEG (but not EOG) for eye blink removal

It is standard to reject eye blink artifacts by excluding the trials in which the blinks occur. This results in substantial loss of data. To reduce data loss, several methods have been developed to eliminate eye blink artifacts, leaving EEG components in the data (Gratton, 1998; Joyce, Gorodnitsky, & Kutas, 2004). These methods require the recording of EOG (electro-oculogram) with an additional two to four electrodes. The current EEG set up only allowed recording from a maximum of 16 electrodes. Recording EOG would reduce examinable sites in the current thesis significantly. An eye blink template matching approach, which did not require additional EOG electrodes, was developed to maximize the number of examinable sites. Although removal of eye blink components from EEG without using EOG is novel, the advantages of the method have led to systematic investigation of its feasibility. For example, Li, Ma and Lu (2006) demonstrated eye blink components removal without obvious distortion to the underlying EEG, without the use of EOG eye blinks.

Gratton (1998) has suggested that the use of only EEG without EOG to remove eye blinks makes the interpretation of large potentials ambiguous. This could be a particular concern for evoked potential studies since these potentials, like eye blinks, are also large compared to rhythmic activity in the EEG. Joyce, Gorodnitsky and Kutas (2004) raised an important issue in their discussion of an alternative method for eye blink removal. That is, "...algorithms are not expected to produce physically meaningful components unless their underlying assumptions present a good fit to the signal properties being estimated" (Joyce, Gorodnitsky & Kutas, 2004, p. 304). The assumptions underlying the current eye blink removal procedure are fitted to estimate rhythmic activities in the 4-12 Hz range. Admittedly, its use in evoked potential studies, where the interpretation of large potentials is important, could be incompatible. However, for the current purpose, it was an efficient way to reduce data loss and maximize the recording capabilities of the 16-channel EEG set up.

3 Goal-conflict in the Stop-Signal Task

3.1 Goal-conflict as a separable process from simple inhibition

The Stop-Signal Task (**SST**) (Logan, Cowan, & Davis, 1984) provides a measure of behavioural inhibition that is relatively uncontaminated by the additional processes involved in related tasks such as the Wisconsin Card Sorting Task, Task Switching, and the Go/No-Go paradigm. It has become an important test of simple behavioural inhibition. Go trials in the **SST** require a motor response to a standard stimulus such as an arrow. Stop trials require the inhibition of the pre-potent tendency to respond to the arrow when a stop signal, for example a tone, is presented. A Stop trial therefore always begins in the same way as a Go trial until the onset of the stop-signal.

The onset of the stop-signal in Stop trials elicits behavioral inhibition. It has consistently modulated activity in the right inferior frontal gyrus (IFG) in functional magnetic resonance imaging *(fMRI)* (Aron & Poldrack, 2006; Chevrier, Noseworthy, & Schachar, 2007; Rubia, et al., 2001). The stop-signal has also modulated changes in right frontal regions in evoked potential studies (Pliszka, Liotti, & Woldorff, 2000; Schmajuk, Liotti, Busse, & Woldorff, 2006). Although Go and Stop activities are independent processes initiated at different times (Boucher, Palmeri, Logan, & Schall, 2007), their time courses overlap in the **SST** after the initiation of the stop-signal. In this period, the co-activations of the incompatible goals of Going and Stopping should according to the BIS theory, activate goal-conflict-related behavioral inhibition processing.

When the stop signal is presented early, the probability of successfully stopping the motor response is high. When the stop signal is presented late, the probability of successfully stopping is low (Logan, et al., 1984). Thus Stop activation should predominate when the stop-signal is presented early while Go activation should predominate when the signal is presented late. Goal-conflict activity, on the other hand, should be minimal when the signal is presented early or late, where net Go and net Stop activations predominate respectively. The effect of goal-conflict should therefore peak

at intermediate Stop-Signal Delays (SSDs) when Stop and Go activations are approximately equal.

It is unclear if previous reports of right frontal activations elicited by the stop-signal included a component of goal-conflict. Therefore, I investigated goal-conflict activations by grouping Stop trials according to the relative level of goal-conflict likely to be operating in different trials (as a result of the variation in SSDs at which the tone is presented). Stop trials were grouped into early, intermediate and late SSD trials. It was predicted that goal conflict should increase EEG theta spectra power maximally at intermediate SSDs. As this could be done without modifications to the standard **SST**, I created a version intended to be identical to the one used by Aron and Poldrack (2006) to facilitate comparison across studies.

3.2 Methods

3.2.1 Participants

Participants were recruited from the University of Otago. The experiment was run in two replications. In replication 1, nine male and nine female students were recruited from the university's "Student Job Search" programme. They responded to an advertisement displayed by Student Job Search for a two-hour psychology experiment. Their age ranged from 18 to 22 years. They were each paid $20 for participating but received no monetary reward or punishment during the task. In replication 2, 13 male and 11 female students, who were enrolled in a Biopsychology course, participated voluntarily as part of the course's practical class requirement. Their age ranged from 18 to 33 years. None of the participants had received any psychological treatment in the past year according to their declarations in the consent forms. One participant was excluded from the data analysis of replication 2 as she was left-handed. With this exception, all participants considered themselves right-handed. The University of Otago Ethics Committee (Approval number: DP 10/07) approved the means of recruiting participants and other experimental procedures described below.

3.2.2 Apparatus/Materials

3.2.2.1 The Stop-signal task – Go trials

The **SST** was set up so as to be as far as possible identical to that used in Aron and Poldrack (2006). This was achieved with assistance from A. R. Aron (email communications, 2007) which included his supplying us with the computer code used to control their task. At the start of each Go trial (see figure 3.1), a white fixation circle was presented in the centre of the screen against a black background. 500 ms later, a white arrow appeared in the circle. A left arrow (<) was a prompt to make a left mouse click and a right arrow (>), a prompt to make a right mouse click. If no response was made 1000 ms after the onset of the arrow, the stimuli disappeared and the inter-trial interval began. When a response was made within 1000 ms, the interval remaining in the 1000 ms period was added to the inter-trial period, which was fixed for that trial, regardless of when the response was made. The inter-trial intervals were sampled from an exponential distribution that was cut off at 4 s. The interval was 1 s on average and ranged from 0.5 s to 4 s.

3.2.2.2 The Stop-Signal Task – Stop trials

A Stop trial was exactly like a Go trial except that a 1000 Hz tone lasting 500 ms was also presented. The tone was a prompt to withhold responding to the arrow. The interval between the onset of the arrow and the onset of the tone – the Stop-Signal Delay (SSD) – was systematically varied between trials. The SSD increased or decreased in steps of 50 ms controlled by four separate "staircases". The four staircases started at 100, 150, 200 and 250 ms, respectively. On any particular trial, failing to inhibit a response would decrease the SSD and withholding a response successfully would increase the SSD by 50ms on the next trial that was controlled by the current staircase. The four staircases ran in parallel with each other. They were pseudo randomly assigned to Stop trials so that each staircase moved eight times within a block of trials that consisted of 32 Stop trials and 96 Go trials. There was one Stop trial in every four trials. Altogether, there were 3 blocks of trials interleaved with rest breaks with no time limit. The rule governing staircase movement generated a tendency for responding to converge on a 50 % probability of inhibition ($P_{inhibit}$), i.e. participants were equally likely to make or withhold a response once the SSD values had converged

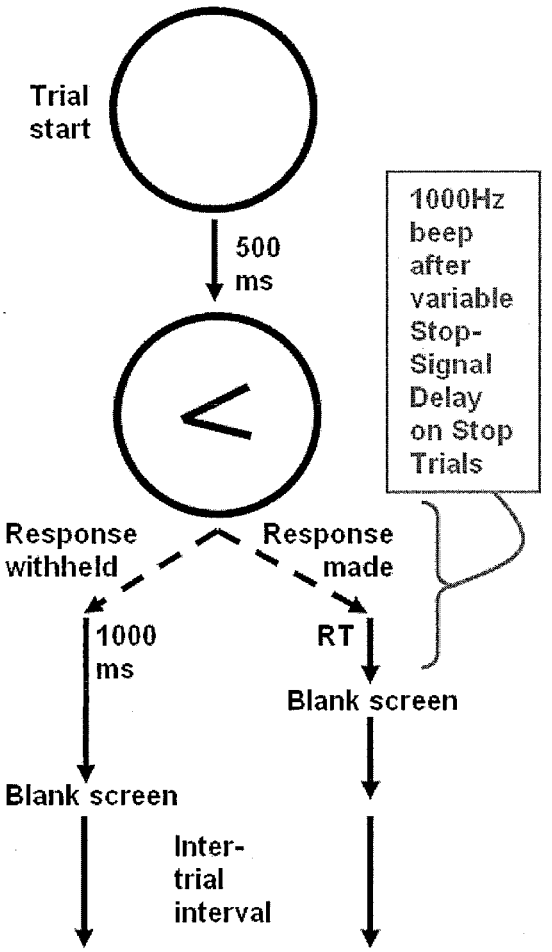

Figure 3.1 SST Events in a trial.
In a Go trial, participants were to make a left mouse click if a left arrow was presented. They were to make a right mouse click if a right arrow was presented. A Stop trial is identical to a Go trial except for the onset of a 1000Hz beep. The beep was presented at variable delays and prompted the participant to withhold a mouse click **Note**: In the actual experiment, the background was black and ink color was white as opposed to white background and black ink shown in this figure.

to a stable average. This occurred by the last 12 moves of each staircase in the study by Aron and Poldrack (2006) as well as in the current experiments.

3.2.3 Procedure

In replication 1, the Eysenck Personality Questionnaire-Revised (EPQ-R) and the Spielberger State-Trait Anxiety Inventory (STAI) were administered when participants arrived at the laboratory, together with the information sheet and consent form, before preparation for the EEG recording. In replication 2, participants filled these out in their own time before coming to the laboratory. The same **SST** instructions used by Aron and Poldrack (2006) were presented on the computer screen. They read

> Remember, respond as FAST as you can once you see the arrow. However, if you hear a beep, your task is to stop yourself from pressing. Stopping and Going are equally important.

Participants had 12 practise trials (this included three Stop trials) before moving on to the actual test. It was emphasized to the participants that they should try not to slow their responses in order to withhold a response successfully.

3.2.4 Data processing

3.2.4.1 Behavioral data

Each participant's number, age, gender and handedness were recorded. Trial and block number, trial type (Go or Stop), SSD values, reaction times, staircase index (1-4), staircase moves for each staircase, left/right/null responses and inter-trial intervals were also recorded for each trial. From these, three summary behavioural measures were calculated for each participant based on Aron and Poldrack's (2006) study: 1) median Go Reaction Time (Go RT (ms)) across all trials; 2) mean SSD (ms) over the last 12 moves for each of the four staircases, after responding stabilized at 50% $P_{inhibit}$; 3) Stop-Signal Reaction Time (SSRT (ms)) was computed by subtracting a participant's average SSD from his median Go RT (ms). To check for stable estimates of SSD values, the averaged value of the SSD values from the first and second staircases and that of the third and fourth staircases were correlated. To ascertain that $P_{inhibit}$ had

indeed converged at 50%, the $P_{inhibit}$ of the four staircases in the last 12 moves were calculated.

To determine trials with SSD values that produced maximal conflict for each participant, the 48 Stop trials (four staircases x 12 moves) in the period after $P_{inhibit}$ converged at 50% were arranged in ascending SSD for each participant. The trials were then divided into those with early, intermediate and late SSDs. Trials with the same SSD values were banded together. As a result, the number of trials in each band was unbalanced for some participants. The number of trials in each band ranged from 8 to 21 trials. The $P_{inhibit}$ for the early, intermediate and late SSD trials were then calculated.

3.2.4.2 Spectral power post-processing – Stop trials

The 0.5s period after the tone in a Stop trial was assigned a power spectrum. The early, intermediate and late SSD trials obtained in the period after responding had converged at 50% $P_{inhibit}$ were then averaged separately.

3.2.4.3 Spectral power post-processing – Go trials

For every Go trial preceding a Stop trial, the same procedure was repeated for the 0.5s period at which the tone was presented in the matching Stop trial. If the trial preceding a Stop trial was also a Stop trial, the Go trial following this Stop trial was used instead.

3.2.5 Statistical analyses – Analysis of variance (ANOVA)

In the current study, the ANOVAs included extraction of orthogonal polynomial contrasts (Snedecor & Cochran, 1967). They were performed with the GenStat statistical package (GenStat, VSN International Ltd, UK) which interpolated missing values and adjusted degrees of freedom for missing values.

A factor of SSD (Stop-Signal Delay) was extracted with three levels: early, intermediate and late SSD trials. The intermediate SSD trials represented maximum conflict with the two other SSD trials representing less conflict. The contribution of conflict was therefore extracted as the orthogonal quadratic contrast of SSD. Given that SSD has only three levels, the "quadratic" component in this case can be thought of as

representing the difference between the intermediate (conflicting) condition and a value obtained by averaging the two adjacent conditions. The term "quadratic" is, therefore, descriptive and does not imply the presence of any underlying quadratic function. A linear contrast of SSD was also extracted to assess proportionate variation with the three levels of SSD.

We extracted a factor of SITE as the variation in log power across the 15 electrodes included in our analyses. We extracted a factor of FREQ as the variation in log power at different frequencies (4 Hz –12 Hz). We extracted a factor of TYPE as the difference between Stop and Go trials. We also extracted a factor of REPL as the variation between replication 1 and 2.

3.2.6 EEG data exclusion

The GenStat statistical package uses a recursive algorithm to estimate values for missing data in its ANOVA calculations. For stable interpolations of missing values, the data to be analysed should contain no more than 10 % of missing values. To determine the percentage of data that were missing, I ran separate ANOVAs on each participant extracting the effect of SITE, SSD, FREQ and TYPE. These analyses were carried out only to determine the missing degrees of freedom. A participant was excluded when the number of degrees of freedom that were missing was more than 10% of the total number of degrees of freedom. As a result of this procedure, I excluded one participant (out of 18) from replication 1 and four participants (out of 24) from replication 2. As noted previously, one more participant from replication 2 was excluded because she was left-handed.

3.3 Results

3.3.1 Behavioral results

The median reaction times in the Go trials, averaged across the two replications, (standard deviation in brackets) was 452.76 (97.20) ms. The averaged Stop-Signal Reaction Time (SSRTs) was 202.00 (65.00) ms. The averaged SSD for staircases 1 and 2 was 246.24 (135.45) and that for staircases 3 and 4 was 258.43 (149.89). Out of the final 48 Stop trials of the **SST**, the intermediate SSD trials produced 50 % $P_{inhibit}$; early

SSD trials produced 75% $P_{inhibit}$ and late SSD trials produced 27% $P_{inhibit}$. When the same 48 SSD trials were averaged together, consistent with Aron and Poldracks' (2006) study, the overall $P_{inhibit}$ was 50%.

3.3.2 EEG: replication

The initial analysis detected no differences between the two replications. Hence only the combined results are presented below.

3.3.3 EEG: Stop minus Go (compared across SSD)

In this analysis, I subtracted Go trial activity from Stop trial activity. The conflict effect represented by a quadratic trend assessed the difference in spectral power between the intermediate SSD and the average of the early and late SSD. Figure 3.2A shows the variation of the quadratic trend in the 4-12 Hz frequency range across the recording sites. At the frontal midline site Fz, and the frontal right electrodes, F4 and F8, the largest conflict effect was observed at the intermediate frequencies 7 Hz and 8 Hz (site x SSD x type x freq, site x quad x type x quad, $F(14, 25200) = 1.82$, $p < 0.05$, see table 3.1 for F ratios of individual recording sites). F3 may show similar effects at 6-8 Hz but these are not reliable. A few other recording sites such as Cz, Pz and P4 also appeared to show relative increases for the intermediate SSD but these occur at sporadic frequencies and are not statistically reliable.

In a post hoc analysis restricted to averaged 7-8 Hz power, as expected, the conflict effect varied across recording sites (site x SSD x type, site x quad x type, $F(14,1575) = 1.97$, $p < 0.05$). Notably, only F4 (SSD x type, quad x type, $F(1,105) = 6.49$, $p < 0.05$) and F8 (SSD x type, quad x type $F(1,105) = 5.35$, $p < 0.05$) showed significant conflict activations. The effect at Fz was non-significant in this sub-analysis.

Note that Stop-Go activity averaged across recording sites showed a proportionate increase with SSD at 4 Hz and 5 Hz activity at the higher frequencies did not appear to show a steady trend (SSD x type x freq, lin x type x lin, $F(1, 25200) = 4.87$, $p < 0.027$). This was the only reliable linear effect of SSD detected in the current study.

3.3.4 EEG: Go only

A positive difference between Stop and Go trials could result from a decrease in Go trials as much as an increase in Stop trials. Thus, significance testing of the effect of SSD at Fz, F4 and F8 in the Go trials (effectively time within trial as the stop signal was not presented) and Stop trials were carried out respectively. In the Go trials (see figure 3.2B), conflict activation was observed at recording site F8, at the lower frequencies, 4 Hz, 5 Hz and 6 Hz, and at the higher frequencies, 11 Hz and 12 Hz. The intermediate frequencies, 7 Hz and 8 Hz showed the opposite trend (F8: SSD x frequency, quad x quad, $F(1,840) = 14.5, p < 0.001$). A similar trend was observed at Fz and F4 (Fz: SSD x freq, quad x quad, $F(1,840) = 4.62, p < 0.05$; F4: SSD x freq, quad x quad, $F(1,840) = 4.95, p < 0.05$).

3.3.5 EEG: Stop only

In the Stop trials, although not statistically reliable, conflict activations appear to occur at 7 Hz and 8 Hz at Fz, F4 and F8 (see figure 3.2C). It appears that the conflict effect observed in the Stop-Go analysis, although inflated by the suppression seen at 7 Hz and 8 Hz in the Go trials, could be taken to reflect genuine increases in Stop trial activity.

3.3.6 EEG: Stop minus Go (averaged across SSD)

Stop trial-related activity in the **SST** has previously been assessed simply via the average signal for all SSDs rather than via the conflict-specific component extracted above. To assess Stop trial theta spectra power in a way comparable to previous studies, I subtracted Go trials spectral power averaged across all SSDs from that of Stop trials (figure 3.3). Stop trials showed the largest relative increase at lower frequencies (4-6 Hz) in the frontal-midline and central sites (site x type x freq, site x type x lin, $F(14, 25200) = 4.8, p < .001$) (see table 3.1 for F ratios of individual recording sites).

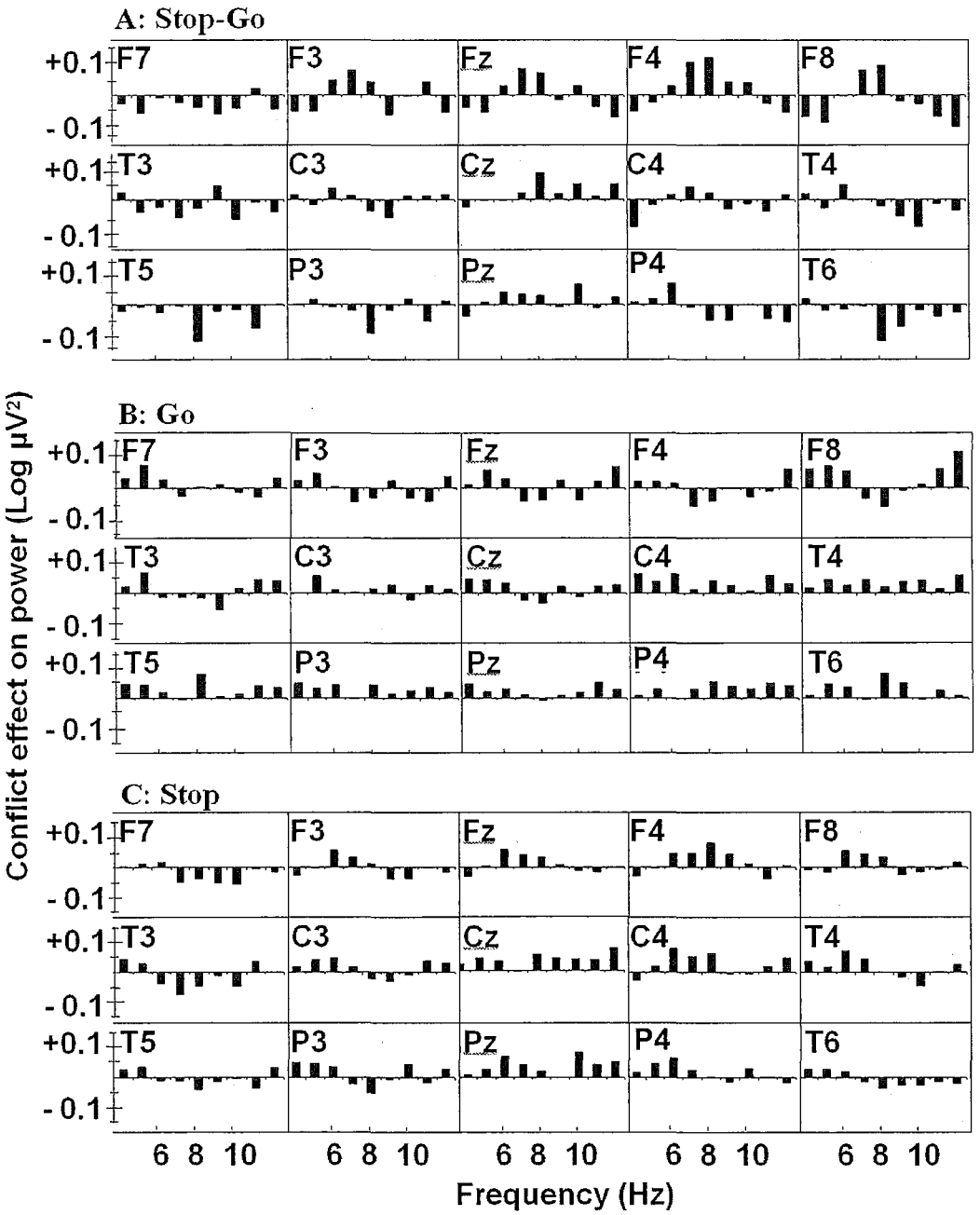

Figure 3.2 SST Variation in conflict-related 4-12 Hz spectra power for Stop-Go, Go and Stop activity Each bar represents the size of the difference between the intermediate SSD trials and the average of the early and late SSD trials as estimated by the quadratic trend of trials. Variations of this quadratic trend are shown for each of the nine frequencies (4-12 Hz) across the recording sites. **A.** The difference in quadratic trend between Stop and Go trials (Stop-Go). **B.** The quadratic trend for Go trials. **C.** The quadratic trend for Stop trials.

Table 3.1: Summary of statistics for individual recording sites obtained in post hoc analyses.

Recording sites	SSD x type x freq, quad x type x quad	type x frequency, type x lin
F7	$F(1, 1680) = 0.02, p = 0.886$	$F(1, 1680) = 14.23, p < .001$
F3	$F(1, 1680) = 2.58, p = 0.108$	$F(1, 1680) = 41.38, p < .001$
Fz	$F(1, 1680) = 5.73, p < 0.05$	$F(1, 1680) = 44.58, p < .001$
F4	$F(1, 1680) = 9.24, p < 0.05$	$F(1, 1680) = 57.25, p < .001$
F8	$F(1, 1680) = 10.04, p < 0.05$	$F(1, 1680) = 11.29, p < .001$
T3	$F(1, 1680) = 0.05, p = 0.820$	$F(1, 1680) = 54.71, p < .001$
C3	$F(1, 1680) = 0.47, p = 0.495$	$F(1, 1680) = 102.77, p < .001$
Cz	$F(1, 1680) = 0.49, p = 0.482$	$F(1, 1680) = 85.4, p < .001$
C4	$F(1, 1680) = 0.94, p = 0.332$	$F(1, 1680) = 108.03, p < .001$
T4	$F(1, 1680) = 0.1, p = 0.754$	$F(1, 1680) = 74.12, p < .001$
T5	$F(1, 1680) = 0.43, p = 0.512$	$F(1, 1680) = 55.01, p < .001$
P3	$F(1, 1680) = 0.6, p = 0.438$	$F(1, 1680) = 65.71, p < .001$
Pz	$F(1, 1680) = 0.45, p = 0.505$	$F(1, 1680) = 74.41, p < .001$
P4	$F(1, 1680) = 0.0, p = 0.978$	$F(1, 1680) = 70.27, p < .001$
T6	$F(1, 1680) = 1.25, p = 0.264$	$F(1, 1680) = 66.1, p < .001$

The second column assesses the effect of conflict as the difference in the orthogonal quadratic component of SSD between the two types of trial (Stop and Go) as plotted in figure 3.2A. The third column assesses the effect of inhibition (as the difference between the two types of trial) averaged across all SSDs as plotted in figure 3.3

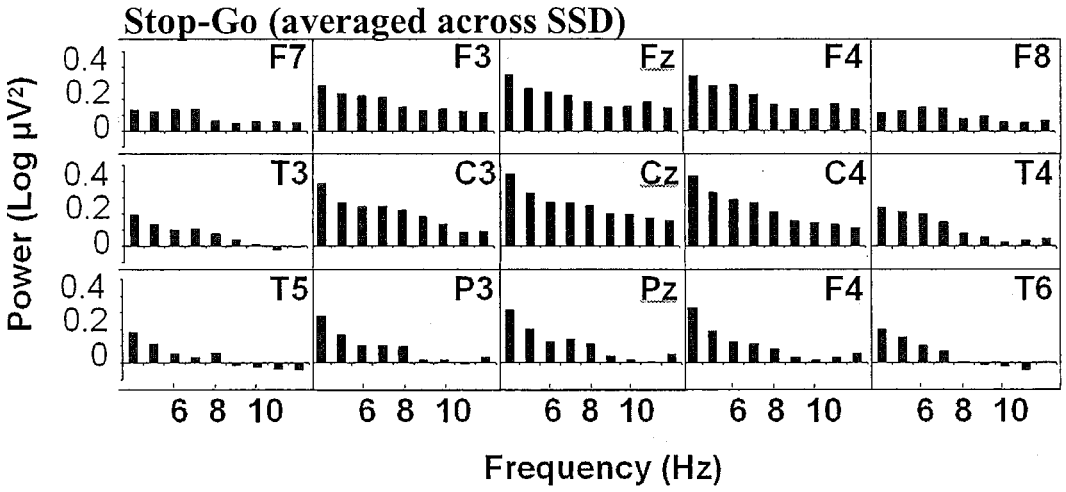

Figure 3.3 SST Variation in 4-12 Hz spectra power averaged across all SSDs across recording sites for Stop-Go activity.

3.3.7 Stepwise regression analyses

Conflict activations measured by the difference between the intermediate SSD and the average of the early and late SSD trials were extracted for individual participants, for frequencies at which reliable activations were observed. Hence, Stop-Go conflict activity for 7 Hz and 8 Hz at Fz, F4 and F8, and Go conflict activity for 4 Hz, 5 Hz, 6 Hz, 11 Hz, 12 Hz at F8 were included as predictor variables in the stepwise regression analyses. Separate stepwise analyses were carried out with Stop-Signal Reaction Times (SSRT), median go times, Speilberger Trait Anxiety (STAI-T) and Eysenck Neuoroticism (N) as dependent variables respectively.

No reliable correlations were observed.

3.4 Discussion

Goal-conflict activity was assessed as the difference between theta power at intermediate SSDs and the average of the activity at early and late SSD trials. At the medial frontal region Fz, and right frontal regions F4 and F8, the difference between Stop and Go activity, representing conflict activation, peaked at 7 Hz and 8 Hz. Stop-Go activation was assessed as the difference in activity immediately following stop-

signal presentation compared to the same time point in the immediately preceding Go trial. This ruled out a contribution from those processes associated with the presentation of the Go signal and preparation and execution of the Go response and any anticipatory activity in expectation of a stop response.

Although Fz, F4 and F8 Stop activity also appeared to show increases in conflict activity, these changes were not reliable. However, reliable Go trials conflict activity was observed at the right frontal site F8, at 4 Hz, 5 Hz, 6 Hz, 11 Hz and 12 Hz.

There are several caveats to interpreting maximal activation in the intermediate SSD trials as being specific to goal-conflict. Firstly, the interpretation of increased activity in the intermediate SSD trials, relative to the adjacent trials, as processing specific to goal-conflict rests on an assumption that simple Go and Stop tendencies scale linearly with SSDs. In early SSD trials, if Go processes were not yet initiated by the onset of the stop signal, due to a lack of attention for example, there could be no inhibitory activity. Successfully stopping in this case was due to a lack of motor output rather than inhibition of an initiated motor output. In the late SSD trials, if Go processes were completed before the onset of the stop-signal, there may not be inhibitory activity. In this case increased Stop-Go activity in the intermediate SSD trials could simply reflect simple inhibitory activity.

Aron and Poldrack (2006) reported that activations in the pre-supplementary motor area, globus pallidus and subthalamic nucleus proportionately increased with SSDs in successful Stop trials. This suggests a mechanism that is sensitive to the time course of Go processes and increases inhibitory activation proportionately, as Go processes are closer to completion. In the present study, Stop-Go activity averaged across electrode sites showed a proportionate increase with SSD at 4 Hz and 5 Hz. Taken together with Aron and Poldrack (2006) findings, this supports the current claim that simple inhibition scales linearly with SSD.

Secondly, the observation of "conflict" activity in the Go trials also raised the possibility that factors other than goal-conflict could have contributed to peak

activations in the intermediate SSD trials. In Go trials, approach activity should predominate. Conflict activity was unlikely unless inhibitory activity was also concurrently activated. It is possible that a motivation for successful stopping led to an anticipation of the stop-signal in Go trials, and thereby generated anticipatory simple inhibitory activity (Chevrier, et al., 2007; Floden & Stuss, 2006). This would result in concurrent activation of going and at least preparation of stopping in a similar fashion and with an approximately similar time course to the Stop trials that immediately followed the selected Go trials. In addition, Go trials conflict activations were observed at the right frontal site F8, where putative Stop-Go conflict activations were observed. If the right frontal region F8 is important for conflict processing, it is likely that maximal activity observed in the intermediate SSD trials in the Go trials represented anticipatory goal-conflict activations.

However, the contribution of non-conflict related factors could not be definitely ruled out. For example, it is possible that activity in the intermediate SSD trials represented activity involved in response preparation immediately preceding response execution. Future assessment of the contribution of goal-conflict in the SST should include a control condition to assess anticipatory slowing in Go trials.

Lastly, the number of trials in each group of SSD trials was unbalanced. The number of trials in the early SSD trials could be twice as many as late SSD trials. The lowest number of trials included in the analyses was 8 compared to the maximum number 21. Eight is an unusually small number of trials in EEG analyses. This raised the chances of activity in a few trials being misrepresented as averaged activity.

The above issues raise doubts that the spectral power variations with SSD were specific to goal-conflict. They do not however, rule out the possibility that goal-conflict contributed to the variations. Importantly, as this related to the findings in the next few chapters, the lateral right frontal site F8 was consistently activated by goal-conflict. This raises the possibility that F8 activation observed in the current SST was specific to goal-conflict.

If F8 activation was specific to goal-conflict, it raises the possibility that right frontal activations in previous SST studies (Aron & Poldrack, 2006; Chevrier, et al., 2007; Rubia, et al., 2001) could include a component of goal-conflict. However, Aron and Poldrack (2006), whose version of the SST was used in the current experiment, found that right IFG activations (*f*MRI) did not vary with SSD in successful trials (they modeled successful stop trials with SSD as a parametric regressor). They found that the pre-supplementary motor area, the globus pallidus and the subthalamic nucleus were proportionately more active as SSD increased. This suggests that the lack of variation with SSD in the right IFG was unlikely to be caused by poor temporal resolution in the recording technique. The above results by Aron and Poldrack (2006) suggest that some aspects of goal-conflict related changes in theta activity might not be sufficiently large to be detected by *f*MRI signals.

When Stop-Go activity was assessed via the averaged activity of early, intermediate and late SSD trials, the frontal midline and central sites showed the highest Stop-Go activity compared to the lateral sites. This is consistent with previous reports of midline activations in the cingulate cortex and pre-supplementary regions in the **SST** (Aron & Poldrack, 2006; Chevrier, et al., 2007; Leung & Cai, 2007). However, there was no evidence of the right frontal dominance normally associated with the right IFG assessed in the same manner (via the averaged signals of SSDs). This again, suggests that some changes in goal-conflict related theta activity might not be sufficiently large to be detected by metabolic signals in *f*MRI.

4 The Choice paradigm –methods

4.1 Assessment of goal-conflict in the "Choice" paradigm

The next three experiments were based on a contrasting appproach to assessment of conflict – termed for short, the "**Choice**" paradigm.

The **Choice** paradigm used simple stimuli and responses, as with the **SST**, but controlled conflict more directly with gain or loss of money as positive and negative reinforcers, and without a time constraint on responding. Monetary gain of a left mouse click was held constant while varying the level of monetary loss with: a) net gain greater than loss so that participants ought to be motivated to make a left mouse click to gain cash; b) gain and loss equally balanced; and c) net loss greater than gain so that participants ought to be motivated to avoid making a left mouse click. Thus, both loss value and net value varied steadily across the conditions. Goal-conflict should be maximal in condition b) where the potential gain equaled loss.

Choice 1, **2** and **3** were variations of the paradigm described above. The methods are described here since they all involve the same basic procedure, to avoid repetitions. Deviations from general methods in each experiment will be specified. The rationale for each experiment, and the report and discussion of the results would be dealt with separately in the following chapters.

4.2 Participants

Participants were recruited from the University of Otago's "Student Job Search" programme. There were 30 participants (15 females and 15 males) in **Choice 1**, 52 participants (25 females and 27 males) in **Choice 2**, and 36 participants (19 females and 17 males) in **Choice 3**. The participants were between 19 and 25 years old. According to their declarations in their consent forms, none of them had received any psychological treatment in the past year. All of them considered themselves right-handed. They responded to an advertisement displayed by Student Job Search for a 2-hour psychology experiment. Participants in **Choice 1** were paid NZ$9.50 while

participants in **Choice 2** and **3** were paid NZ$10.25 per hour due to a rise in the legal minimum wage rate. Participants had the opportunity to make more than the advertised wages depending on their performance on the computer task in all the experiments. They were not aware of this until after their arrival at the laboratory. The Lower South Regional Ethics Committee (Approval number: OTA/04/03/019) approved the means of recruiting participants and other experimental procedures described below.

4.3 Apparatus/Materials

4.3.1 Behavioural stimuli and payoffs

Figure 4.1 illustrates the stimulus sequence presented on each trial. The payoffs for making a left click varied according to four payoff conditions in **Choice 1** and **2**. In **Choice 3**, the continuous reward condition was excluded. The payoff conditions were coded with colours (shaded areas in figure 4.1). The colour coding was not mentioned to participants. Continuous reward was coloured green (IBM colour &H00404000), the net rewarding condition aquamarine (IBM colour &H00808000&), the conflicting condition brown (IBM colour &H00404080&) and the net punishing condition dark purple (IBM colour &H00400040&). Practise trials were coloured grey (IBM colour &H80000004&). The stimuli were presented against a blue background (&H00800000&).

Each payoff condition was presented in blocks of 10 trials. A rest break was inserted between each 10-trial block. Eight 10-trial blocks from each condition were presented. The order of presenting the trial blocks was pre-determined and counter-balanced:

Choice 1 & 2	**Choice 3**
1234	234
4321	432
2143	243
3412	342
3241	324
1423	423
4132	432
2314	234

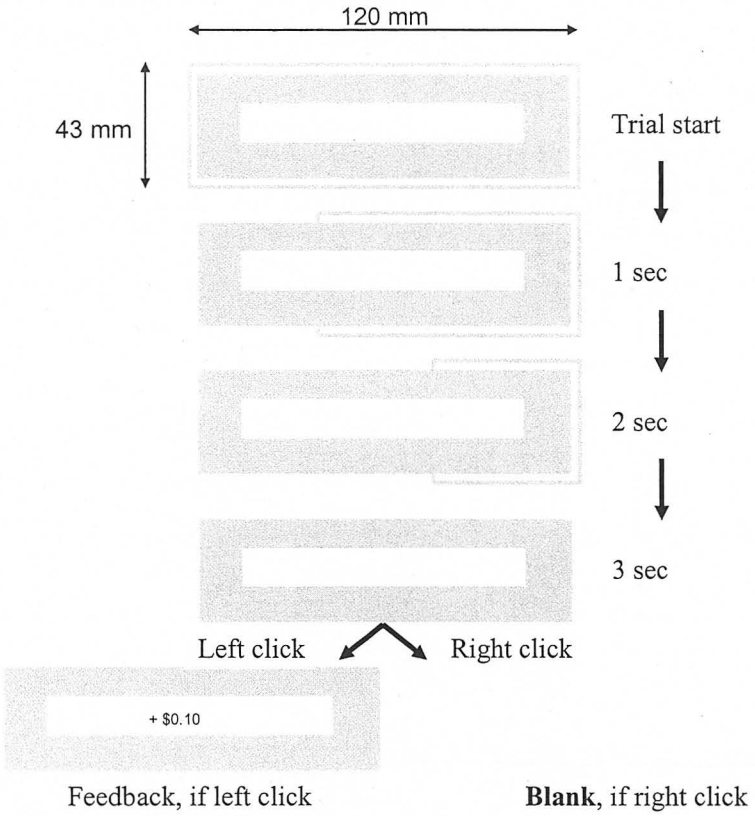

Figure 4.1 Choice Sequence of stimulus presented on each trial
After a left click, the feedback was presented for 2 s (in **Choice 3**, the countdown and feedback periods were shortened to 1 s). A blank screen was then presented for 2 s before a new trial began. After a right click, the blank screen was presented for 4 s before a new trial began. The interval between a click and the start of the next trial was the same with both left and right clicks even though a left click produced feedback and a right click did not. There was, thus, no time incentive for participants to either make a left or right click. Participants were not given details of the timing of the task components and were only informed that the computer task would take about 45 minutes (20 minutes for **Choice 3**).

For practise, participants were presented with 10 trials. For these trials, participants had an equal chance of either nominally gaining or losing 10 cents for making a left click (the payoffs were determined unpredictably by the computer program). The sum gained or lost on the practise trials did not contribute to their final pay.

Figure 4.2 shows the actual payoffs and the pre-determined sequences of the payoffs from a left click. Right clicks did not alter the programmed consequences of the next left click. Hence regardless of when a left click was made, participants with different response patterns received the same sequence of left click payoffs. In all three **Choice** experiments, the interaction of the gain/loss sequences with the payoff values produced,

on average over trials, a net gain in the rewarding condition, no gain or loss in the conflicting condition and a net loss in the punishing condition.

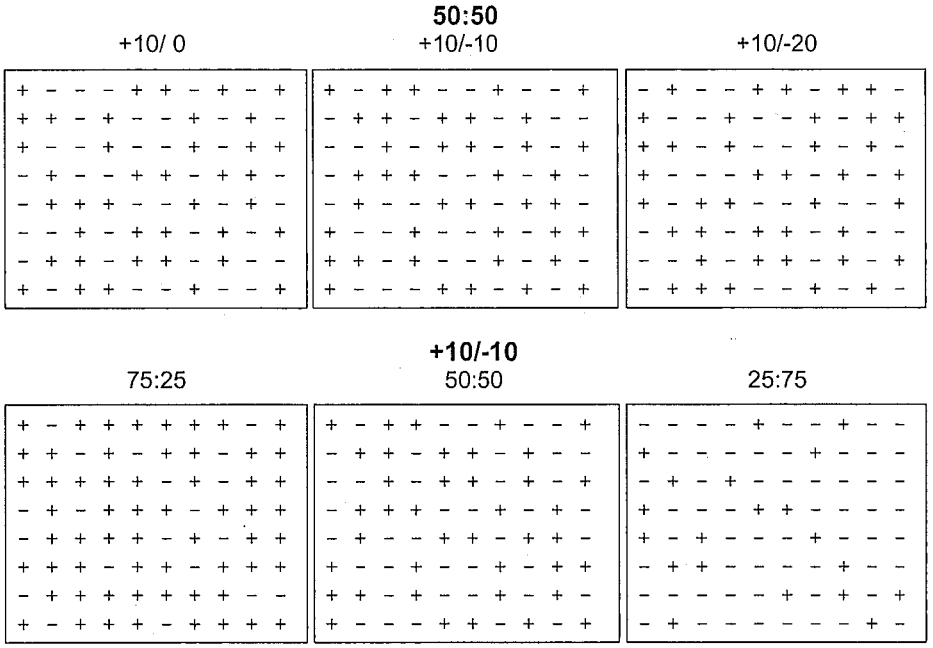

Figure 4.2 Choice Gain/loss sequences for left clicks
In **Choice 1** and **2**, left clicks produced a continuous gain of 10 cents in the continuous reward condition (not shown in here). The left click sequence of the conflicting condition in all three experiments was identical (middle sequence). *Top*: In **Choice 1**, the ratio of gains to losses is 50:50 in each condition. The conditions differed on the value of losses produced by left clicks. In the +10/-10 condition, left clicks produced either a gain or loss of 10 cents. In the +10/-20 condition, left clicks produced either a gain of 10 cents of a loss of 20 cents. *Bottom*: In **Choice 2** and **3**, left clicks always produced either a gain or a loss of 10 cents. The ratio of gains to losses varied between payoff conditions (from 75:25 to 25:75). + : gain; - : loss

4.3.2 Feedback questionnaires

In addition to Eysenck Personality Questionnaire-Revised (EPQ-R) and the Spielberger State-Trait Anxiety Inventory (STAI) personality scales, feedback questionnaires were created and administered to detect aberrant behaviour and response patterns to the tasks (see appendix 3). In **Choice 1**, the questionnaires were administered after 12 participants were tested so only 18 participants filled out the questionnaires.

4.4 Procedure

4.4.1 Basic instructions

The same basic instructions were given to participants in all three experiments. The participants were told to make a mouse click when the frame (see figure 4.1) disappeared at the end of a countdown period. Three aspects of the task were emphasized to the participants. First, the payoffs were not determined by how quickly they responded. Second, they had to make a click in order to move to the next trial. Third, they would only get a monetary win/loss feedback if they made a left click. If they made a right click there was no consequence. That is, they gave up the chance to win cash but also avoided losing cash for that trial. The participants were told to try and make as much money as possible. After the appropriate instructions were given, participants were given 10 practise trials. The experimental task took 45 minutes in **Choice 1** and **2** and about 25 minutes in **Choice 3.** Participants were informed how much they had earned from the task (their total earnings were not displayed during the task, only individual trial feedback) at the end of the experiment. They were then debriefed and thanked for their participation.

4.4.2 Cash reward in Choice 1 and 2

Regardless of their minimum wage rates, if participants had nominally earned less than NZD$9.50 then they received the advertised wages. If they earned more than NZD$9.50, they could keep the amount earned in excess of NZD$9.50, in addition to the minimum wage. For example, if the participants made $11 during the task, they would be paid $1.50 in addition to their advertised wage. They were not penalized if they ended up with losses.

4.4.3 Cash reward in Choice 3

Unlike **Choice 1** and **2**, participants did not have to meet the target of NZD$9.50. Participants kept the actual amount earned during the task on top of their minimum wage rate. They were not penalized if they ended up with losses.

4.4.4 Instructions on payoffs in Choice 1

In addition to the basic instructions, participants were informed that there were four payoff conditions. In order to make more than NZD$9.50, they should aim to maximise their gains and minimise their losses for all the conditions. They were informed that the payoffs for each of the four conditions would be presented on the screen before each trial-block began. The actual instructions given for condition one were,

> "For the next 10 turns, you will earn $0.10 if you click the left button. Click the right button to skip a turn"

For the remaining conditions, apart from the actual $ values, the instructions were the same as the following instructions used for condition four,

> "For the next 10 turns, you may gain $0.10 or lose $0.20 if you click the left button. Click the right button to skip a turn. The outcomes are randomised and there is no pattern to it."

4.4.5 Instructions on payoffs in Choice 2 & 3

In contrast to **Choice 1**, participants were not told how many payoff conditions there were. No instructions on the payoff values were given at any time. Participants were only given the basic instructions at the start of the experiment. However, there was a consistent relation of stimulus colour to payoff that permitted them to learn by experience what payoff condition was in place.

4.5 Data processing

4.5.1 Behavioural data

The type of responses made (left versus right click) and reaction times in milliseconds in each trial were recorded. The number of times participants made a left click within each 10-trial block (there were eight trial-blocks per payoff condition) was calculated post data collection and then converted into percentage scores. The percentage scores were then angular transformed to normalise error variance (Zar, 1974). Reaction times

were measured from the time the countdown period ended to the time a participant made a mouse click. To normalise error variance, individual participant's reaction times in each trial were log transformed (X' = Log10(X)).

4.5.2 Scoring feedback questionnaires

The number of "Yes" answers to each question were calculated and converted to percentage scores. Their answers to open-ended questions were coded and then converted into percentage scores. Participants' answers to the question "What was your responding strategy?" were classified into three categories. The first included strategies adopted according to the payoffs produced by left clicks. The second included non-specific response patterns. Participants in this category reported that they were guessing or responding according to instinct most of the time. The third category included participants who made only left clicks and those who responded fast because they thought response speed was important.

Participants' responses to whether they dozed off or felt sleepy during the task were classified according to their markings on a timeline divided into three sections: Early, Halfway and End. For "Yes" responses to the question, "Did you feel anxious at any point in the experiment? If yes, please note down when and why", the reasons for feeling anxious were classified into task and environment-related reasons.

4.5.3 Spectral power post-processing

The 0.5s period after the onset of the countdown stimulus was assigned a power spectrum (this was the period of interest in the **Choice** experiments). The computer task was divided into early and late phases. Early task phase included trials from the first, second and third 10-trial blocks. Late task phase included trials from the sixth, seventh, seventh and eighth trial blocks. For each participant, individual trials were averaged by task phase and payoff condition.

4.6 Statistical analyses - Analysis of variance (ANOVA)

In all three **Choice** experiments, the ANOVAs included extraction of orthogonal polynomial contrasts (Snedecor and Cochran 1967). They were performed with the GenStat statistical package (GenStat, VSN International Ltd, UK) which also interpolated missing values and adjusted degrees of freedom for missing values.

4.6.1 Factors extracted for behavioral and EEG analyses

A factor of PAYOFF was extracted from the three payoff conditions that involved both gains and losses on left click. Payoff condition 1 in **Choice 1** and **2**, which produced a continuous gain on left clicks, was excluded from the analyses. The three levels of the payoff factor represented a linear progression from overall reward through neutral to overall loss. However, the middle condition (payoff condition three) represented maximum conflict with the two other conditions representing equivalent conflict to each other – but with a greater tendency to press the left or the right button, respectively. The contribution of conflict was extracted as the quadratic component of PAYOFF. Given that PAYOFF had only three levels, the "quadratic" component in this case can be thought of as representing either any deviation from a simple linear effect of reinforcement, or as representing the difference between the intermediate (conflicting) condition from a value obtained by averaging the two adjacent conditions.

4.6.2 Factors extracted for behavioral analyses

A factor of TRIAL BLOCK was extracted from the eight trial blocks in each payoff condition. The eight levels of this factor represent the progression of the task. The first level represents the first trial block from each payoff condition that was presented. The last level represents the last trial block from each payoff condition that was presented.

4.6.3 Factors extracted for spectral power analyses

Separate ANOVAs were extracted for different phases within the task. The early phase represents the average log power of individual trials from the first, second and third 10-trial block. The late task phase represents the average log power of trials from the sixth, seventh and eighth trial blocks.

For the ANOVAs, we extracted a factor of FREQ as the variation in log power at different frequencies (4 Hz –12 Hz). A factor of BAND was also extracted in post-hoc analyses as the variation in averaged log power at different theta frequency bands. The first level of this factor represents the average of 4 Hz and 5 Hz log power. The second level of this factor represents the average of 6 Hz and 7 Hz log power.

A factor of SITE was extracted as variation of log power across the 15 recording sites.

In separate analyses, ANPO (anterior/posterior) and MED (medial/lateral) were extracted as variation in log power across different recording sites along two dimensions. As shown figure 4.3 the three levels of the ANPO factor represent how log power averaged across lateral recording sites varied from the anterior to the posterior of the scalp. With this factor the linear trend represented differences between the front and the back array of electrodes while the quadratic trend represented differences between the middle array and the average of the front and the back. The five levels of the MED factor represented how log power averaged across frontal-posterior sites varied medially, from the left to the right of the scalp. With this factor, the linear trend represented effects that increase steadily from one side to the other, the quadratic trend represents effects that are either bilateral or medial, and higher order trends represent more localised effects. The interaction of the ANPO and MED factors tests the fitting of a two dimensional surface over the entire electrode array. It should be noted that these statistics are purely descriptive of significant systematic deviations from a plane surface and do not assume any specific underlying spatial function generating the observed distribution of power.

A factor of EXPT was extracted as the variation between the three experiments.

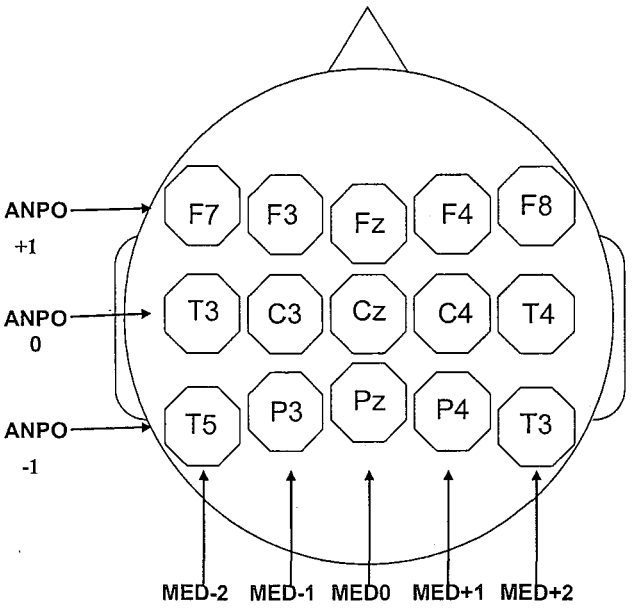

Figure 4.3. Choice Headmap of electrode sites showing levels of the ANPO and MED factors extracted to examine variations of log power across recording sites.
ANPO +1 represents the average log power of F7, F3, Fz, F4 and F8 and ANPO -1 represents the averaged log power of T5, P3, Pz, P4 and T3. MED -2 represents the averaged log power of F7, T3 and T5 and MED +2 represents the averaged log power of F8, T4 and T3.

4.7 EEG data exclusion

The GenStat statistical package uses a recursive algorithm to estimate values for missing data in its ANOVA calculations. For stable interpolations of missing values, the data to be analysed should contain no more than 10 % of missing values. To determine the percentage of data that were missing, I ran separate ANOVAs on each participant extracting the effect of SITE, PAYOFF and FREQ. These analyses were carried out only to determine the missing degrees of freedom. A participant was excluded when the number of degrees of freedom that were missing was more than 10% of the total number of degrees of freedom. This procedure was repeated for the early and late task phases. Different participants were therefore excluded in each task phase depending on the extent of each individual participant's artifact contamination in each phase. 28 out of 30 participants were included in the early task phase analyses in **Choice 1**. 24 participants were included in the late phase. In **Choice 2**, 39 out of 52 participants were included in the early phase and 27 participants were included in the late phase. In **Choice 3**, only one participant out of 36 had to be excluded in the late task phase analyses due to artifact contamination.

5 Goal- conflict in Choice experiment 1

5.1 Addressing limitations in the Stop-Signal Task (SST)

As discussed in section 3.4, there are several caveats to the interpretation of goal-conflict activity in the **SST**. The key challenge is the possibility that there was minimal simple inhibitory activity in the early and late stop-signal delay (SSD) trials. Simple inhibition could also be maximal in the intermediate SSD trials where goal-conflict was also maximal. The failure to resolve these issues was partly a consequence of a lack of direct control of goal-conflict. In the **SST**, estimating the level of goal-conflict likely to operate in different SSD trials relied on the *interpretation* of the variation of neural activity with time i.e. stop-signal delays. Whereas, in the **Choice** paradigm, goal-conflict was experimentally manipulated by varying monetary reward and punishment. The use of money and its omission as positive and negative reinforcers allowed for a direct and *objective* valuation of the level of goal-conflict in the experimental conditions. The lack of previous *f*MRI work with this paradigm, however, makes it relatively less easy to link any observed changes with specific neural substrates.

In the present experiment, participants made left mouse clicks to earn cash in four payoff conditions. If they made a right click this avoided the programmed consequences for a left click and result in neither gain nor loss. In the continuous reward condition, a left click always produced a gain of +10 cents. In the remaining three conditions, the probability of gain versus loss was fixed at 50%. The value of gain was fixed at +10 cents. Loss was 0 or –10 or –20 cents, resulting in averages of +5, 0 and -5c/left click respectively. Goal-conflict was expected to be maximal when the payoff was +10 versus –10 cents. Goal-conflict was assessed as the difference between the +10/ -10 condition and the average of the +10/ 0 and +10/ -20 conditions. Note that the value of loss/punishment was scaled linearly, gain/reward value was constant, and both were under direct experimental control. Activity that peaked at the +10/ -10 condition was interpreted as being specific to goal-conflict, ruling out the contributions of reward (which did not change) and net payoff and simple punishment (both of which varied linearly).

The assessment of goal-conflict required only three payoff conditions. The continuous reward condition was not intended as part of the assessment of goal-conflict. Its inclusion was to create motivation for the experimental task. Participants had the opportunity to make extra cash only if they met a target amount of earnings. The continuous reward condition was included to ensure it was possible to meet the target in practise. By imposing a target, real interest in performance on the task ought to increase, and hence elicit the intended perception of the payoffs.

5.2 Results

5.2.1 Behavioural analyses

5.2.1.1 Number of left clicks

As shown in Figure 5.1, in the +10/ 0 payoff condition, the number of left clicks remained constant at close to 100% over trials, whereas, in the +10/-20 condition, left clicks decreased during the experiment from about 60% to about 20%. Interestingly, despite an average net loss, responding did not drop to 0%. In the +10/-10 condition number of left clicks also decreased somewhat over trial blocks and was intermediate between the other two conditions (trial block x payoff, lin x lin, $F(1,464)= 18.83$, $p < 0.001$).

5.2.1.2 Reaction times

As shown in Figure 5.2 reaction times were initially high and then decreased to about 310ms over trials in the +10/ 0 condition. In the +10/-10 condition, reaction times also decreased steadily but to a greater extent to about 274ms. Unlike the other two conditions, reaction times in the +10/-20 condition did not decrease but remained relatively constant at 300ms to 316ms over trials. Except in the early trials, reaction times in the +10/-20 condition stayed intermediate between the other two conditions. In the early trials, the +10/-20 condition produced the quickest reaction times (trial block x payoff, lin x lin, $F(1,4784)= 5.04$, $p < 0.05$).

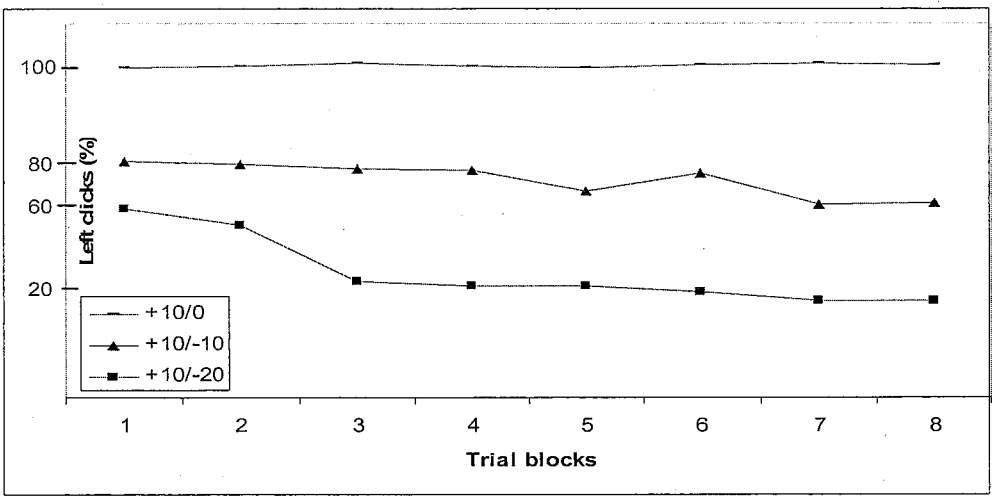

Figure 5.1 Choice 1 Percentage of left clicks made in each 10-trials block
Left clicks in the +10/0 payoff condition produced either a gain of 10 cents or no gain/loss. In the +10/-10 condition, left clicks produced either a gain or loss of 10 cents. In the +10/-20 condition, left clicks produced either a gain of 10 cents or a loss of 20 cents. The nonlinear response axis is a result of an angular transform.

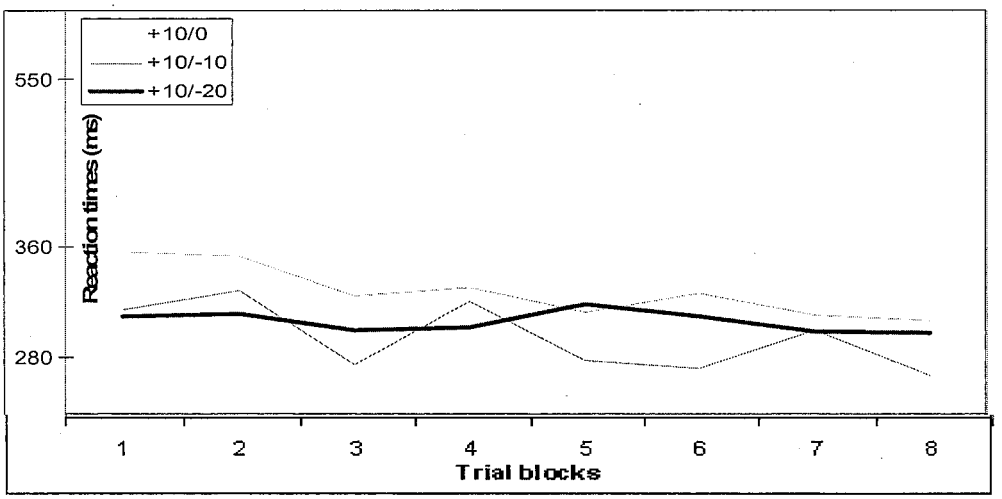

Figure 5.2 Choice 1 Time taken to make a left/right click
Reaction time was recorded from the end of the countdown period. Left clicks in the +10/0 payoff condition produced either a gain of 10 cents or no gain/loss. In the +10/-10 condition, left clicks produced either a gain or loss of 10 cents. In the +10/-20 condition, left clicks produced either a gain of 10 cents or a loss of 20 cents. The nonlinear response is a result of a log transform (X' = Log10(X).

5.2.1.3 Feedback

Participants were given a feedback form at the end of the experiment. Their feedback is summarized in table 5.1, which shows that none of the participants thought that response speed was vital in the experiment. 72 % of the participants reported responding according to the payoffs. All of the participants reported feeling sleepy at some point in the experiment. 33 % of the participants reported feeling anxious. All of them reported feeling anxious in the +10/-20 condition. About five also reported feeling anxious in the +10/-10 condition.

5.2.2 Spectral analyses

5.2.2.1 Preliminary analyses

Preliminary inspection of the data suggested that theta spectra power varied over trials in the experiment. 4-12 Hz theta spectra power averaged over the first 30 trials (early task phase) was analyzed separately from the last 30 trials (late task phase). This separation was based on the behavioral response. Active learning, if evident, tended to occur in the first 30 trials (see response trend for +10/-20 condition in figure 5.1). Responses appeared to stabilize by the late task phase (trials 51-80). In the late task phase, the number of participants producing excessive movement artifacts increased, resulting in their exclusion from the final analyses. To ensure a maximum number of participants for the analyses of variances (ANOVAs), early and late task phases were thus not examined as within-participant factors. Separate ANOVA was carried out for the early and late phases.

Table 5.1 Participants' feedback

Feedback questions	Experiment 1
Did you think response speed was important?	0% "Yes"
What was your response strategy?	72% payoffs 22% instinct 6% others
Did you change your strategy at all?	56% "Yes"
What was your response strategy at the beginning?	NA
What was your response strategy at the end?	NA
Please indicate if you either dozed off or felt sleepy during the experiment. Start Half-way End	100% "Yes" 17 % Start 44% Half-way 39% End
Did you feel anxious at any point? If yes, please note down when and why.	NA
Did you feel anxious during the countdown period in any of the scenarios? Always earn $0.10 Earn $0.10 or nothing Earn $0.10 or lose $0.10 (+10/-10) Earn $0.10 or lose $0.20 (+10/-20)	33% "Yes" 50 % +10/-10 100% +10/-20
Did you try to spot a pattern in the outcomes?	33% "Yes"
Did you pay attention to the frame during the experiment?	83% "Yes"
Were you counting down as the frame was disappearing?	78% "Yes"
When you started feeling sleepy, were you still paying attention to the frame?	56% "Yes"
Did you notice that the different coloured boxes represent different probabilities in the outcome?	NA

The variation in spectral power (averaged over 4-12 Hz) over the countdown period within a trial, averaged across recording sites, in the early and late task phase is shown in Figure 5.3. Averaged 4-12 Hz spectral power peaked in the 0.5s immediately after the onset of the countdown stimuli. This suggests that 4-12 Hz activity on average showed active processing in the period of interest.

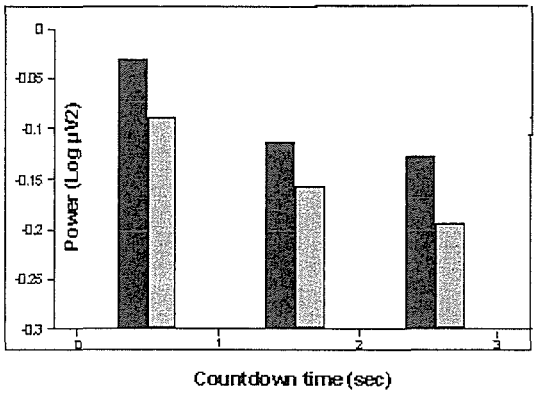

Figure 5.3 Choice 1 Variations in averaged 4-12 Hz power across recording sites in the countdown period in the early (black bar) and late (grey bar) task phases

Goal-conflict was assessed via the quadratic component of payoff, i.e. as the difference between the +10/ -10 condition and the average of the +10/ 0 and +10/ -20 conditions. Figure 5.4A shows the variations of 4-12 Hz conflict activity across recording sites in the early task phase. Figure 5.4B shows the variations of 4-12 Hz conflict activity across recording sites in the late task phase. Although goal conflict activity appeared to vary across frequencies (4-12 Hz) and recording sites, the variation across frequency was not reliably detected. Separate analyses were thus carried out for the standard human theta (4-7 Hz) and alpha (9-12 Hz) bands. As 8 Hz activity could represent a mixture of theta and alpha activity, it was excluded in the analyses to keep representation of the two classes of activity separate. Within each class of activity, frequencies were further banded into a lower and upper band. In the human theta band, 4-5 Hz and 6-7 Hz power were pooled together. In the alpha band, 9-10 Hz and 11-12 Hz power were pooled together. Separate analyses were carried out on the lower and upper bands only when the pattern of conflict activations differed between the two bands. Reliable goal-conflict activity was not detected in the alpha band. Hence, only results for the human theta band are reported below.

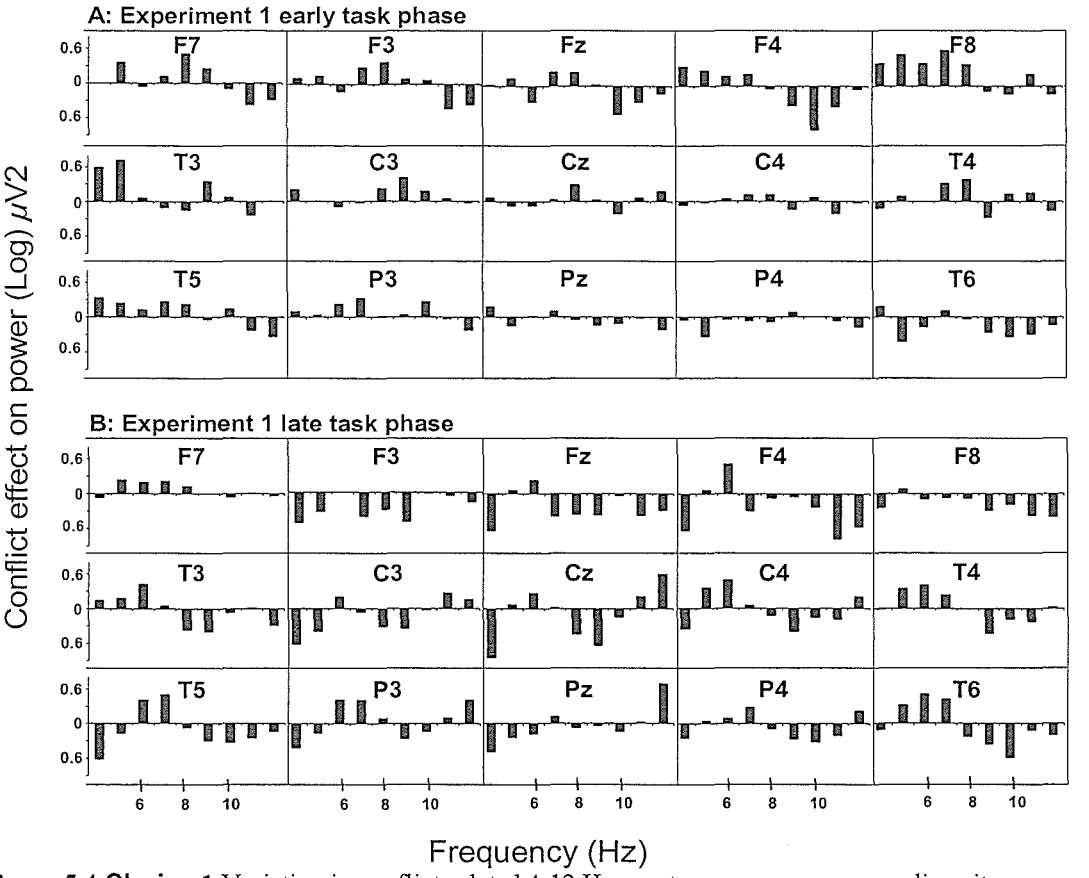

Figure 5.4 Choice 1 Variation in conflict-related 4-12 Hz spectra power across recording sites. Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for each of the nine frequencies (4 – 12 Hz) across the recording sites. Spectra power shown represents power in the 0.5 s after the onset of the countdown period. **A.** The quadratic trend in the early task phase (first 30 trials). **B.** The quadratic trend in the late task phase (last 30 trials).

5.2.2.2 Assessing variations of 4-7 Hz spectra power across recording sites

Figure 5.5 shows the variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activities across recording sites in the early phase (left hand pair of columns) and late task phase (right hand pair of columns). Although goal-conflict appears to vary with recording sites, the variations between individual sites were not sufficiently different to be reliably detected (Early phase: payoff x site x band, quad x site x band, $F(14,1215) = 0.46$, $p = 0.956$; late phase: payoff x site x band, quad x site x band, $F(14,810) = 0.79$, $p = 0.677$). However, the variation between recording sites appears systematic across the head and from front to back. Polynomials were therefore fitted to the recording sites for significance testing (see section 4.6.3 for explanation of ANPO and MED factors). Bonferroni correction was used to safeguard against multiple testing since the polynomials were fitted after significance testing with SITE as a factor (see 4.6.3). Thus, only interactions with p value less than 0.025 (0.05/2) are reported for goal-conflict variations with recording sites.

5.2.2.3 4-7 Hz early task phase spectral analyses

Reliable variations between the lower and upper bands were not detected. The variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activities across recording sites in the early phase are shown in figure 5.5 (left hand pair of columns). As shown in figure 5.5 , in both the lower and upper bands, the conflict effect increases steadily as we move from F7 on the left to F8 on the right. At the posterior sites on average across upper and lower bands, the conflict effect was evident only in the left hemisphere at T3 and T5. Conflict therefore affected 4-7 Hz power more to the right at the front and more to the left at the back of the head (payoff x anpo x med, quadratic x linear x linear, $F(1,810) = 5.93$, $p < 0.025$).

5.2.2.4 4-7 Hz late task phase spectral analyses

Figure 5.5 shows the variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activities across recording sites in the late phase (right hand pair of columns). There may be signs of conflict effects in the 6-7 Hz band at T5, P3 and T6 but these were not reliable.

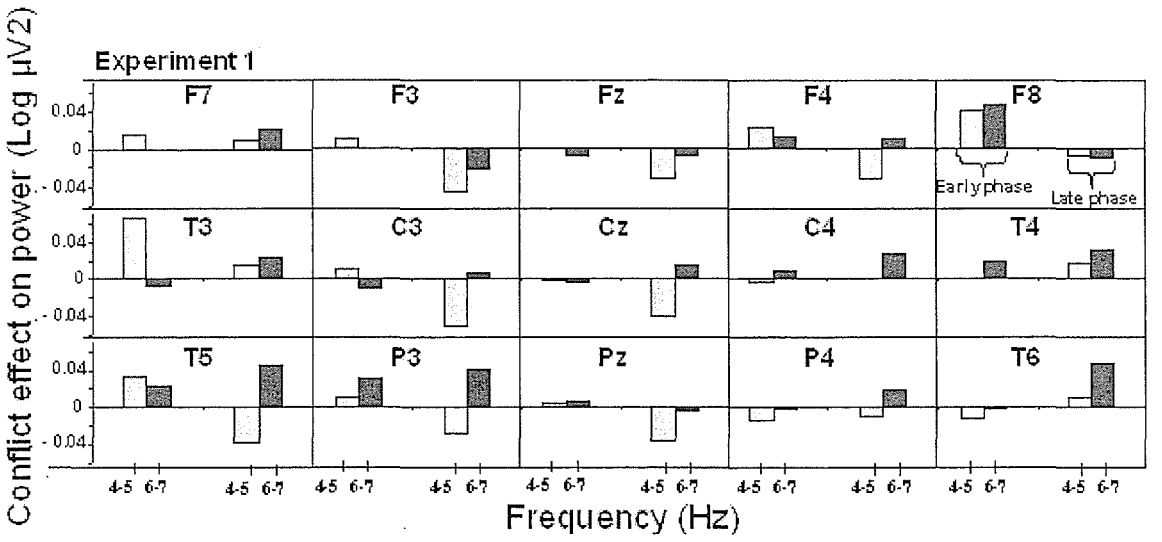

Figure 5.5 Choice 1 Variation in conflict-related 4-12 Hz spectra power across recording sites. Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for averaged 4-5 Hz (grey bar) and 6-7 Hz (black bar) power. Left hand column shows quadratic trend in the early task phase (average of first 30 trials). Right hand column shows the quadratic trend in the late task phase (average of last 30 trials).

5.2.3 Stepwise regression analyses

Conflict activations measured by the difference between the conflicting and the average of the rewarding and punishing conditions were extracted for individual participants for recording sites that showed reliable conflict activations. Averaged 4-5 Hz and averaged 6-7 Hz activities in the early task phase at F8, T3 and T5 were included as predictor variables. Separate stepwise analyses were carried out with the number of left clicks made in the conflicting condition, Spielberger Trait Anxiety (STAI-T) and Eysenck Neuoroticism (N) as dependent variables.

4-5 Hz conflict activations at T3 predicted fewer left clicks in the conflicting condition $F(1, 26) = 9.472$, $p < 0.005$ ($r^2 = 0.267$) in the stepwise analysis. No other reliable correlations or partial correlations were observed.

5.3 Discussion

Goal-conflict activity was assessed as the difference between the conflicting (+10/ -10 cents) condition and the average of the rewarding (+10/ 0 cents) and punishing (+10/ -20 cents) conditions. This ruled out a contribution of simple reward, net payoff and

punishment. In the early task phase (trials 1-30), goal-conflict activity was maximal in the lateral frontal site at F8 in the right hemisphere, in the human theta frequency band (averaged 4-7 Hz theta activity). In the posterior sites, averaged 4-7 Hz goal-conflict activities were also maximal in the lateral sites, but at T3 and T5 in the left hemisphere. In addition, early task phase 4-5 Hz conflict activations at T3 predicted fewer left clicks in the conflicting condition. Reliable conflict activity was not observed in the late task phase (trials 51-80).

In the current experiment, unlike the **SST**, the contribution of simple reward and punishment was ruled out. Goal-conflict was experimentally controlled with monetary reward and punishment rather than estimated post experiment in the **SST**. The number of trials in each experimental group was kept balanced. 30 trials from each experimental condition were processed for significance testing compared to as low as eight trials in the **SST.** Including more trials minimized chances of activity in a few trials being taken as representative of averaged activity. Taken together, these data suggest that the increase in human theta activity observed in the conflicting condition could be reliably attributed to goal-conflict processing. Importantly, the observation of F8 goal-conflict activity, i.e above the right frontal area, supports the hypothesis that there was a contribution of goal-conflict to right frontal **SST** activity at F8.

In the late task phase of the current experiment, there appeared to be an increase in movement artifacts, resulting in more participants being excluded from the final analyses due to data loss (2 excluded in the early phase versus 6 in the late phase). All participants reported feeling sleepy at some point. However, participants made fewer left clicks as the monetary loss increased. They were not randomly making responses even though they reported feeling sleepy. It appears that participants were motivated to solve the task but might have difficulty sustaining their attention during the experiment, particularly in the late task phase. It is unclear if the lack of goal-conflict activity in the late task phase was due to a loss of attention on the task, or due to a genuine lack of goal-conflict effect in the late task phase. A variation of the current task intended to capture their attention more effectively was therefore devised (see next chapter).

6 Goal-conflict in Choice experiment 2

6.1 Addressing limitations in Choice experiment 1

In **Choice 1**, theta spectra power in the human theta band (4-7 Hz), specific to goal-conflict, was evident in the early task phase (trials1-30). It is unclear if the lack of goal-conflict activity in the late task phase (trials 51-80) was due to a loss of attention during the experiment, or due to a genuine lack of a goal-conflict effect in the late task phase. The current experiment aimed to replicate the early phase effects and to reassess goal-conflict effects in the late phase. Changes were made to make the task more interesting and ought to have increased sustained attention during the experiment, particularly in the late phase.

Two changes were made. Firstly, the instructions presented at the start of each block of trials in **Choice 1** were removed. Only the basic instructions common to all three experiments were given in **Choice 2,** the current experiment (see section 4.4). At the start of each block of trials in **Choice 1**, participants were presented with instructions on the payoff condition they were in. An example of the instructions is as follows: "For the next 10 turns, you may gain $0.10 or lose $0.20 if you click the left button. Click the right button to skip a turn. The outcomes are randomised and there is no pattern to it." In **Choice 2**, the payoff instructions were removed. Participants had to learn the payoff conditions by associating the colour of the stimulus with the payoffs they received.

Secondly, the values of the payoffs were fixed but the probabilities of reward and punishment across the payoff conditions were varied. In **Choice 1**, the level of goal-conflict was manipulated by varying the value of the punishment while keeping the value of reward fixed at +10 cents. Punishment ranged from 0 to –10 and –20 cents. In **Choice 2**, the values of the reward and punishment were fixed at 10 cents and -10 cents. The probabilities of the reward and punishment were manipulated to vary the level of conflict across the payoff conditions. In **Choice 1**, this was fixed at 50% across conditions. In **Choice 2**, the probability of reward to punishment was 75:25, 50:50 and 25:75 in the three key experimental conditions respectively. Goal-conflict

was assessed, via the quadratic component as before, as the difference between the 50:50 and the average of the 75:25 and 25:75 conditions. Note that the parameters of the conflicting condition (50:50) were unchanged from **Choice 1**.

6.2 Results

6.2.1 Behavioural analyses

6.2.1.1 Number of left clicks

As shown in figure 6.1, in the 75:25 condition, the number of left clicks remained constant at about 90% over trials whereas in the 25:75 condition the number of left clicks decreased from 80% to about 20%. In the 50:50 condition responding also decreased somewhat and was intermediate between the other two conditions (trial block x payoff, lin x lin, $F(1,816)=66.84$, $p < 0.001$).

6.2.1.2 Reaction times

Reaction times in all three conditions tended to increase and then decrease again over the trials (figure 6.2). This trend however occurred earliest and was weakest when payoffs were rewarding (in the 75:25 condition). As the payoffs became more punishing, the trend occurred later and became stronger (trial block x payoff, quad x quad, $F(1, 8304)= 5.25$, $p < 0.05$; trial block x payoff, cub x lin, $F(1, 8304)= 9.4$, $p < 0.01$).

6.2.1.3 Feedback

Participants were given a feedback form at the end of the experiment. Their feedback is summarized in table 6.1. 8 % of the participants thought response speed was important in the experiment. 79 % of the participants responded according to the payoffs. 58 % of the participants changed their response strategies at some point. Only 71 % of the participants, as opposed to 100 % in Choice 1, reported feeling sleepy at some point in the experiment. 35 % of the participants reported feeling anxious. 27 % of the anxious participants reported being anxious due to concerns over their performance.

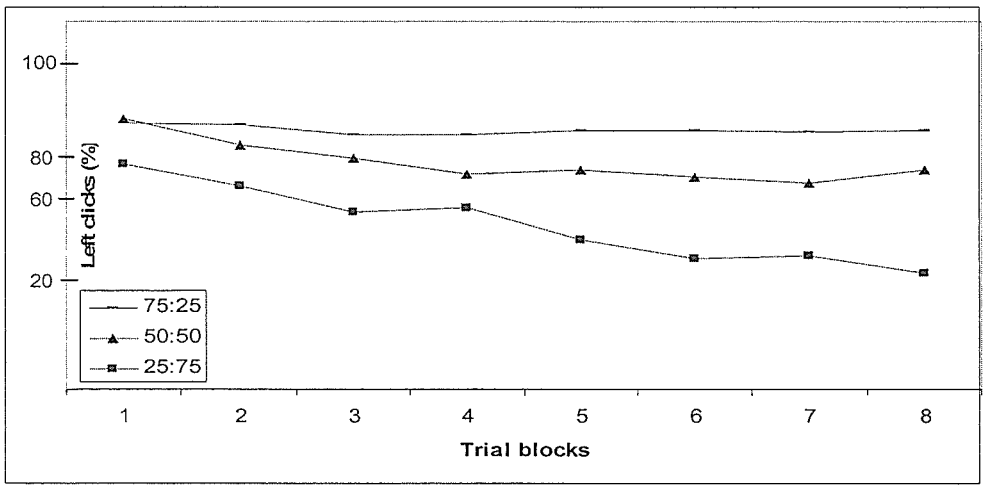

Figure 6.1 Choice 2 Percentage of left clicks made in each 10-trials block
Left clicks always produced either a gain or loss of 10 cents. The payoff conditions differed in terms of the gain to loss ratio produced by left clicks (from 75:25 to 25:75). The nonlinear response axis is the result of an angular transform.

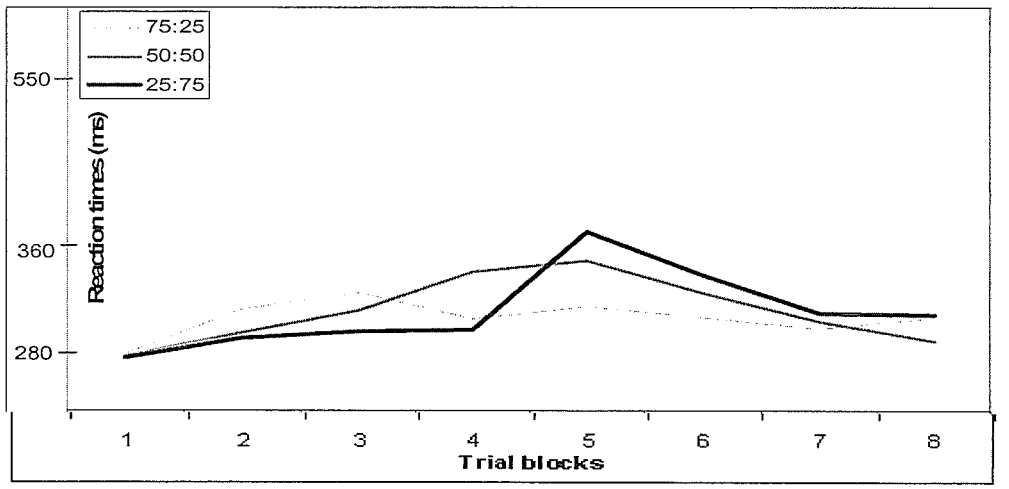

Figure 6.2 Choice 2 Time taken to make a left/right click.
Reaction times were recorded from the end of the countdown period. Left clicks always produced either a gain or loss of 10 cents. The payoff conditions differed in terms of the gain to loss ratio produced by left clicks (from 75:25 to 25:75). The nonlinear response axis is the result of a log transform (X' = Log10(X)).

Table 6.1 Participants' feedback

Feedback questions	Experiment 1	Experiment 2
Did you think response speed was important?	0% "Yes"	8% "Yes"
What was your response strategy?	72% payoffs 22% instinct 6% others	79% payoffs 15% instinct 6% others
Did you change your strategy at all?	56% "Yes"	58% "Yes"
What was your response strategy at the beginning?	NA	NA
What was your response strategy at the end?	NA	NA
Please indicate if you either dozed off or felt sleepy during the experiment. Start Half-way End	100% "Yes" 17 % Start 44% Half-way 39% End	71% "Yes" 15 % Start 57% Half-way 28% End
Did you feel anxious at any point? If yes, please note down when and why.	NA	35% "Yes" 27% "Yes", task-related 8% "Yes" environment-related
Did you feel anxious during the countdown period in any of the scenarios? Always earn $0.10 Earn $0.10 or nothing Earn $0.10 or lose $0.10 (+10/-10) Earn $0.10 or lose $0.20 (+10/-20)	33% "Yes" 50 % +10/-10 100% +10/-20	NA
Did you try to spot a pattern in the outcomes?	33% "Yes"	NA
Did you pay attention to the frame during the experiment?	83% "Yes"	NA
Were you counting down as the frame was disappearing?	78% "Yes"	NA
When you started feeling sleepy, were you still paying attention to the frame?	56% "Yes"	NA
Did you notice that the different coloured boxes represent different probabilities in the outcome?	NA	96% "Yes"

6.2.2 Spectral analyses

6.2.2.1 Preliminary analyses

To keep the analyses consistent across the two **Choice** experiments (see section 5.2.2.1) separate Analysis of variance (ANOVA) was carried out for early (trials 1-30) and late task phases (trials 51-80).

The variation in spectral power (averaged over 4-12 Hz) over the countdown period within a trial, averaged across recording sites, in the early and late task phase is shown in figure 6.3. Consistent with **Choice 1**, averaged 4-12 Hz spectral power peaked in the 0.5s immediately after the onset of the countdown stimuli. This suggests that 4-12 Hz activity on average showed active processing in the period of interest

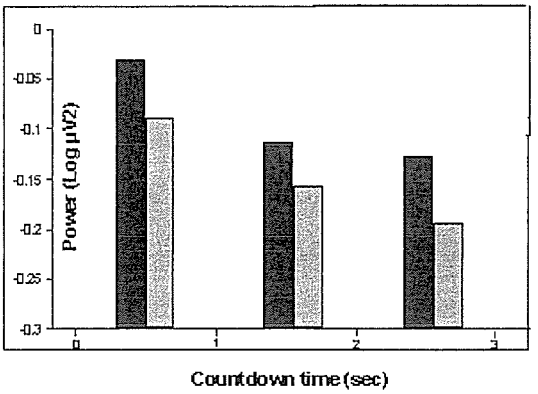

Figure 6.3 Choice 2 Variations in averaged 4-12 Hz power across recording sites in the countdown period, in the early (black bar) and late (grey bar) task phases.

Goal-conflict was assessed as the difference between the 50:50 condition and the average of the 25:75 and 75:25 conditions. Figure 6.4A shows the variations of 4-12 Hz conflict activity across recording sites in the early task phase. Figure 6.4B shows the variations of 4-12 Hz conflict activity across recording sites in the late task phase. Like **Choice 1**, although goal conflict activity appears to vary across frequencies (4-12 Hz) and recording sites, this was not reliably detected. Separate analyses were thus carried out for the standard human theta (4-7 Hz) and alpha (9-12 Hz) bands. As 8 Hz activities could represent a mixture of theta and alpha activity, it was excluded in our analyses to keep representation of the two classes of activity separate. Within each class of activity, frequencies were further banded into a lower and upper band. In the theta band, 4-5 Hz and 6-7 Hz power were pooled together. In the alpha band, 9-10 Hz and 11-12 Hz

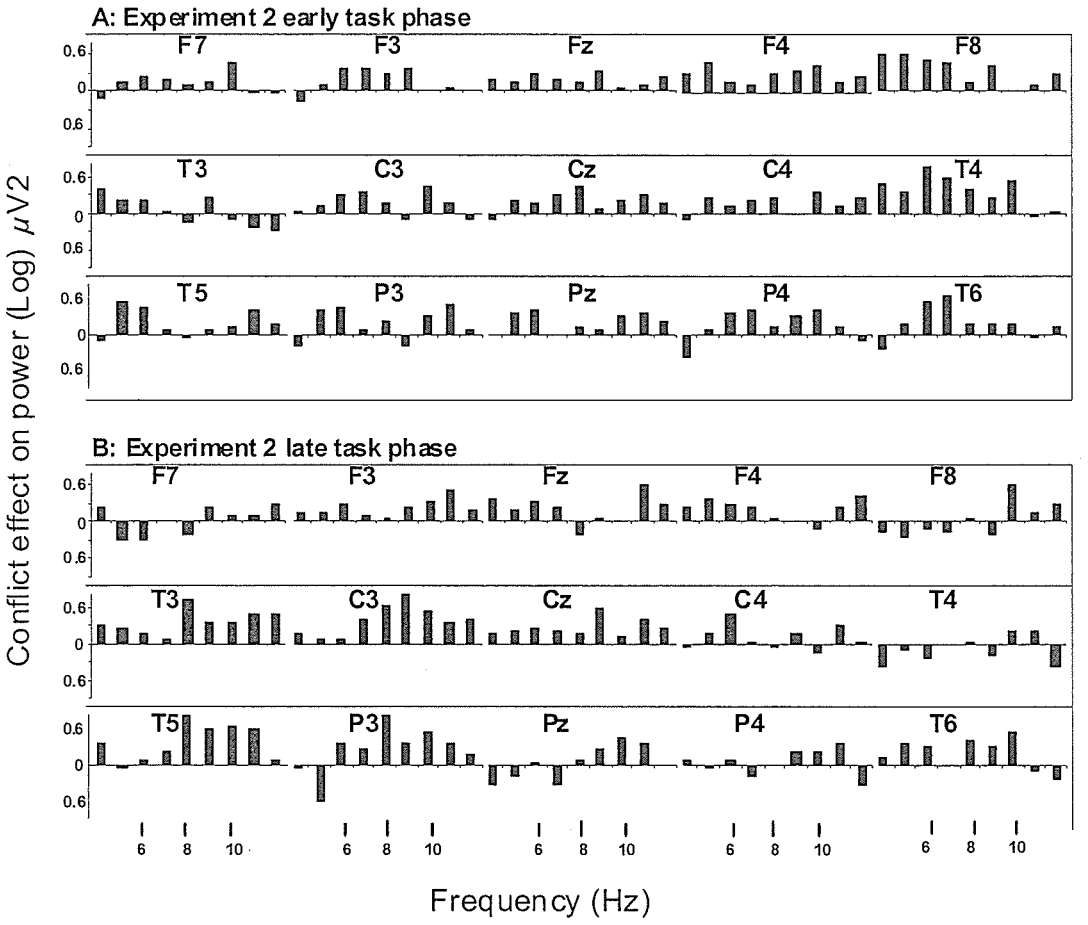

Figure 6.4 Choice 2. Variation in conflict-related 4-12 Hz spectra power across recording sites.

Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for each of the nine frequencies (4 – 12 Hz) across the recording sites. Spectra power shown represents power in the 0.5 s after the onset of the countdown period. **A.** The quadratic trend in the early task phase (first 30 trials). **B.** The quadratic trend in the late task phase (last 30 trials).

power were pooled together. Separate analyses were carried out on the lower and upper bands only when the pattern of conflict activations differed between the two bands. Reliable goal-conflict activity was not observed in the alpha band in any of the analyses. Only results for the human theta band are reported below.

6.2.2.2 Assessing variations of 4-7 Hz spectra power across recording sites

Figure 6.5 shows the variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activities across recording sites in the early (left hand pair of columns) and late (right hand pair of columns) task phase. As in **Choice 1**, although goal-conflict appears to vary with recording sites, the variations between individual sites were not sufficiently different to be reliably detected (Early phase: payoff x site x band, quadratic x site x band, $F(28,1710) = 0.37$, $p = 0.999$; payoff x site x band; late phase: quad x site x band, $F(28,1140) = 0.68$, $p = 0.894$). However, the variation between recording sites appears systematic across the head and from front to back. Polynomials were therefore fitted to the recording sites for significance testing (see section 4.6.3 for explanation of ANPO and MED factors). Bonferroni correction was used to safeguard against multiple testing since the polynomials were fitted after significance testing with SITE as a factor (see section 4.6.3). Hence, only interactions with p value less than 0.025 (0.05/2) are reported for goal-conflict variations with recording sites.

6.2.2.3 4-7 Hz early task phase spectral analyses

Figure 6.5 shows the variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activities across recording sites, in the early phase (left hand pair of columns). Unlike **Choice 1**, conflict appeared to affect the two bands differently (payoff x band x anpo x medl, quad x band x lin x lin, $F(1,1710) = 3.71$, $p = 0.054$). Significance testing was therefore carried out for lower and upper bands separately. Note that the interaction between spectra power bands, payoffs, and brain regions reported above only approaches significance. The individual upper and lower band analysis was thus Bonferroni corrected.

Conflict affected averaged 4-5 Hz activity in a similar fashion as in **Choice 1** (payoff x anpo x medl, quad x lin x lin, $F(1,1140) = 7.93$, $p < 0.01$). As in **Choice 1**, conflict

increased 4-5 Hz spectra power steadily as we move from the left at F7 to F8 on the right.

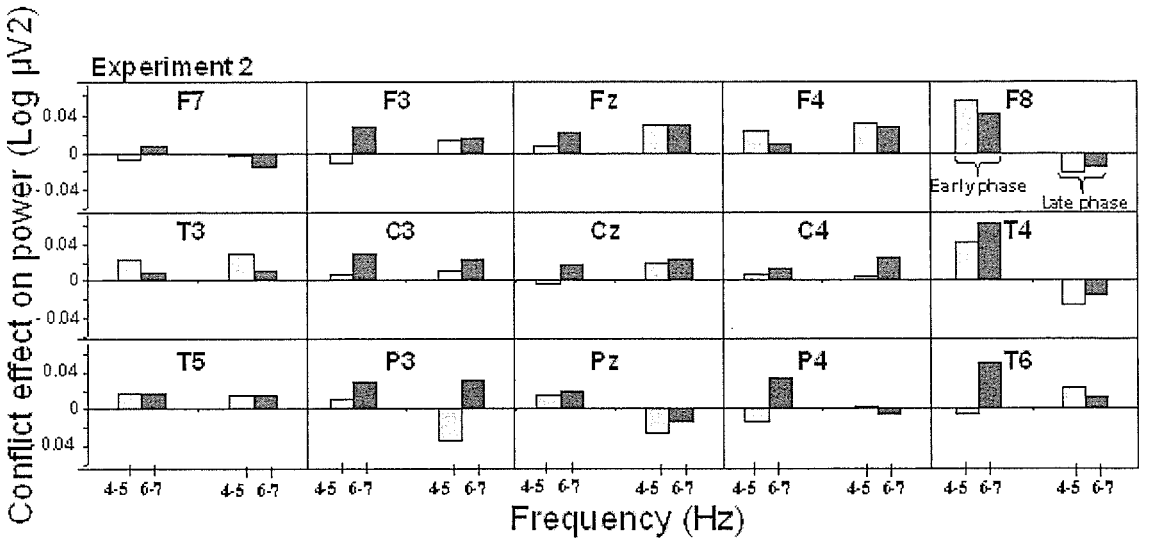

Figure 6.5 Choice 2 Variation in conflict-related 4-12 Hz spectra power across recording sites

Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for averaged 4-5 Hz (grey bar) and 6-7 Hz (black bar) power. Left hand column shows quadratic trend in the early task phase (average of first 30 trials). Right hand column shows the quadratic trend in the late task phase (average of last 30 trials).

Unlike **Choice 1**, a conflict effect of the same order as that at F8 was evident at T4. Conflict therefore increased 4-5 Hz spectra power steadily from T3 on the left to T4 on the right. In the posterior sites, the size of the conflict effect at T5 on the left was negligible, unlike T5 in **Choice 1**. There also appear to be a weak trend of 4-5 Hz power increasing as we move from T6 on the right to T5 on the left.

6-7 Hz conflict activity appeared to occur at right frontal sites F8 and T4, and the posterior site T6 (payoff x medl, quad x lin, $F(1,1140) = 4.03$, $p < 0.05$). These effects were not reliable after Bonferoni correction (after Bonferoni correction: payoff x medl, quad x lin, $F(1,1140) = 4.03$, $p > 0.0125$).

6.2.2.4 4-7 Hz late task phase spectral analyses

Figure 6.5 shows the variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related spectra power across recording sites in the late phase (right

hand pair of columns). Conflict increased power in both the lower and upper bands at the frontal midline sites Fz and F4 more than at Pz to the back, and F7 and F8 to the sides. At the back of the head, conflict increased spectra power in both power bands at the lateral sites T5 and T6 more than Pz at the midline and F7 and F8 to the front. Hence, conflict affected 4-7 Hz theta power more in the midline area at the front and the lateral areas in the back (payoff x anpo x medl, quad x lin x quad, $F(1,780) = 5.63$, $p < 0.025$).

6.2.3 Stepwise regression analyses

Conflict activations measured by the difference between the conflicting and the average of the rewarding and punishing conditions were extracted for individual participants for recording sites that showed reliable conflict activations. Separate stepwise analyses were carried out with the number of left clicks made in the conflicting condition, Spielberger Trait Anxiety (STAI-T) and Eysenck Neuoroticism (N) as dependent variables.

In the early task phase, averaged 4-5 Hz activity at F8 and T4 were included as predictor variables. Reliable correlations were not observed.

In the late task phase, averaged 4-5 Hz and 6-7 Hz activities at Fz, T5 and T6 were included as predictor variables. Increased 4-5 Hz conflict activations at T5 predicted fewer left clicks in the conflicting condition, $F(1,25) = 6.514$, $p < 0.05$ ($r^2 = 0.207$). Higher 6-7 Hz goal-conflict activity at Fz, predicted lower scores on Eysenck Neuroticism scale, $F(1,25) = 6.074$, $p < 0.05$ ($r^2 = 0.195$). Higher 4-5 Hz goal-conflict activity at T5 predicted lower scores on the Spielberger Trait Anxiety scale, $F(1,25) = 8.346$, $p < 0.01$ ($r^2 = 0.25$). When scores on left clicks and trait anxiety were entered together as predictor variables of T5 activity, they explained almost half of the variance in activity at T5, $F(1,25) = 10.302$, $p = 0.001$ ($r^2 = 0.462$). Left clicks and Trait Anxiety did not share common variance in activity at T5.

6.3 Discussion

Goal-conflict activity was assessed as the difference between the conflicting (50:50) cents condition and the average of the rewarding (75:25) and punishing (25:75) conditions. This ruled out the contribution of simple reward and punishment. In the early task phase, goal-conflict elicited maximal activity in the human lower theta band (averaged 4-5 Hz) from the right frontal site at F8 and right temporal site T4. Although right lateral sites F8, T4 and T6 appeared to show conflict activity, this was not reliable after Bonferroni correction.

In the late task phase (trials 51-80), conflict activity was stronger in the middle and weaker at the sides in the frontal regions, peaking at the midline site Fz. In the posterior regions, conflict was weaker in the midline and stronger at the sides, at T4 and T5. This pattern of activity was observed in both lower and upper human theta band (averaged 4-7 Hz).

Increased late task phase conflict activations at T5, in the 4-5 Hz band, predicted fewer left clicks in the conflicting condition. Higher late phase 4-5 Hz goal-conflict activity at T5 predicted lower scores on Spielberger Trait Anxiety scale. Left clicks and trait anxiety scores together explained half the variance in T5 conflict activity. Higher late task phase 6-7 Hz activity at Fz predicted lower scores on Eysenck Neuroticism scale.

Only 39 out of 52 participants were included in the early phase and 27 out of 52 participants were included in the late phase in the current experiment. This compares with 28 out of 30 participants in the early phase; and 24 out of 30 in the late phase in **Choice 1**. A large amount of data had to be thrown out in this experiment due to movement artifacts. It appeared that changes planned to capture participants' attention more effectively produced an undesired effect – increased EEG artifacts such as movements and eye blinks. Increased artifacts in the early phase could result from excitability over the challenge of figuring out how to make as much money as possible from the task (participants were not given instructions on payoffs conditions). In the late task phase, increased artifacts could reflect frustration and tiredness. The task lasted about 45 minutes. As feedback on accumulated earnings over trials was not

given, participants did not know how they had performed. In **Choice 1**, participants were clearly instructed on the different payoff conditions. Responding by the late task phase would have become automatic and relatively non-taxing. In **Choice 2**, participants could not know for certain if they had adopted a correct responding strategy due to the lack of information on the payoff conditions. They, however, appeared to have learned that there were different payoff conditions, probably by associating the color of the stimulus in each condition with the particular payoffs. Hence, as in **Choice 1**, participants responded according to the payoffs on average i.e., they made fewer left clicks as the punishment increased. The higher degree of uncertainty, the pressure to perform well (participants had to meet a target amount of earnings), and the length of the experiment – taken together – could elicit more tiredness and frustration towards the end of the experiment and increased movement artifacts.

Interestingly, although the changes made in **Choice 2** appeared to produce more artifacts, they elicited goal-conflict effects not evident in the late task phase of **Choice 1**. The combination of higher pressure and uncertainty could have produced task-dependent conflict effects in the late phase in the current experiment.

7 Goal- conflict in Choice experiment 3

7.1 Addressing limitations in Choice experiment 2

The increase in EEG artifacts in **Choice 2** compared to **Choice 1**, raised concern over the effectiveness of the changes made to the paradigm in **Choice 2**. Proportionately more participants had to be excluded from **Choice 2**. Since the number of participants that reported feeling sleepy during the task went from 100 % in **Choice 1** to 71 % in **Choice 2**, changes made in **Choice 2** appeared somewhat effective in capturing attention. Hence, changes already made were retained. Other properties of the **Choice 2** paradigm were examined for more effective measures of capturing interest and attention without excessive artifacts.

Choice 1 and **2** took 45 minutes. It could be difficult to sustain attention and interest in just making left and right mouse clicks over such a long period. Particularly, in **Choice 1** and **2**, the mandatory waiting period before a response could be made was three seconds. This period could have been unnecessarily long. The countdown period was shortened to 1 second in **Choice 3**, so that participants could get through each trial quicker.

Two other changes were made to **Choice 2** to shorten the task. Firstly, the fourth condition, the continuous reward condition, was removed. Note that in **Choice 1** and **2,** this condition was not included in the analyses of variances (ANOVAs). Secondly, participants could keep the nominal amount of cash they made from the task – the earnings target was removed. Previously, participants could only keep the amount in excess of NZD $9.50 (the earnings target). For example if the participants made $11 during the task, they would be paid $1.50 in addition to their advertised wages. In **Choice 3**, participants were paid what they earned from the experimental task on top of their advertised wages. This change was made as a result of removing the continuous reward condition. The change ensured that the amount of money participants could make in excess of the advertised wages would be comparable to **Choice 1** and **2**. Altogether, the changes made shortened the task from 45, to 25 minutes. Otherwise, the task was run as for **Choice 2**.

7.2 Results

7.2.1 Behavioural analyses

7.2.1.1 Number of left clicks

As shown in figure 7.1, in the 75:25 condition, the number of left clicks remained constant at about 80% over trials. In the 50:50 condition, there was a modest decrease from 80 % to about 70%. A larger decrease could be seen in the 25:75 condition where responding fell from about 60% to 20% (trial block x payoff, lin x lin, $F(1,560) = 31.88, p < 0.001$).

7.2.1.2 Reaction times

Overall, reaction times were quicker at the end of the experiment compared to the start in all three conditions (trial block, lin, $F(1,245)=78.92$, $p< 0.001$). There were considerable fluctuations in between the trial blocks, particularly noticeable in the 75:25 and 25:75 conditions. There was a tendency for reaction times to peak in alternate trial blocks in the 75:25 condition. The 25:75 condition showed a similar trend but with the peaks occurring at the troughs of the 75:25 condition (trial x payoff, quartz x lin, $F(1, 5744)= 10.04, p < 0.05$).

7.2.1.3 Feedback

Participants were given a feedback form at the end of the experiment. Their feedback is summarized in table 7.1. 5 % of the participants thought response speed was important in the experiment. 72 % participants responded according to the payoffs. Only 56 % of the participants, as opposed to 71 % in **Choice 2** and 100 % in **Choice 1**, reported feeling sleepy at some point in the experiment. 30 % of the participants reported feeling anxious. 25 % of the anxious participants reported being anxious due to concerns over their performance.

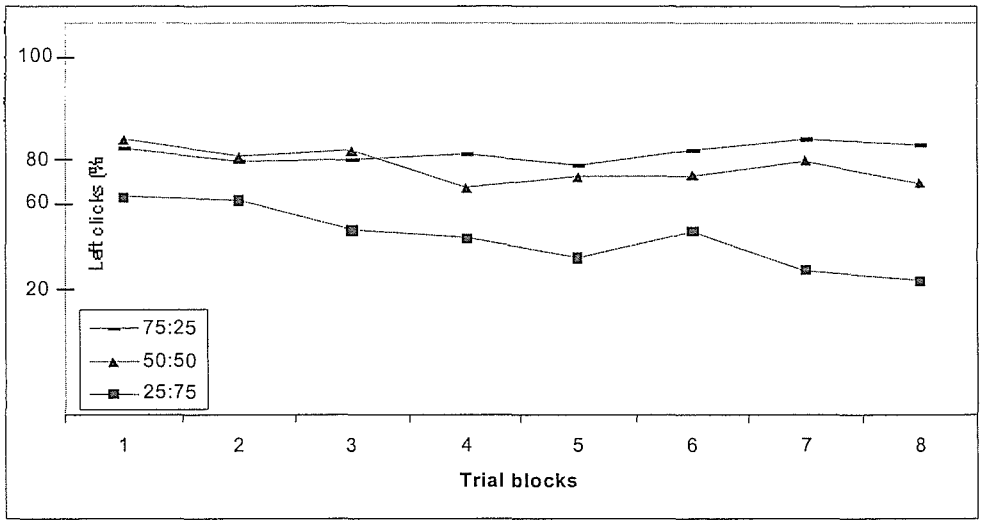

Figure 7.1 Choice 3 Percentage of left clicks made in each 10-trials block
Left clicks always produced either a gain or loss of 10 cents. The payoff conditions differed in terms of the gain to loss ratio produced by left clicks (from 75:25 to 25:75). The nonlinear response axis was a result of an angular transform.

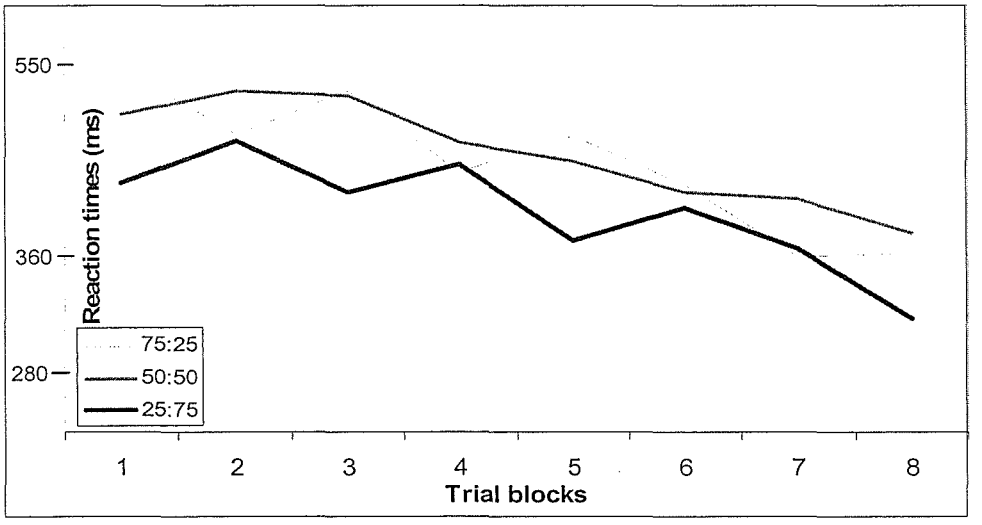

Figure 7.2 Choice 3 Time taken to make a left/right click.
Reaction times were recorded from the end of the countdown period. Left clicks always produced either a gain or loss of 10 cents. The payoff conditions differed in terms of the gain to loss ratio produced by left clicks (from 75:25 to 25:75). The nonlinear response axis was a result of a log transform (X'= Log10(X)).

Table 7.1 Participants' feedback

Feedback questions	Experiment 1	Experiment 2	Experiment 3
Did you think response speed was important?	0% "Yes"	8% "Yes"	5% "Yes"
What was your response strategy?	72% payoffs 22% instinct 6% others	79% payoffs 15% instinct 6% others	72% payoffs 22% instinct 6% others
Did you change your strategy at all?	56% "Yes"	58% "Yes"	NA
What was your response strategy at the beginning?	NA	NA	77% payoffs 4% instinct 11% others
What was your response strategy at the end?	NA	NA	75% payoffs 5% instinct 14% others
Please indicate if you either dozed off or felt sleepy during the experiment. Start Half-way End	100% "Yes" 17 % Start 44% Half-way 39% End	71% "Yes" 15 % Start 57% Half-way 28% End	56% "Yes" 3 % Start 25% Half-way 28% End
Did you feel anxious at any point? If yes, please note down when and why.	NA	35% "Yes" 27% "Yes", task-related 8% "Yes" environment-related	30% "Yes" 25% "Yes", task-related 6% "Yes" environment-related
Did you feel anxious during the countdown period in any of the scenarios? Always earn $0.10 Earn $0.10 or nothing Earn $0.10 or lose $0.10 (+10/-10) Earn $0.10 or lose $0.20 (+10/-20)	33% "Yes" 50 % +10/-10 100% +10/-20	NA	NA
Did you try to spot a pattern in the outcomes?	33% "Yes"	NA	NA
Did you pay attention to the frame during the experiment?	83% "Yes"	NA	NA
Were you counting down as the frame was disappearing?	78% "Yes"	NA	NA
When you started feeling sleepy, were you still paying attention to the frame?	56% "Yes"	NA	NA
Did you notice that the different coloured boxes represent different probabilities in the outcome?	NA	96% "Yes"	NA

7.2.2 Spectral analyses

7.2.2.1 Preliminary analyses

To keep the analyses consistent across the **Choice** experiments (see section 5.2.2.1) separate analysis of variance (ANOVA) was carried out for early (trials 1-30) and late task phases (trials 51-80).

Goal-conflict was assessed as the difference between the 50:50 condition and the average of the 75:25 and 25:75 conditions. Figure 7.3A shows the variations of 4-12 Hz conflict activity across recording sites in the early task phase. Figure 7.3B shows the variations of 4-12 Hz conflict activity across recording sites in the late task phase. Like **Choice 1** and **2**, although goal conflict activity appeared to vary across frequencies (4-12 Hz) and recording sites, this was not reliably detected. Separate analyses were thus carried out for the standard human theta (4-7 Hz) and alpha (9-12 Hz) bands. As 8 Hz activities could represent a mixture of theta and alpha activity, it was excluded in our analyses to keep representation of the two classes of activity separate. Within each class of activity, frequencies were further banded into a lower and upper band. In the theta band, 4-5 Hz and 6-7 Hz power were pooled together. In the alpha band, 9-10 Hz and 11-12 Hz power were pooled together. Separate analyses were carried out on the lower and upper bands only when the pattern of conflict activations differed between the two bands. Reliable goal-conflict activity was not observed in the alpha band in any of the analyses. Only results for the human theta band are reported below.

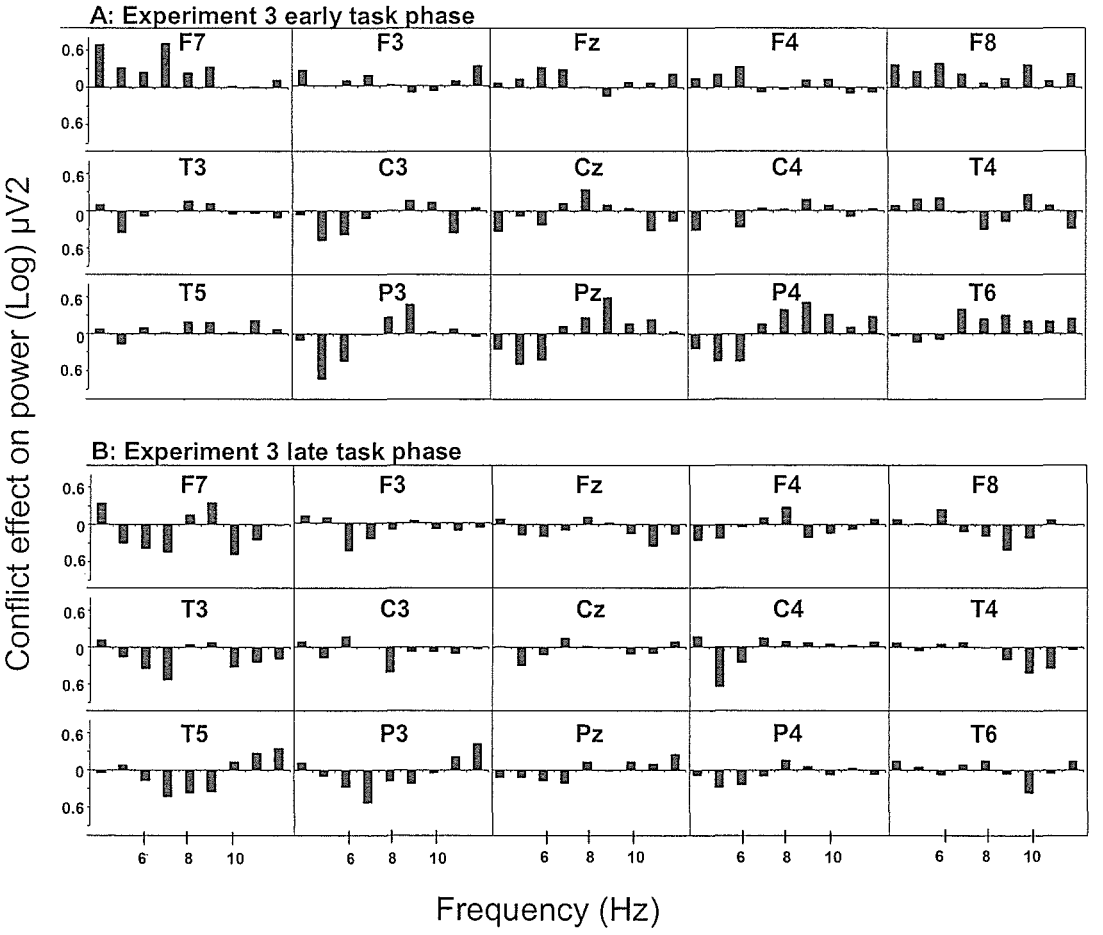

Figure 7.3 Choice 3 Variation in conflict-related 4-12 Hz spectra power across recording sites. Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for each of the nine frequencies (4 – 12 Hz) across the recording sites. Spectra power shown represents power in the 0.5 s after the onset of the countdown period. **A.** The quadratic trend in the early task phase (average of first 30 trials). **B.** The quadratic trend in the late task phase (average of last 30 trials).

7.2.2.2 4-7 Hz early task phase spectral analyses

The variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activity across recording sites, in the early phase, is shown in figure 7.4 (left hand pair of columns). Conflict-specific changes did not differ between the two bands.

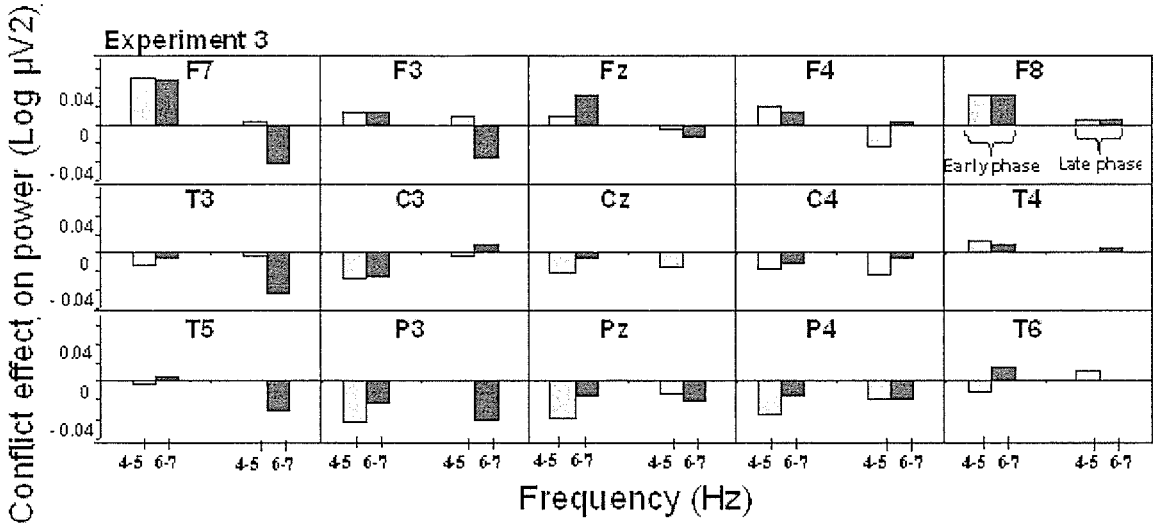

Figure 7.4 Choice 3 Variation in conflict-related 4-12 Hz spectral power across recording sites. Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for averaged 4-5 Hz (grey bar) and 6-7 Hz (black bar) power. Left hand column shows quadratic trend in the early task phase (average of first 30 trials). Right hand column shows the quadratic trend in the late task phase (average of last 30 trials).

Conflict activity varied significantly across the recording sites (site x payoff, site x quad, $F(14,1050) = 2.41$, $p < 0.05$). Only the lateral frontal site in the left hemisphere, F7, showed a reliable conflict effect (F7: payoff, quad, $F(1,70) = 9.54$, $p < 0.05$)). The effect at F8 approached statistical significance (F8: payoff, quad, $F(1,70) = 3.82$ $p = 0.055$). Reliable conflict effects were not detected in the remaining recording sites.

7.2.2.3 4-7 Hz late task phase spectral analyses

The variation in averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) conflict-related activity across recording sites in the late phase is shown in figure 7.4 (right hand pair of columns). There were no signs of conflict effects.

7.2.3 Stepwise regression analyses

Conflict activation measured by the difference between the conflicting and the average of the rewarding and punishing conditions was extracted for individual participants for recording sites that showed reliable conflict activations. Separate stepwise analyses

were carried out with the number of left clicks made in the conflicting condition, Spielberger Trait Anxiety (STAI-T) and Eysenck Neuoroticism (N).

Increased 4-5 Hz conflict activations at F8 predicted fewer left clicks in the conflicting condition $F(1,34) = 7.699$, $p < 0.01$ 9 ($r^2 = 0.185$). No other reliable correlations were detected.

7.2.4 Spectra power data pooled from Choice experiment 1, 2 and 3

Although conflict activity at F8 only approached significance in the current experiment, the consistency with which goal-conflict increased theta activity at this site, across the **Choice** experiments, should rule out any concerns over its occurrence by chance. Figure 7.5 shows the effect of conflict on averaged 4-5 Hz (grey bar) and averaged 6-7 Hz (black bar) theta activity across recording sites, pooled from the three **Choice** experiments. On average, across the three experiments, a conflict effect was observed at F8 and T4 in the right hemisphere (payoff x site, quad x site $F(14,3000) = 1.98$, $p < 0.05$; F8: payoff, quad, $F(1,204) = 17.8$, $p < 0.001$; T4: payoff, quad, $F(1,204) = 17.8$, $p < 0.05$). There was no evidence that the conflict effect at F8 varied in size across the three experiments (F8: expt x payoff, expt x quad $F(2, 200) = 0.32$, $p < 0.728$). Unlike the conflict effect at F8, the effect at T4 was not evident in all of the **Choice** experiments. The T4 effects in **Choice 1** and **3** were negligible. The T4 effect observed in the pooled data appeared to be an artifact of the averaging technique and was mainly contributed by the large effect seen at T4 in **Choice 2**.

7.3 Discussion

Goal-conflict activity was assessed as the difference between the conflicting (50:50 cents) condition and the averaged of the rewarding (75:25) and punishing (25:75) conditions. This rules out the contribution of simple reward and punishment. Conflict increased human theta activity (averaged 4-7 Hz) at the lateral frontal site in the left hemisphere at F7. Conflict also tended to increase averaged theta activity (4-7 Hz) at F8 but this effect only approached statistical significance. Increased 4-5 Hz conflict activations at F8 predicted fewer left clicks in the conflicting condition.

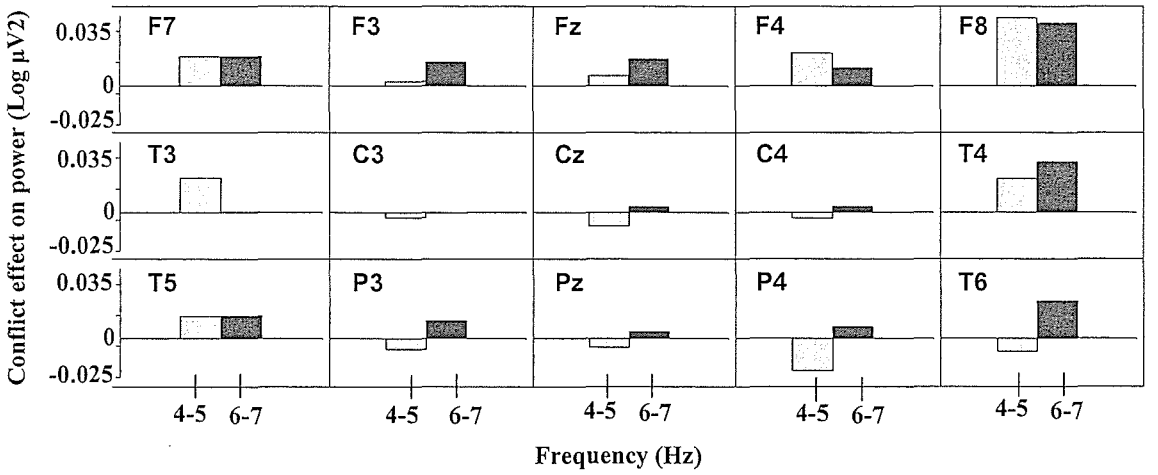

Figure 7.5 Combined data of **Choice 1, 2** and **3**. Variation in conflict-related 4-12 Hz spectra power across recording sites.
Each bar represents the size of the difference between the conflicting payoff condition and the average of the rewarding and punishing conditions as estimated by the quadratic trend of payoff conditions. Variations of this quadratic trend are shown for each of the nine frequencies (4 – 12 Hz) across the recording sites. Spectra power shown represents power in the 0.5 s after the onset of the countdown period. **A.** The quadratic trend in the early task phase (average of first 30 trials). **B.** The quadratic trend in the late task phase (average of last 30 trials).

Only 56% of the participants reported feeling sleepy compared to 100 % in **Choice 1** and 71 % in **Choice 3**. Changes made in the current experiment appeared effective in sustaining participants' attention in the task. This was also evident in the reduction of participants being excluded due to EEG artifacts. Only one participant had to be excluded due to movement artifacts in the late task phase as opposed to 25 participants.

Changes in the current experiment appeared to eliminate the temporal lobe conflict activity observed in **Choice 1** and **2** and elicited lateral frontal activity in the left hemisphere. Despite these changes, goal-conflict activation was still observed in the right frontal site F8. Although this effect only approached statistical significance, data pooled across the three **Choice** experiments suggests that there was a conflict effect at F8 across all three **Choice** experiments. Hence, ruling out the chance occurrence of the F8 conflict effect observed here in **Choice 3**.

8 Was there theta phase-locking during goal-conflict processing

8.1 Theta phase-locking during goal-conflict

In the current thesis, the examination of 4-12 Hz theta spectra power for an effect of goal-conflict is theoretically driven. Detection of theta activations associated with conflict implicates the involvement of the Behavioural Inhibition System (BIS). The increase in theta spectra power observed in the current experiments could reflect phase-locking of event-related theta oscillations between the cortex and key BIS modules such as the hippocampus during goal-conflict processing. The phases of *phase-locked* EEG (eg, evoked potentials) occur at fixed time delays to an event. Although *event-related* EEG is time-locked to an event, the oscillations may begin at different phases to the event on separate occasions. Averaging untransformed EEG over trials increases the signal-to-noise ratio for phase-locked EEG and attenuates that of event-related EEG. Untransformed averaged EEG records thus show clear phase-locked EEG if they are present. Although phase-locked and event-related EEG have been treated as uncorrelated activities, it has been suggested that phase-locked EEG can be a result of a reorganization of the phases of event-related EEG (Kalcher & Pfurtscheller, 1995; Pfurtscheller & Lopes da Silva, 2002). If an event, such as conflict processing, resets and causes the phases of the underlying-event related EEG to become phase-locked, this should be detectable in untransformed averaged EEG. Hence, the untransformed EEG for periods matching the spectra power data that showed conflict effects in the current experiments is analysed below for evidence of phase-locking.

8.2 Methods

In the Fourier analysis of the **SST** task, the 0.5s period after the tone in a Stop trial was assigned a power spectrum. For every Go trial preceding a Stop trial, the same procedure was repeated for the 0.5s period at which the tone was presented in the matching Stop trial. If the trial preceding a Stop trial was also a Stop trial, the Go trial following this Stop trial was used instead. The untransformed EEG traces for the same 0.5s period of interest, and the 0.5s before and after were averaged. For the analyses of

variances (ANOVAs), a factor of SSD representing early, intermediate and late stop-signal delay trials in the 0.5s after the onset of the stop-signal was extracted (see section 3.2.5).

In the **Choice** experiments, the 0.5s period after the onset of the countdown stimulus was assigned a power spectrum. The untransformed EEG traces for the 0.5s period after the onset of the countdown period, and the 0.5s before and after, were averaged by early (trials 1-30) and late (trials 51-80) task phase. For the ANOVAs, a factor of PAYOFF representing the rewarding, conflicting and punishing conditions was extracted (see section 4.6.1)

For both the **SST** and **Choice** paradigms, variations in the size of evoked potentials were assessed with the factor SAMPLE, representing the 64 samples sampled during the EEG recording.

8.3 Results

Figure 8.1 shows Stop trials EEG traces across recording sites for the early, intermediate (conflict) and late SSD trials in the **SST**. Although evoked potentials were evident, the size of the potentials did not differ between SSD trials.

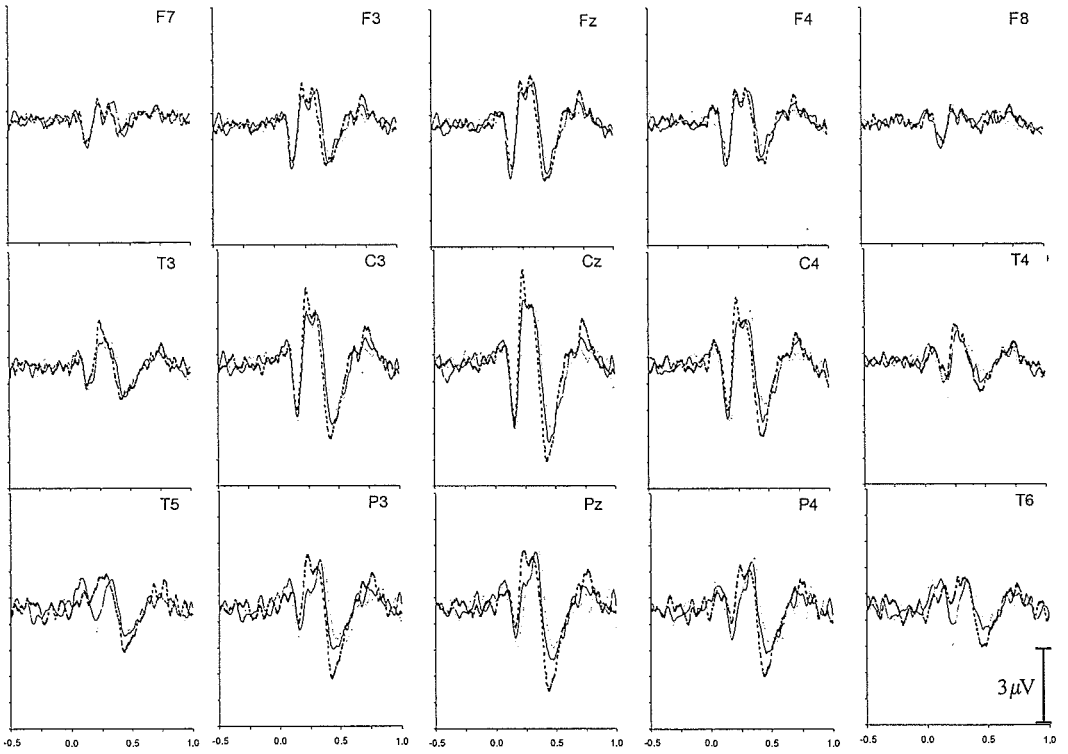

Figure 8.1 SST Evoked potentials in the Stop trials
Figure shows variations across recording sites, in averaged EEG traces for the 0.5s after the tone and the 0.5s before and after. 0s represents the onset of the tone (stop signal). Dotted black line represents early SSD trials. Black line represents intermediate SSD trials (conflict). Grey line represents late SSD trials.

Figure 8.2 shows Go trials untransformed EEG traces across recording sites for the early, intermediate (conflict) and late SSD trials in the stop signal inhibition task. No tone was actually presented in the Go trial and the Go trials activity presented here was not consistently time-locked to the start of the Go trial. The activity was time-locked to the onset of the tone in the following or preceding Stop trial. There was no evidence of increased activity in the intermediate SSD trials (conflict).

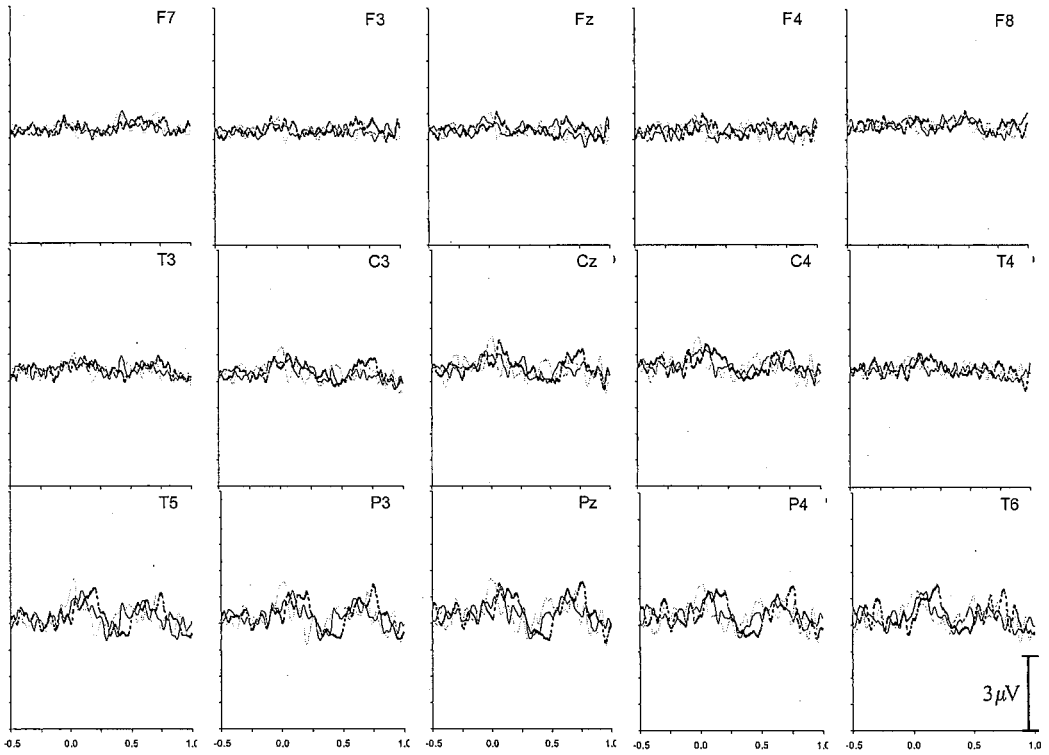

Figure 8.2 SST Evoked potentials in the Go trials.
Figure shows variations across recording sites, in averaged EEG traces for the 0.5s after the tone and the 0.5s before and after. 0s represents the onset of the tone in a stop trial following or preceding a Go trial. Dotted black line represents early SSD trials. Black line represents intermediate SSD trials (conflict). Grey line represents late SSD trials.

Figure 8.3 shows early task phase EEG traces across recording sites for the rewarding, conflicting and punishing trials in **Choice 1**. Evoked potentials in the conflicting trials did not differ from the rewarding and punishing trials.

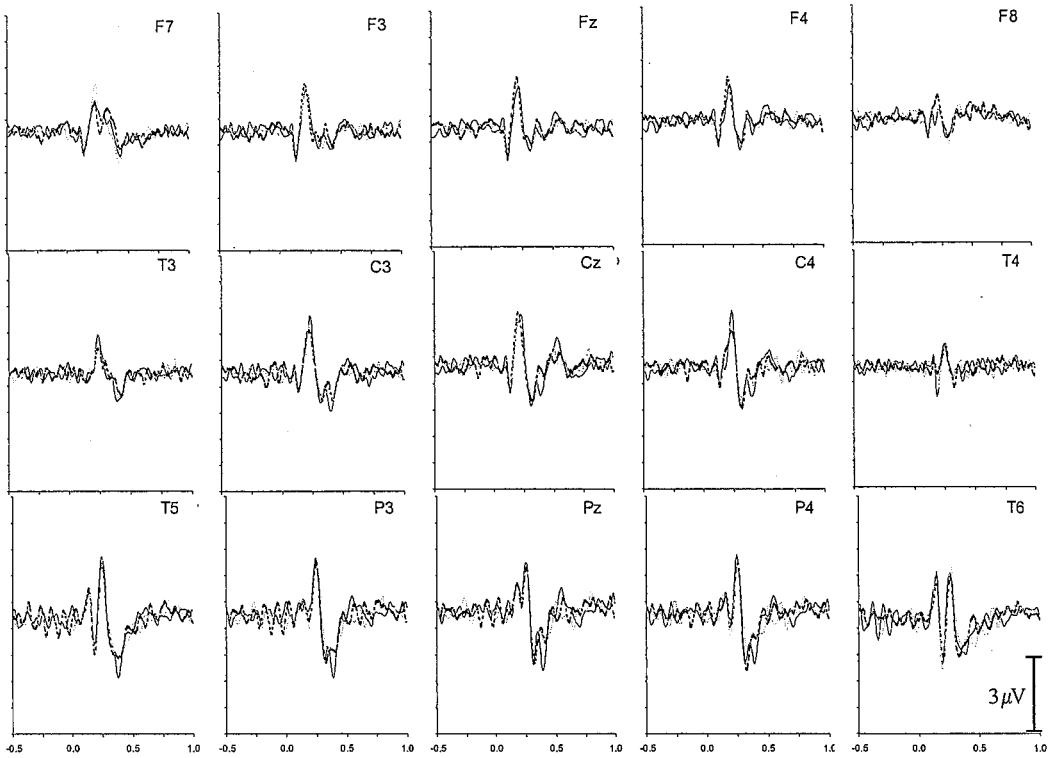

Figure 8.3 Choice 1 Evoked potentials in the early task phase.
Figure shows early task phase (trials 1-30) variations across recording sites, in averaged, EEG traces for the 0.5s after the onset of the countdown stimuli, and the 0.5s before and after. 0s represents the onset of the countdown stimuli. Dotted black line represents rewarding trials (trials 1-30). Black line represents conflicting trials (conflict). Grey line represents punishing trials.

Figure 8.4 shows early task phase EEG traces across recording sites for the rewarding, conflicting and punishing trials in **Choice 2**. Evoked potentials in the conflicting trials did not differ from the rewarding and punishing trials.

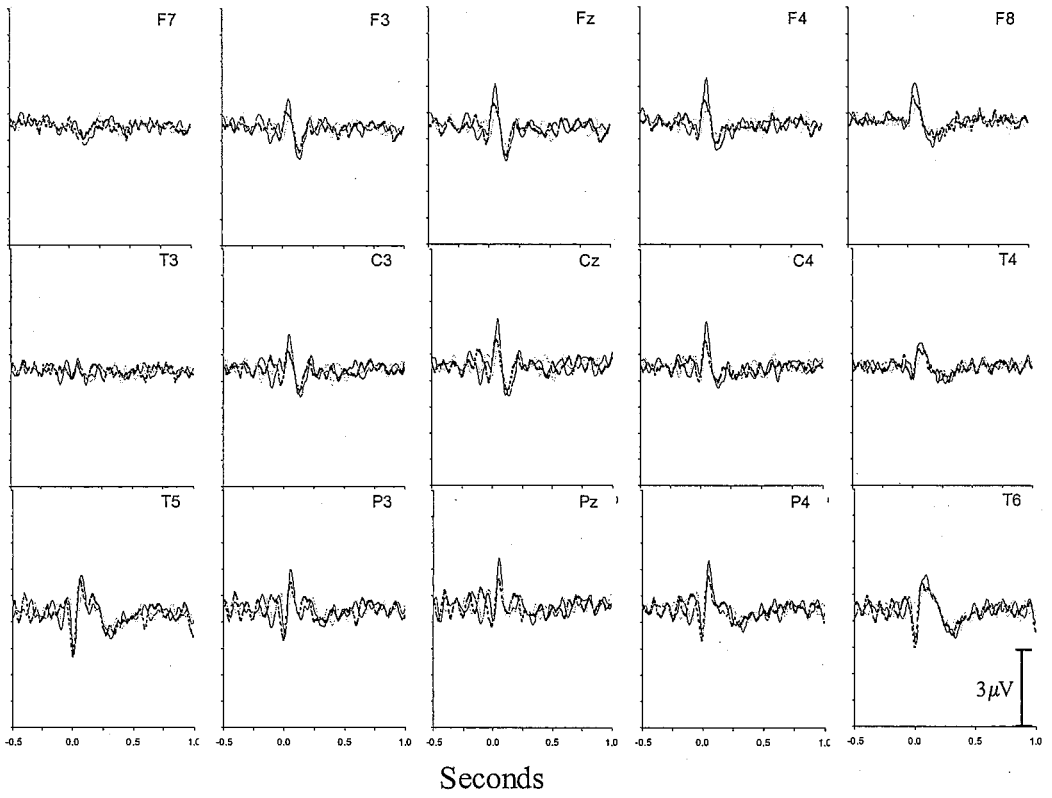

Figure 8.4 Choice 2 Evoked potentials in the early task phase
Figure shows early task phase (trials 1-30) variations across recording sites, in averaged EEG traces for the 0.5s after the onset of the countdown stimuli, and the 0.5s before and after. 0s represents the onset of the countdown stimuli. Dotted black line represents rewarding trials. Black line represents conflicting trials (conflict). Grey line represents punishing trials.

Figure 8.5 shows late task phase EEG traces across recording sites for the rewarding, conflicting and punishing trials in **Choice 2**. Evoked potentials did not differ across conditions. Although evoked potentials at Fz in the conflicting trials appear larger, this was not reliable.

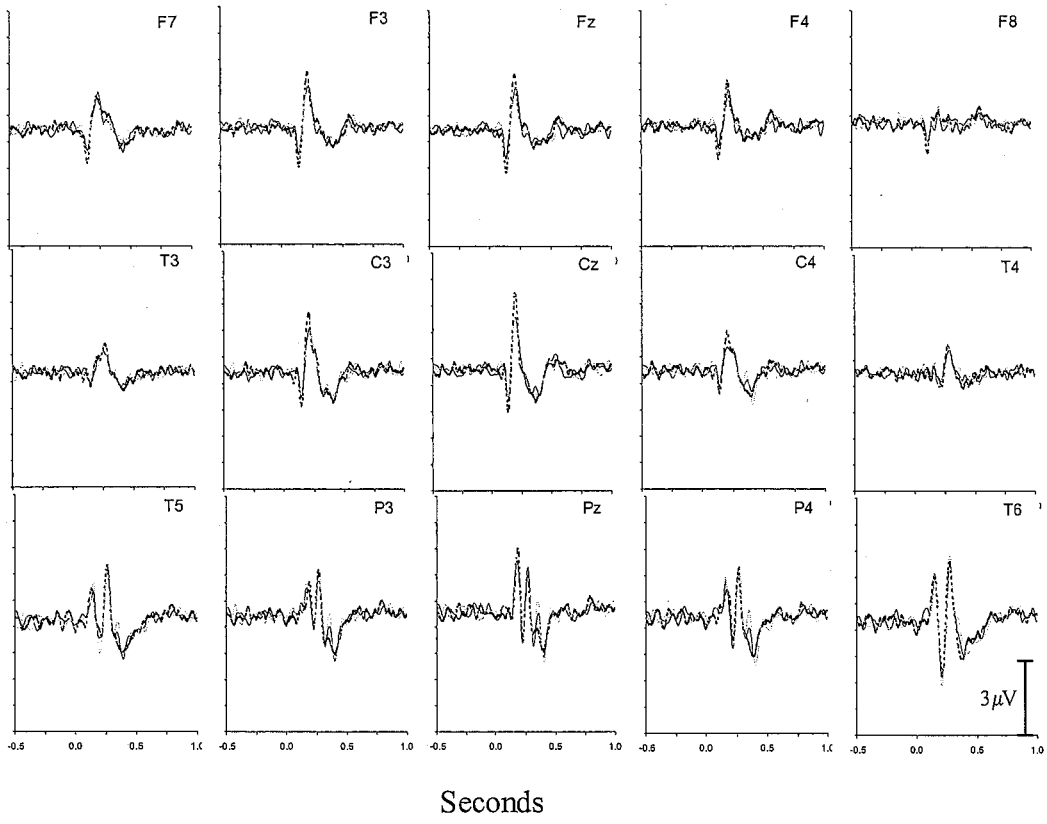

Figure 8.5 Choice 2 Evoked potentials in the late task phase
Figure shows late task phase (trials 61-90) variations across recording sites, in averaged EEG traces for the 0.5s after the onset of the countdown stimuli, and the 0.5s before and after. 0s represents the onset of the countdown stimuli. Dotted black line represents rewarding trials. Black line represents conflicting trials (conflict). Grey line represents punishing trials.

Figure 8.6 shows early task phase EEG traces across recording sites for the rewarding, conflicting and punishing trials in **Choice 3**. Evoked potentials in the conflicting trials at these sites did not differ from the rewarding and punishing trials.

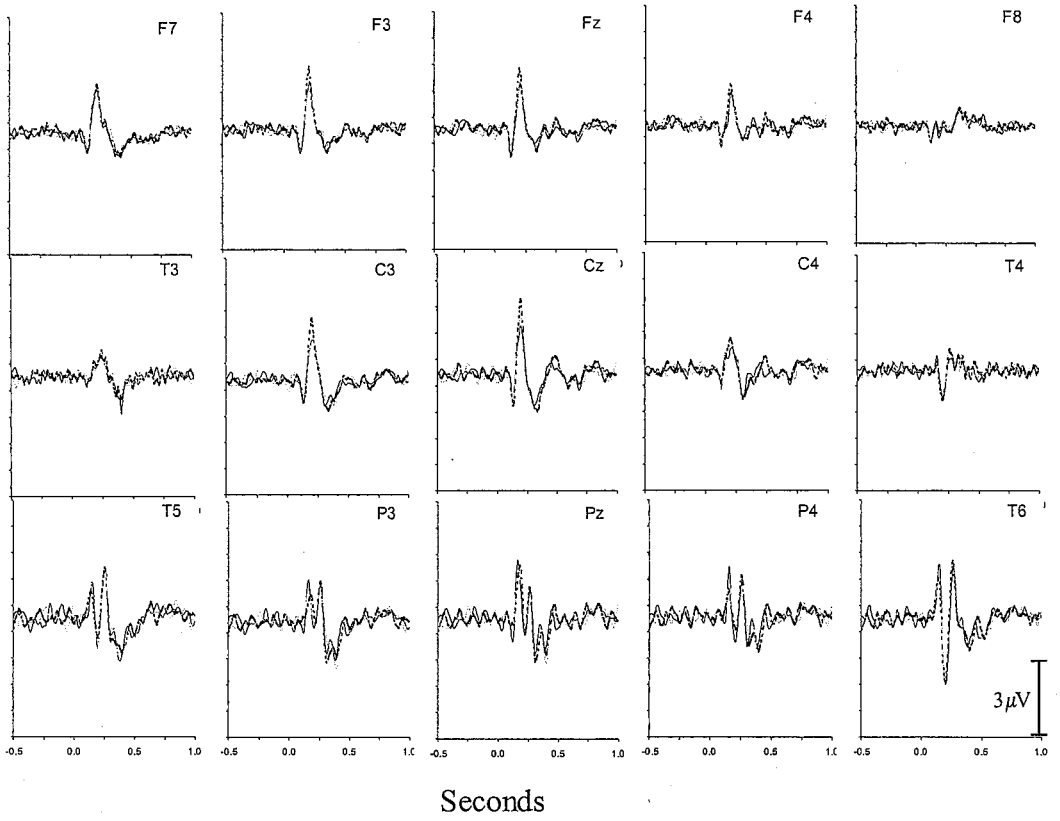

Figure 8.6 Choice 3 Evoked potentials in the early task phase.

Figure shows early task phase (trials 1-30) variations across recording sites, in averaged EEG traces for the 0.5s after the onset of the countdown stimuli, and the 0.5s before and after. 0s represents the onset of the countdown stimuli. Dotted black line represents rewarding trials. Black line represents conflicting trials (conflict). Grey line represents punishing trials.

8.4 Conclusions

There was no evidence of variations in the size of the evoked potentials across experimental conditions in the **SST** and **Choice** experiments. This suggests that evoked potentials detected in these records were likely to be uncorrelated to the increase in theta spectra power elicited by conflict. It appeared that goal-conflict did not lead to detectable phase-locking activities in the **SST** and **Choice** experiments.

9 Discussion

9.1 Summary of EEG results [2]

In the Stop Signal Task (**SST**), over the midline and right frontal areas (Fz, F4 and F8), conflict between Stop and Go appeared to produce a change in theta power that peaked in the intermediate stop-signal delay trials at 7 and 8 Hz. Conflict activation was assessed as the difference in activity immediately following stop-signal presentation compared to the same time point in the immediately preceding Go trial (Stop-Go). This rules out a contribution from processes associated with the presentation of the Go signal and preparation and execution of the Go response, and any anticipatory activity in expectation of a Stop response.

Although Fz, F4 and F8 also appeared to show overall increases in conflict activity in the Stop trials, these changes were not reliable. Reliable conflict activity was observed in Go trials at the right frontal site F8, at 4, 5, 6, 11 and 12 Hz.

In **Choice 1**, the probability of gain versus loss from making a left click was fixed at 50%. The value of gain was fixed at +10 cents. The value of loss was fixed at 0, –10 or –20 cents. Goal-conflict activation was assessed as the difference between the conflicting (+10/-10) and the average of the rewarding (+10/ 0) and punishing (+10/ -20) conditions. In the early task phase (trials 1-30), goal-conflict elicited maximal activity in the human theta frequency range (averaged 4-7 Hz). Conflict activity was detected from the lateral frontal site F8 in the right hemisphere and from the lateral posterior sites at T3 and T5 in the left hemisphere. Reliable conflict activity was not observed in the late task phase (trials 51-80).

In **Choice 2**, goal-conflict was manipulated in a different way from **Choice 1**. Other task parameters remained unchanged. The values of the reward and punishment were fixed at +10 and –10 cents. The probabilities of reward to punishment varied from

[2] Note that significant liner trends across the three key experimental conditions were not detected in any of the statistical analyses in the **SST** and **CHOICE.**

75:25, 50:50 and 25:75 across the rewarding, conflicting and punishing conditions respectively. Goal-conflict activity was assessed as the difference between the conflicting condition (50:50) and the average of the rewarding (75:25) and punishing conditions (25:75). In the early task phase, goal-conflict elicited maximal activity in the human lower theta band (averaged 4-5 Hz) from the right frontal site at F8 and right temporal site T4. Although right lateral sites F8, T4 and T6 appeared to show averaged 6-7 Hz conflict activity, this was not reliable after Bonferroni correction.

In the late task phase (trials 51-80) of **Choice 2**, averaged 4-7 Hz conflict activity was stronger at the midline and weaker at the sides in the frontal regions, peaking at the midline site Fz. In the posterior regions, conflict activations (averaged 4-7 Hz) were weaker in the midline and stronger at the sides, peaking at T4 and T5.

In **Choice 3,** changes made to the paradigm pertained to shortening the time it took to complete the task. Since goal-conflict was manipulated across the rewarding, conflicting and punishing conditions in the same way as in **Choice 2,** its effects were assessed in the same way as in **Choice 2**. In **Choice 3**, goal-conflict increased human theta activity (averaged 4-7 Hz) at the lateral frontal site in the left hemisphere at F7. There also appeared to be conflict activation (averaged 4-7 Hz) at F8 in the right hemisphere but the reliability of this effect only approached statistical significance. However, when data were pooled from all three **Choice** experiments, a reliable conflict effect was observed at F8. There was no evidence that this effect varied in size across the **Choice** experiments.

In none of the four experiments was there any evidence of goal-conflict related changes in evoked potentials as estimated by untransformed waveforms averaged across trials. This rules out a contribution of evoked potentials to goal-conflict related changes in rhythmic activity assessed by spectral power.

9.2 Summary of correlations between goal-conflict and behavioral measures of avoidance

Gray and McNaughton (2000) viewed a pre-potent response as approach behavior. The inhibition of the pre-potent response is seen as avoidance behavior. In the **SST**, Go trials required participants to make a mouse click in response to an arrow. The mouse click was, therefore, the pre-potent response. If the stop-signal (a tone) was later presented, participants were required to withhold (inhibit) their response. The time taken to stop the Go response, the Stop-Signal Reaction Times (SSRT), was estimated by subtracting a participant's average Stop-signal delays (SSDs) in the Stop trials from his median Reaction Times (ms) in the Go trials. Faster SSRT provided a measure of increased avoidance tendencies.

In the **Choice** tasks, a left click produced monetary rewards and was the pre-potent response. In the conflicting condition in all three **Choice** tasks, a left click either produced a gain or loss of 10 cents with equal probability. If a participant made a right click, the participant gave up the chance to make money but also avoided the risk of losing money. Avoidance tendencies were thus estimated with the reduction in the number of left clicks.

In the **SST**, no significant correlations were detected between conflict activity and SSRT. In **Choice 1**, in the early task phase, higher 4-5 Hz conflict activations at T3 predicted fewer left clicks in the conflicting condition. In **Choice 2**, higher 4-5 Hz conflict activations at T5 in the late task phase predicted fewer left clicks in the conflicting condition. In **Choice 3**, higher 4-5 Hz conflict activations at F8 predicted fewer left clicks in the conflicting condition.

9.3 Goal-conflict as a class of mechanisms separable from simple approach/avoidance

In the three **Choice** experiments, goal-conflict was experimentally manipulated. Monetary punishment was proportionately varied, keeping reward constant. This ruled out a contribution of simple reward, net payoff and simple punishment to the quadratic

trend used to estimate conflict since all of these are linear with respect to changes in punishment. Theta activity peaked in the intermediate condition where goal-conflict was the greatest, compared to activity in the adjacent conditions where simple approach/avoidance predominated. This suggests that goal-conflict, and not simple avoidance elicited the increase in spectral power. Notably, goal-conflict specific theta activity was consistently observed at the right lateral frontal site F8 in the **Choice** tasks. The **SST**, a different paradigm, also appeared to elicit conflict-specific theta activity at F8. Therefore, goal-conflict specific theta activations were consistently observed at F8 across all four experiments conducted here. This rules out the detection of goal-conflict specific theta by chance.

The current results support Gray and McNaugthon's (2000) view that goal-conflict is a class of mechanism separable from simple approach and avoidance. This is consistent with Perkins, Kemp and Corr (2007) findings of separate personality constructs for anxiety and fear, which are currently viewed as the emotional dimensions of goal-conflict related avoidance and simple active avoidance respectively.

9.4 Goal-conflict activity predicted increased avoidance tendencies

Gray and McNaughton (2000) proposed that goal-conflict induces changes in brain processing and behaviors when incompatible, concurrently activated, approach and avoidance tendencies are detected as approximately equal in strength. The effects of goal-conflict are superimposed on simple effects and could have similar outcomes such as increasing avoidance, attention and arousal. This makes it difficult to assess their unique contributions on behaviors. The index of goal-conflict developed here allowed us to identify goal-conflict specific activations and assessed their impact on behaviors.

Across the three **Choice** experiments, the observed relations between goal-conflict specific theta and avoidance were consistently in the lower human theta band (4-5 Hz). Critically, the relations were consistently in the direction predicted by Gray and McNaughton (2000). Goal-conflict theta accounted for 27 %, 20 % and 18 % of the variances in avoidance behaviors in **Choice 1, 2, 3** respectively. On average, they accounted for about 20 % of the variances in avoidance behaviors. This suggests that

goal-conflict processing could have amplified avoidance behavior in the current experiments by about 1.25 times (100% divided by 80%). The present findings support Gray and McNaughton's (2000) proposition that goal-conflict is resolved via recursive amplifications of existing avoidance tendencies.

However, note that in the **Choice** experiments, the relations between goal-conflict activations and increased avoidance shifted between regions and task phases. In **Choice 1,** T3 in the left hemisphere predicted increased avoidance in the early phase. In **Choice 2**, conflict activations also predicted increased avoidance in the left temporal cortex but at T5 and only in the late phase. Although goal-conflict activations were observed consistently at F8 above the right frontal cortex, it only predicted increased avoidance in **Choice 3.**

Also note that goal-conflict activations did not predict inhibition times (SSRTs) in the **SST**. The **SST** was a speeded response task. It is possible that goal-conflict related information could not reach the motor system in time to effect any observable impact (see section 9.7.2 for the discussion on its neural basis). In the **Choice** experiments, participants had to wait between one to three seconds before they could make a response. This should allow sufficient time for information to reach the motor system to exert observable changes on behaviors. Therefore, effects of increased avoidance were detected.

9.5 Cortical rhythms within rodent hippocampal theta frequency range (4-12 Hz) as an index of goal-conflict

In the current experiments, goal-conflict specific rhythmic activity, estimated by Fourier transform, was detected in the human theta frequency range (4-7 Hz) in the **Choice** tasks. This is consistent with previous findings (Cohen, et al., 2007; Moore, et al., 2006) implicating human theta in goal-conflict processing. However, in the **SST**, goal-conflict specific activity was observed at 8, 11 and 12 Hz, which are frequencies in the human alpha band (8-12 Hz). Taken together, the current findings support Gray and McNaughton (2000) suggestion that goal-conflict processing recruits and increases

cortical rhythmic activity within the same frequency range as rodent hippocampal theta (4-12 Hz).

9.6 Assessing the involvement of the hippocampal system

Gray and McNaughton (2000) viewed the hippocampus as a goal comparator that detects and resolves goal-conflict. In the rodent hippocampus, theta activity is predominant and is necessary but not sufficient for functional output from the hippocampus. The presence of theta appears crucial for efficient processing of information and, according to Gray & McNaughton (2000), packages information when it is being recursively processed between hippocampus and other brain areas. Therefore, the transmission of hippocampal output to neural areas mediating goal-directed behaviors, such as the motor system, is likely to involve superimposition of the phasic aspects of hippocampal theta activity on the receiving neurones.

In humans and rodents, it has also been demonstrated that cortical 4-12 Hz rhythmic activity can be coherent with hippocampal 4-12 Hz activity (Ekstrom, et al., 2005; Jones & Wilson, 2005). In particular, Siapas, Lubenov and Wilson (2005) showed that rodent hippocampal theta could modulate cortical theta (coherent prefrontal theta occurred later than hippocampal theta). If the cortical theta observed here is the result of modulation by hippocampal theta, it should show hippocampal theta-like characteristics.

In rodents, hippocampal theta frequency changes when the intensity of motor movements is changed (Vanderwolf, 1969). More intense motor movements like rearing and running are associated with high frequency theta (more than 6 Hz). Less intense motor movements such as lever pressing is associated with lower frequencies (Vanderwolf, 1969). In the current work, the **Choice** tasks required relatively less intense motor movements than the **SST** since response speed was not a task demand. Hippocampal-like cortical theta should therefore occur at relatively lower frequencies in the **Choice** tasks compared to the **SST**. In the **Choice** tasks, conflict theta occurred at 4-7 Hz. In the **SST**, Stop-Go conflict theta occurred at higher frequencies, at 7 and 8 Hz in the Stop trials, and at 11-12 Hz in the Go trials. Cortical theta observed here,

therefore, showed hippocampal theta-like frequency characteristics. So it appears that goal-conflict specific theta observed here could, in principle, reflect related hippocampal activity.

If the hippocampus modulates cortical activity during goal-conflict resolution, we should see hippocampal activation in existing studies that include components of goal-conflict, particularly, the **SST**. To my current knowledge, there are no existing iEEG studies on the **SST**. Hippocampal activations measured with *f*MRI were implicated only in a related paradigm, the Go/NoGo task (Goldstein, et al., 2007). *f*MRI hippocampal activations have not been reported in the **SST**. This could be because activations in the hippocampus were not examined given the current focus on frontal cortical involvement in the **SST**. It is also possible, that some goal-conflict related changes in theta do not induce sufficiently large metabolic changes to be detected by *f*MRI.

An equally likely possibility is that there was no functional hippocampal output to the frontal cortex in the present experiments. There is evidence of cortical generation of theta activity that is independent of hippocampal theta (Raghavachari, et al., 2006; Young & McNaughton, 2008). Further, in Gray and McNaughton's (2000) theory, the hippocampus is only one node (albeit the central one) in a hierarchy of modules, each of which can control some aspects of behavioural inhibition. These modules range from the periaqueductal gray to the dorsal lateral prefrontal cortex and cingulate cortex. The precise cortical modules allocated to specific functions by Gray and McNaughton (2000) are based more on general theoretical considerations than detailed data.

Currently, there is little empirical data that identify specific cortical units with goal-conflict resolution. However, the critical point in the current context is that Gray and McNaughton (2000) explicitly stated that modules other than the hippocampus could resolve goal-conflict under appropriate conditions. Interestingly, although their analysis of the BIS was primarily based on data on the effects of anxiolytic drugs, they considered the possibility that the prefrontal or cingulate cortex may not only operate

independently of the hippocampus but control anxiety and behavioural inhibition that is anxiolytic insensitive, unlike hippocampal dependent conflict processes.

The above statements by Gray and McNaughton (2000) suggest that the involvement of the hippocampal system can be assessed with the effects of anti-anxiety drugs on cortical theta. Gray and McNaughton (2000) found that anti-anxiety drugs share common behavioral effects with hippocampal lesions and that all classes of anti-anxiety drugs appear to produce similar changes in hippocampal theta (McNaughton, et al., 2007). If the effects of anti-anxiety drugs on 4-12 Hz rhythmic activity are specific to the hippocampal system, cortical theta that is *dependent* on the hippocampal system should be s*ensitive* to anxiolytic actions. Cortical theta that is *independent* of the hippocampal system should be *insensitive* to anxioytic actions.

9.7 Roles of goal-conflict specific theta across different recording sites

Across the four experiments, goal-conflict consistently elicited theta activations at the right lateral frontal site F8. Goal-conflict theta was also observed at a) the temporal sites represented by T3, T4, T5 and T6; b) the frontal sites represented by Fz and F4 and c) the left lateral frontal site represented by F7. In the Gray and McNaughton (2000) model, goal-conflict resolution produces several outputs. When goal-conflict is detected, pre-potent overt responses are inhibited; existing simple avoidance tendencies are amplified; exploration is initiated (including memory scanning); and attention and arousal increase. The current data could not separate these outputs. The following discussion on the possible roles of goal-conflict theta is, therefore, speculative.

9.7.1 Conflict activations at F8

As discussed in chapter 3, there are caveats to interpreting maximal activity in the intermediate trials in the **SST** as being specific to goal-conflict. If simple inhibitory activity did not scale linearly with SSDs (see section 3.4), "conflict" activity in the **SST** could just reflect simple avoidance-related activity. However, goal-conflict-related activity was consistently observed in the right lateral frontal region (F8) not only in the **SST** but also in the **Choice** tasks. If we accept that the parallel with the **Choice** tasks shows that goal-conflict activity was observed in the **SST**, we then open

up the possibility that the right inferior frontal gyrus (IFG) was the source of the EEG at F8.

A study by Okamoto et al., (2004) tried to identify neural structures that are under the cortical surface of electrodes placed according to the international 10-20 system (electrode placement system used in the current work). They found that F8 is likely to be placed above the right IFG (Brodmann's area 47 and 45). Admittedly, the projection of EEG signals is three-dimensional and may not necessarily project to the cortical surface directly above. But in *f*MRI studies, the stop-signal in the **SST** consistently activated the right IFG (Aron, Robbins, & Poldrack, 2004). Given the right IFG's links with the **SST,** the right IFG was the most likely source of the EEG at F8 in the current **SST.**

The right IFG is thought to play a role in response inhibition (Aron, 2007; Aron, Robbins, et al., 2004; Robbins, 2007) and may have functional significance (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003). A key study by Aron et al.(2003) showed that damages in the right IFG during stopping in the **SST** slowed inhibition times (estimated with SSRTs). The right IFG could be a key node in one of many pathways responsible for relaying "what not to do" information to the motor system. How "what not to do" information from the right IFG is relayed to the motor system to produce behavioural inhibition is still unclear. But there is evidence of a circuit involving the subthalamic nucleus (Aron, 2007; Aron, Behrens, Smith, Frank, & Poldrack, 2007). Aron (2007) suggested that information from the right IFG is relayed to the motor system via a pathway involving the subthalamic nucleus, the globus pallidus pars interna (Gpi) and the thalamus (see also Nambu, Tokuno, & Takada, 2002). This pathway is shown in figure 9.1. Figure 9.1 shows the neural circuits in goal-conflict processing detailed as a result of the current work.

Gray and McNaughton (2000) suggested during goal-conflict resolution, hippocampal outputs are likely relayed to the cortical regions via the Papez circuit involving the mamillary bodies (MB) and the thalamus. However, Gray and McNaughton (2000) has not detailed the pathways hippocampal outputs could be relayed to the motor system to

control behavioral inhibition. If goal-conflict theta activations at F8 reflected right IFG activity and was hippocampal related, then Aron's (2007) right IFG pathway could be part of a circuit that relays "what not to do" information from the hippocampus to the motor system. Thus, in figure 9.1, I have linked the Papez circuit to the right IFG to form a more detailed circuit than previously suggested by Gray and McNaughton (2000).

Goal-conflict specific theta activations at F8 were consistent across the current experiments and so appeared task-independent. This suggests that the right IFG could itself be a conflict-detector and mediator. It could have similar functions to those attributed to the hippocampus by Gray and McNaughton (2000), and so require phasic theta activity, but operate independently of the hippocampus.

The right IFG is currently not an explicit module in the Gray and McNaughton (2000) model of goal-conflict resolution. In either case, the current findings raise the possibility that the IFG should be included in the Gray and McNaughton (2000) model as another key module.

9.7.2 Conflict activations in other frontal sites

In the **SST**, the frontal midline site Fz and the adjacent site to the right, F4, showed conflict processing (Stop-Go activations) in addition to F8. Activity at these sites could also reflect the relay of "what not to do" information to the motor system. But they are likely to be recruited to inhibit very fast responses. Activity at F8/right IFG could be recruited to inhibit slower responses.

Floden and Stuss (2006) reported that patients with right superior medial lesions such as the presupplematary motor area (preSMA) showed slower SSRTs in the **SST**. Their findings suggest that the preSMA could also be important for behavioral inhibition, in addition to the right IFG. An earlier Go/NoGo study by Garavan et al. (2002) found that right lateral frontal regions including the IFG were associated with successful stopping when Go speed was slow. The frontal regions closer to the midline such as the anterior cingulate and preSMA were associated with successful stopping when Go

speed was fast. Critically, patients in the study by Floden and Stuss (2006) had faster reaction times in the Go trials compared to patients with right IFG lesions in Aron et al (2003) study, who had also shown slower SSRTs. Hence, Floden and Stuss (2006) proposed a "kill-switch" inhibitory system that recruits frontal sites closer to the midline to inhibit very fast responses. The more lateral regions, such as the right IFG, are recruited when responses are slower.

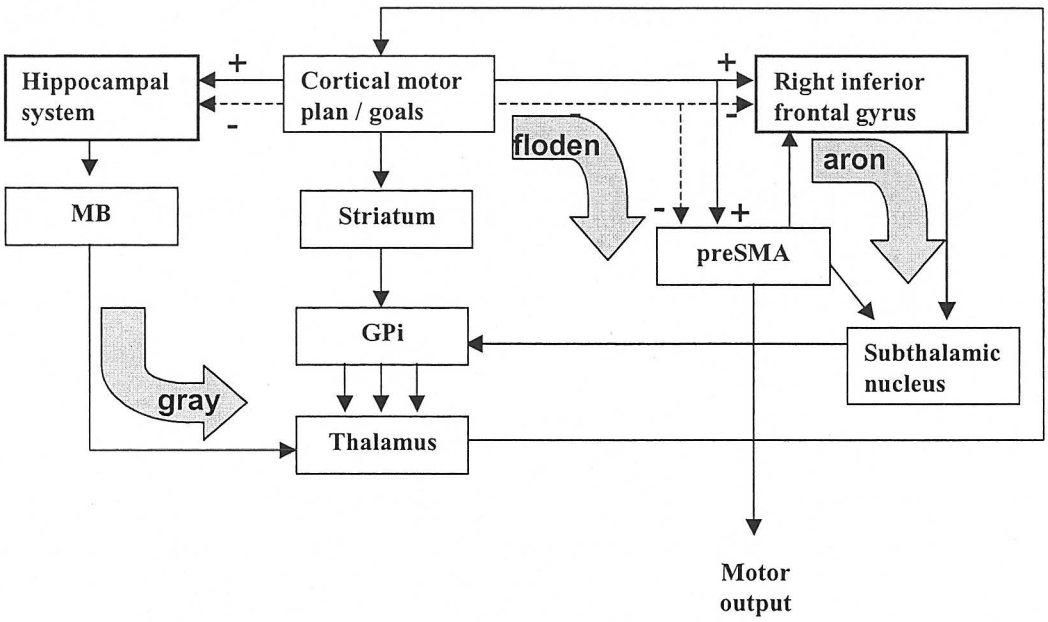

Figure 9.1 Neural circuits of goal-conflict processing.
The figure is adapted from Aron (2007); Floden and Stuss (2006); and Gray and McNaughton (2000). Positive and negative inputs represent efferent copies of goal information on activated approach (+) and avoidance (-) tendencies. They indicate areas that could detect concurrently activated approach and avoidance tendencies, i.e. areas that could function as goal-conflict detectors, for example, the hippocampus. Dotted arrows denote goal information on avoidance tendencies. The interconnections between the right inferior frontal gyrus, the preSMA and the subthalamic nucleus are added based on diffusion-weighted imaging tractography work by Aron et al. (2007). **MB**: mamillary bodies **Gpi:** Globus pallidus pars interna **preSMA**: presupplementary motor area

In the current **SST**, the medial and lateral right frontal regions (Fz, F4 and F8) were co-activated. Varying speed of Go responses across trials and participants could lead to the co-activations of both the "kill-switch" and the "right IFG" circuits in the relay of "what not to do information" during goal-conflict resolution. The extent each system controls behavioral inhibition depends on the response speed. The right IFG has a bigger impact when response is *slow*. The preSMA has a bigger impact when response is *fast*. Note that when response speed is *very fast*, these systems could be activated but the "what not to do" information may not reach the motor system in time to have any impact on behavior. This could explain why there was no relation between SSRTs in the current **SST** and goal-conflict theta activations. This is supported by a comparison between the Go trials reaction times in the current **SST** and the Go trials reaction times in the healthy controls in Floden and Stuss (2006) study. Participants in the current **SST**, on average, had faster reaction times (about 450 ms) than controls (490ms) in Floden and Stuss (2006) study.

The likelihood of Fz and F4 conflict activations observed in the current **SST** reflecting anterior cingulate and preSMA activity is unclear. For theoretical considerations, as in the case with right IFG, I incorporated Floden and Stuss's (2006) "kill switch" system represented by the preSMA into the neural circuits of goal-conflict processing in figure 9.1. This represents another pathway that hippocampal outputs could be relayed to the motor system to control behavioral inhibition during goal-conflict resolution. As in the case with the right IFG, the preSMA could also be in itself a conflict detector and mediator. It could have similar functions attributed to the hippocampus in Gray and McNaughton's (2000) model of goal-conflict resolution, but operate independently of the hippocampus.

Note that the "kill-switch" explanation cannot account for the Fz conflict activation observed in **Choice 2**, because response speed was not a task requirement. It is possible that Fz activations in **Choice 2** represented different goal-conflict processing from that in the **SST**. Fz activity observed in **Choice 2** could be related to arousal as a

result of the high pressure and unpredictability generated by the task demands in **Choice 2.**

Apart from the **SST**, Fz conflict activity was observed only in the late phase (trials 51-80) in **Choice 2.** The behavioral responses in the conflict conditions across the **Choice** tasks suggest that the early phase (trials 1-30) represented active resolution of the conflict. The number of left clicks being made decreased steadily over trials, stabilizing by the late phase. The stabilization of the responses in the late phase suggests that the conflict had been resolved and replaced by simple habit. The combination of high pressure (due to participants having to meet a target before they could make extra cash) and unpredictability (not being informed of the payoffs) in **Choice 2** could have created the urgency to check if the experimental conditions had changed. This could lengthen the conflict resolution process and account for conflict effects related to arousal in the late phase.

In **Choice 3**, the left prefrontal site F7 showed goal-conflict activity in addition to F8 in the right hemisphere. Robbins (2007) suggested that the left prefrontal cortex could be involved in maintaining current task demands (Aron, Monsell, Sahakian, & Robbins, 2004; D'Esposito, Postle, Jonies, & Smith, 1999; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; Robbins, 2007). Aron, Monsell, Sahakian and Robbins (2004) compared performance deficits in a task-switching experiment between patients with left or right frontal lesions. Patients with left frontal cortical lesions, compared with controls and with right frontal lesion patients, took longer to respond if the previous trial involved different task demands. Patients with right lesions, however, made more mistakes. The left lateral frontal cortex could be important for a sufficiently quick response to the current task when there was interference from the previous trial. It could be important for increasing attention to resolve the conflict. In **Choice 3**, there was less time for deliberation before a mouse click had to be made, compared to **Choice 1** and **2** (one second versus three seconds). It is possible that F7 was activated to suppress interference from previous trials, given it was now important to allow more focused attention in the relatively less time available to resolve the conflict in the current trial.

9.7.3 Conflict activations in the temporal cortex

Temporal site conflict activations (T3, T4, T5 and T6) were observed in **Choice 1** and **2**. Lesions to the neo-cortical regions of the temporal lobes sparing the hippocampus in human patients have caused memory deficits (see Lah & Miller, 2008 for a recent review). It is possible that conflict processing in the neo-cortical regions of the temporal lobe in **Choice 1** and **2** represented some form of memory-related activity. It could reflect the amplification of the loss aversion from previous trials during the scanning for information to resolve the goal-conflict. In **Choice 1** and **2**, participants had three seconds to deliberate over their previous and/or next moves before they could make a response. It is likely that in this period, participants would try to recall outcomes of previous trials to solve the task. In this case, altering the memories of the loss aversion from previous trials should be the most efficient way to change the balance of concurrently activated tendencies. The lack of conflict activations in the temporal cortex in **Choice 3** and the **SST** support the above suggestion. In **Choice 3,** there was only a one second wait before participants could make a response. So a less deliberative and more intuitive strategy was probably adopted to solve the task. The **SST** was a speeded response task and should not recruit deliberative memory processes.

9.8 Future directions

The current investigation on goal-conflict processing has raised several issues that future studies should address. Clarifying the conditions in which goal-conflict processing affects overt behavior should explain why behaviorally related goal-conflict theta was not consistently observed across experiments, brain regions and task phases. Identifying the roles of goal-conflict theta in the different regions should partly resolve the above issue. Determining the source of the EEG would be critical for clarifying their functional roles. This is likely to be pursued with *f*MRI studies. However, note that *f*MRI may not be informative on goal-conflict changes dependent on theta activity that do not involve large changes in metabolic demand.

Gray and McNaughton (2000) explicitly stated that modules other than the hippocampus could resolve goal-conflict under appropriate conditions. They raised the possibility that the prefrontal or cingulate cortex may not only operate independently of the hippocampus but control anxiety and behavioural inhibition that is anxiolytic insensitive, unlike hippocampal dependent conflict processes. Future studies should attempt to ascertain hippocampal related and hippocampal independent goal-conflict processes. The theta index of goal-conflict developed in the current work could be used in future studies to profile axiolytic actions on goal-conflict related theta and its relations with changes in behaviours.

9.9 Conclusions

Gray and McNaughton's (2000) theory of a neural system involved in goal-conflict resolution implies that there are at least two classes of avoidance processes. One is goal-conflict related and the other simple avoidance related. Goal-conflict effects are superimposed on simple approach/avoidance effects. Therefore, their effects on brain processing and behaviors are often confounded. The method developed here using superficial theta to index goal-conflict effects was crucial for identifying goal-conflict as a class of mechanisms, separable from simple avoidance. The method also made it possible to assess the contribution of at least one measurable aspect of goal-conflict processing in the brain to avoidance behaviour. The current work showed that goal-conflict theta predicted increased avoidance under some conditions. This is consistent with Gray and McNaughton's (2000) view that goal-conflict is resolved by increasing the subjective value of punishment, thereby increasing avoidance tendencies.

Goal-conflict specific theta activations within the human theta frequency range (4-7 Hz) were consistently activated in the **Choice** tasks. However, in the **SST**, conflict-related activations spanned the conventional human theta and alpha frequencies and appeared specific to the same phenomenon – goal-conflict. This suggests that future studies on goal-conflict processing in humans should continue to examine both human theta and alpha activity.

The current work also identified possible neural modules and circuits that are not explicit in the current Gray and McNaughton (2000) model of goal-conflict resolution. The right IFG and its related circuit could be recruited to inhibit relatively slow responses. The preSMA could be recruited to inhibit faster responses. Although speculative, the current findings suggest that the right IFG and preSMA could be incorporated into existing modules in Gray and McNaughton's (2000) model of goal-conflict resolution.

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Appendix 1: Information sheet and consent form for SST

STOP SIGNAL INHIBITION INFORMATION SHEET FOR PARTICPANTS

This project investigates how fast we make and withhold responses to environmental stimuli. Your reaction times will be recorded during a computer-based task. You will also be asked to complete questionnaires that measure aspects of your mood and personality. If you are participating in the EEG version of this experiment, we will also record your brain activities during the task The behavioural experiment will take about 1 hour and the EEG version may take up to 2 hours. Please read the information in the following paragraphs carefully if you are participating in the EEG experiment.

People in the categories listed below will not be able to participate **in the project because it may involve an unacceptable risk to them:**

- a prior history of affective disorder
- received any medical or psychological treatment for anxiety, depression or emotional disorder within the last 12 months
- a prior history of drug abuse
- previous allergic skin reactions to chemical agents including detergents
- if taking aspirin or any other drugs that irritate the stomach, such as steroids or anti-inflammatory drugs
- if suffering from acute or chronic physical disease such as heart and lung disease, influenza, diabetes, epilepsy or acute infections
- if recovering from an accident, injury or operation
- if drinking regularly to relieve stress or get to sleep
- if you are pregnant

Brain activities can vary substantially between different age groups. There are also left and right brain differences. For these reasons, we are *only recruiting right-handed participants between 18 and 25 years old.*

Preparation for the experiment

Hair products and natural oils on our scalp make it difficult to record your brain rhythms. It is important to us that you come with a clean scalp. *Avoid using any hair products* on the day of the experiment. For participants with glasses, we recommend that you wear contact lenses if possible for your own comfort.

Brain rhythms recording procedure

You will put on an electro-cap as shown in the picture. We will fill the electrodes (small metal discs) attached to the cap with a gel that conducts brain signals from your scalp to our recording system. To achieve good recordings, we will abrade your skin gently after applying the gel. The electrodes are then connected to an amplifier that allows us to record your brain rhythms. The whole system has been tested and passes the current standards for connecting electrical equipment to people.

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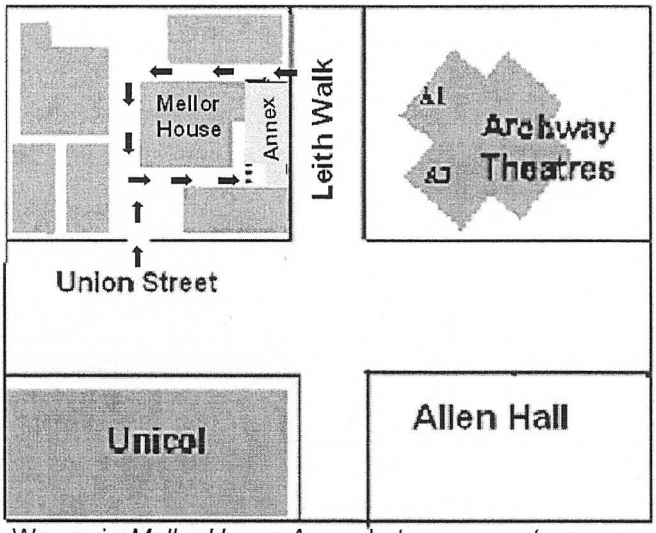

We are in *Mellor House Annex* but you *cannot access* us *from Mellor House*. There is only one access to our laboratory. Please *follow the arrows on the map*. You should come to a white wooden gate if you are in the right place.

This project has been reviewed and approved by _____

UNIVERSITY OF OTAGO

CONSENT FORM FOR

PARTICIPANTS

I have read the Information Sheet concerning this project. All my questions have been answered to my satisfaction. I understand that I am free to request further information at any stage.

I know that:

1. I am free to withdraw from experimental testing at any time without any disadvantage;
2. I have not received any medical or psychological treatment for anxiety, depression or emotional disorder within the last 12 months, I have never suffered from drug abuse and I am not subject to skin allergic reactions;
3. I am not taking aspirin or any other drugs that irritate the stomach, such as steroids or anti-flammatory drugs;
4. I am not suffering from acute or chronic physical disease such as heart and lung disease, influenza, diabetes, epilepsy or acute infections;
5. I am not recovering from an accident, injury or operation;
6. I am not drinking regularly to relieve stress or get to sleep;
7. the data will be destroyed at the conclusion of the project but any raw data on which the results of the project depend will be retained in secure storage for five years, after which it will be destroyed;
8. there may be some discomfort from the attachment and removal of the cap holding the electrodes and there will be a need to clean off the electrode gel;
9. the results of the project may be published but my anonymity will be preserved.

I agree to take part in this project.

.....
(Full name)

....
(Signature of participant) (Date)

This project has been reviewed and approved by _____

UNIVERSITY of OTAGO

Te Whare Wānanga o Otāgo

Appendix 2: Information sheet and consent form for the Choice paradigm

CHOICE EEG INFORMATION SHEET FOR PARTICPANTS

This project investigates how the electrical activities of our brain relate to our responses to monetary gains and losses. We will record your brain activities during a computer-based task. You will also be asked to complete questionnaires that measure aspects of your mood and personality before and after the task. The whole experiment will take about *1 hour and 30 minutes (may take up to 1 hour and 45 minutes).*

People in the categories listed below will not be able to participate **in the project because it may involve an unacceptable risk to them:**

- a prior history of affective disorder
- received any medical or psychological treatment for anxiety, depression or emotional disorder within the last 12 months
- a prior history of drug abuse
- previous allergic skin reactions to chemical agents including detergents
- if taking aspirin or any other drugs that irritate the stomach, such as steroids or anti-inflammatory drugs
- if suffering from acute or chronic physical disease such as heart and lung disease, influenza, diabetes, epilepsy or acute infections
- if recovering from an accident, injury or operation
- if drinking regularly to relieve stress or get to sleep
- if you are pregnant

Brain activities can vary substantially between different age groups. There are also left and right brain differences. For these reasons, we are *only recruiting right-handed participants between 18 and 25 years old.*

Preparation for the experiment

Hair products and natural oils on our scalp make it difficult to record your brain rhythms. It is important to us that you come with a clean scalp. *Avoid using any hair products* on the day of the experiment. For participants with glasses, we recommend that you wear contact lenses if possible for your own comfort.

Brain rhythms recording procedure

You will put on an electro-cap as shown in the picture. We will fill the electrodes (small metal discs) attached to the cap with a gel that conducts brain signals from your scalp to our recording system. To achieve good recordings, we will abrade your skin gently after applying the gel. The electrodes are then connected to an amplifier that allows us to record your brain rhythms. The whole system has been tested and passes the current standards for connecting electrical equipment to people.

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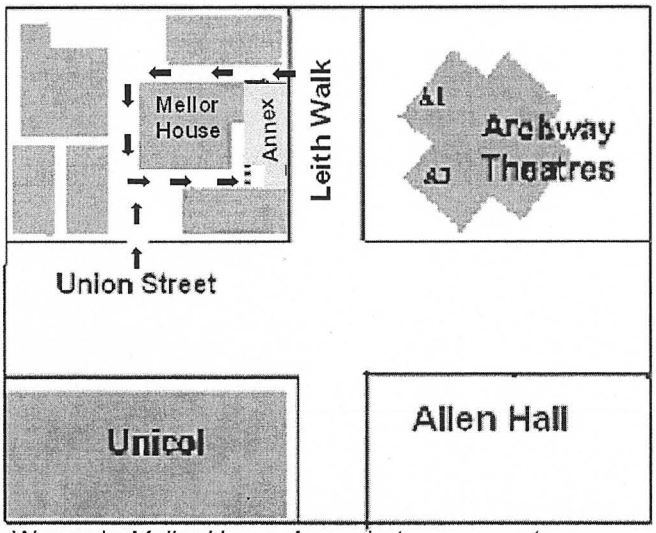

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This project has been reviewed and approved by the Lower South Regional Ethics Committee

UNIVERSITY OF OTAGO

CONSENT FORM FOR

PARTICIPANTS

I have read the Information Sheet concerning this project. All my questions have been answered to my satisfaction. I understand that I am free to request further information at any stage.

I know that:

- I am free to withdraw from experimental testing at any time without any disadvantage;
- I have not received any medical or psychological treatment for anxiety, depression or emotional disorder within the last 12 months, I have never suffered from drug abuse and I am not subject to skin allergic reactions;
- I am not taking aspirin or any other drugs that irritate the stomach, such as steroids or anti-flammatory drugs;
- I am not suffering from acute or chronic physical disease such as heart and lung disease, influenza, diabetes, epilepsy or acute infections;
- I am not recovering from an accident, injury or operation;
- I am not drinking regularly to relieve stress or get to sleep;
- the data will be destroyed at the conclusion of the project but any raw data on which the results of the project depend will be retained in secure storage for five years, after which it will be destroyed;
- there may be some discomfort from the attachment and removal of the cap holding the electrodes and there will be a need to clean off the electrode gel;
- the results of the project may be published but my anonymity will be preserved.

I agree to take part in this project.

.....
(Full name)

....
(Signature of participant) (Date)

This project has been reviewed and approved by the Lower South Regional Ethics Committee

UNIVERSITY of OTAGO

Te Whare Wānanga o Otāgo

Appendix 3: Feedback questionnaires used in the Choice paradigm

Choice 1

Feedback Sheet for participants

Thank you for participating in our study. Please answer the following questions as truthfully as possible; your answers may help us interpret any unexpected findings.

1. Did you try to spot a pattern in the outcomes?
   Yes/No (The outcomes were randomised.)

2. Did you think responding speed was important?
   Yes/No (It wasn't a determinant of the outcomes)

3. What was your strategy for responding?

4. Did you change your strategy at all?
   Yes/No

5. Has anyone discussed the responding strategy with you before?
   Yes/No

6. Did you doze off or feel sleepy during the experiment? If yes, please mark on the line below to indicate when?

Start Half-way through experiment End

7. Did you pay attention to the frame during the experiment?
   Yes/No

8. Were you counting down as the frame was disappearing?
   Yes/No

9. When you started feeling sleepy, were you still paying attention to the frame? Yes/No

Choice 1

Feedback Sheet for participants

10. Did you feel anxious during the countdown period in any of the scenarios?
    Yes/No

    If yes, please put a tick besides the scenario that you felt anxious.

    1) Always earn $0.10

    2) Earn $0.10 or nothing

    3) Earn $0.10 or lose $0.10

    4) Earn $0.10 or lose $0.20

Choice 2

Feedback Sheet for participants

Thank you for participating in our study. Please answer the following questions as truthfully as possible; your answers may help us interpret any unexpected findings.

1 Did you think responding speed was important?
Yes/No (It wasn't a determinant of the outcomes)

2 Did you notice that the different coloured boxes represent different probabilities in the outcome?
Yes/No

3 What was your strategy for responding?

4 Did you change your strategy at all?
Yes/No (If yes, please state how)

5 Has anyone discussed the responding strategy with you before?
Yes/No

6 Did you doze off or feel sleepy during the experiment? If yes, please mark on the line below to indicate when?

Start Half-way through experiment End

Choice 2

Feedback Sheet for participants

7 Did you feel anxious at any point during the experiment?

Yes/No

If yes, please note down when you felt anxious

Choice 3

Feedback Sheet for participants

Thank you for participating in our study. Please answer the following questions as truthfully as possible; your answers may help us interpret any unexpected findings.

1. Did you think response speed was important?
   a) Yes b) No

   c) If you changed your mind, please indicate below when you started thinking speed was important and when you started thinking it was not.

Start Half-way through experiment End

2. What was your response strategy at the beginning?

3. What was your response strategy at the end?

Choice 3

Feedback Sheet for participants

4 Has anyone discussed the response strategy with you before?

Yes/No

5 Please indicate if you either dozed off or felt sleepy during the experiment

a) Dozed off b) Felt sleepy

c) Others:_____

Please mark on the line when and for how long the above occurred:

Start alf-way through experiment End

6 Did you feel anxious at any point?

Yes/No

If yes, please note down when and why you felt anxious.