

1 Introduction

In 2007 national Australian newspapers reported that a 60 year old Australian woman visiting Florida in the USA died tragically as she attempted to cross a four lane highway after reaching a *median strip*. Reports indicated that the woman *standing on a median strip* looked to her left as Australia has left hand traffic and believing that the road was clear stepped straight into the path of a moving 4WD which was travelling on the right hand side of the road as the USA has right hand traffic. In 2008, a 65 year old American man visiting Australia was driving on the right hand side of the road when he caused a head-on collision, killing his wife and severely injuring two others. In 2009, a custodial sentence for him was ruled out as not in the interests of justice.

The above are tragic examples of failure in cognitive control where habitual, automatic responses were executed in an inappropriate context, and raise questions how such tragic sequences of events developed. For example, was it a monitoring system that failed to recognise that a new context required overriding of an automatic response and signal to facilitate execution of less practised behaviour? That is, was it because a correct, but less practised response was not amplified enough? Or was it because an incorrect, but automatic response was not inhibited soon or strongly enough? Or was it because of combined failure of both amplification of weak, but correct response, and inhibition of a strong competing, but incorrect response? The current project aimed to systematically examine the amplification of correct, and inhibition of incorrect information processes in what has become an important paradigm of cognitive control. The introduction aims to provide the broad context which influenced the design of the following four experiments and the background for the interpretation of the ensuing results.

Attention is a cognitive process of selectively focusing on some feature/s of the stimulus while ignoring others and it can be focused intentionally by top down signals driven by internal goals and automatically by bottom up signals driven by stimuli. Bottom up signals are initiated by physical data streaming into sensory receptors, while top down processes originating most likely from prefrontal cortex (PFC) interpret their meaning. In a healthy brain these two processes are inevitably linked (Miller, 1999). Hence, top down and bottom up signals arise from frontal and sensory cortices respectively (Buschman & Miller, 2007), with bottom up signals providing raw data

which is then processed, interpreted and managed by higher cognitive processes according to shifting goals and contexts.

Habitual responses to well known environmental stimuli are automatic and can be implemented by bottom up neural processes alone. For example, crossing a familiar street or travelling a familiar route home require minimal effort as the stimuli themselves provoke highly established, predictable behavioural responses. Novel responses to unpredictable situations must, however, be context sensitive, rapid, flexible and open to constant strategic adjustment requiring an active interplay between top down and bottom up neural processes. For example, an unexpected road disruption en route home requires effortful, strategic adjustment to produce effective behaviour. A major unresolved issue is how this strategic adjustment, in response to changing environmental demands, is achieved in order to produce effective behaviour. For example, disruption to the usual course home requires abandoning automatic responses and finding new effective ones and it is matter of intense debate whether this strategic adjustment is achieved by amplifying correct information (e.g., finding another street that leads home), inhibiting incorrect (e.g., returning to the usual route home) or both.

Apart from theoretical significance, knowledge about processes involved in strategic, flexible adjustment of behaviour has great value in extending knowledge not only about normal development, but also about such devastating disorders as schizophrenia, autism and brain injury among others. For example, those suffering from extensive frontal brain lesions often show utilisation behaviours where responses are dominated by the stimulus (e.g., a plate of food triggers eating) and, in effect, behavioural control is external, rigid with a stimulus triggering prepotent, “default” responses regardless whether they are context appropriate or not (Craik & Bialystok, 2006). Toddlers of ~24 months of age tend to display prepotent, “default” responses to stimulus, but by the end of the third and the beginning of the fourth year (Posner & Rothbart, 2007) they start showing signs that the external stimulus starts losing its hijacking power over behaviour, indicating that internal, top down control of behaviour is emerging. In Piaget’s developmental A-not-B search task, infants initially learn to reach container A to retrieve a hidden object. After a certain number of trials, the object is hidden in container B in full view of the infant. Infants 7 – 12 months of age consistently make errors and still reach

for the object in container A (Aron, 2007; Tipper, 2004). Thus, effectiveness of behaviour is greatly dependent on the ability to resist inappropriate automatic responses.

In the laboratory, strategic adjustment of behaviour can be studied using selective attention tasks such as the Stroop task. In the standard Stroop task (Stroop, 1935) participants view colour name words (e.g., GREEN) written in different ink colours which can be congruent (e.g., GREEN) or incongruent (e.g., RED) and are instructed to name the ink colour and ignore the meaning of the word. However, it is very difficult not to read the word since reading is an overlearned and thus automatic process. Consequently, participants are unable to completely suppress involuntary processing of the irrelevant dimension (MacLeod, 1991; Cohen et al, 1990) which affects performance. The degree to which interference or conflict affect performance can be measured by comparing reaction times (RT) and accuracy in congruent or incongruent conditions with either control trials (e.g., a string of xxxxxx) or each other. A reduction in RT in colour naming (i.e. Stroop facilitation effect) is often observed for congruent versus control stimuli, and an increase in RT (i.e. Stroop interference effect) for incongruent versus control stimuli.

Thus in the Stroop task, a target is presented with distracters that produce cognitive conflict. Distracters, in turn, can be manipulated by varying their in/congruency dimension which is thought to result in either increase for incongruent stimulus or decrease for congruent stimulus in the need for cognitive control or top down regulation which guides behaviour according to goals. In addition to measuring behavioural responses, measurement of neurophysiological effects involved in the resolution of cognitive conflict provides invaluable information about related cortical structures and processes. For example, cognitive conflict can be studied under low and high cognitive control and analysis can be performed to identify the role of specific cortical regions, processes which may help to resolve cognitive conflict (Egner & Hirsch, 2005).

One critical step required before strategic adjustment of behaviour can be implemented is the ability to detect the need for that strategic adjustment. This detection may result from cognitive conflict, for example, when two stimuli interfere with each other as in the Stroop task or when intended goals are not met, for instance, by the production of errors. For example, a sign warning that the road ahead is closed can be

expected to trigger conflict between goals, intended actions and expected consequences as it warns the driver to change a previously initiated action as proceeding ahead will result in unfavorable outcomes. Thus, the ability to detect conflict and react accordingly to improve performance is critical for effective and adaptive behaviour. Neurophysiological studies of brain regions engaged by cognitive and behavioural conflict and error effects indicate that the anterior cingulate cortex (ACC) Brodmann area (BA) 24, 32 is consistently activated during conflict and errors across a variety of tasks regardless of whether errors are consciously or unconsciously detected (Hester et al, 2005).

The ACC is a structurally and functionally heterogeneous region divided into dorsal (dACC) and rostral (rACC) parts involved in processing cognitive-motor and affective information respectively. The rACC has strong connectivity with limbic structures such as the amygdala and orbitofrontal cortex (Fitzgerald et al, 2005) which influence autonomic arousal. The ACC is densely interconnected with other frontal lobe regions especially the prefrontal cortex (PFC), parietal and motor cortices. The ACC is involved in performance, error monitoring and reward assessment. It is thus assumed to play a central role in action selection and in mediating the relationship between previous action reinforcement history and selecting the next action, in other words operant conditioning learning. According to this view the ACC is involved in the transformation of intentions into actions, playing the role of an assessment filter regulating which executive commands gain control of the motor system (Holroyd et al, 2004) with the chief function of increasing positive outcomes and decreasing aversive outcomes.

Cognitive conflict, envy, grief, being unfairly treated and social exclusion also activate the dorsal anterior cingulate cortex (dACC) (Lieberman & Eisenberger, 2009). The ACC appears to be activated when habitual, well learnt behaviours are insufficient to guide actions (Paus, 2001) with consequent increases in arousal suggesting that in response to difficult tasks the ACC acts to marshal response relevant resources including peripheral arousal and the stress response. For example, pain is the primal form of error feedback and pain strongly increases activity in the ACC. Pain usually results in alerting and orienting response to potentially threatening stimulus and triggers a search for an appropriate escape response (Hutchison et al, 1999).

Some authors argue that the ACC detects conditions under which errors are likely to occur rather than errors per se (Carter et al, 1998) and it may detect errors as mismatches between actual and intended events or as conflict between mutually incompatible response processes such as correct versus incorrect responses. Nevertheless, some authors maintain that the ACC does not monitor conflict (Burle et al, 2008; Mansouri et al, 2007) and may not be necessary for cognitive control (Fellows & Farah, 2005). However, the majority of studies provide evidence to support the role of the ACC in the detection and resolution of conflict including clinical studies which suggest that lack of activity in the ACC during heightened processing conflict may result in behavioural and cognitive impairments in performance, like, for example, those observed in attention deficit hyperactivity disorder (ADHD) (Bush, 2004). This also extends to animal research. For example, monkeys with lesions in the ACC were able to use reward information to modify their strategy in a single trial, but could not sustain this new behavioural adjustment in subsequent trials (Kennerley et al, 2006). Hence, the role of the ACC in reinforcement guided behaviour may not necessarily be detecting or correcting errors, but rather learning the value of actions since actions in some circumstances are not categorically correct or erroneous and the ACC is sensitive to both errors and rewards (Kennerley et al, 2006).

Nonetheless, hyperactivity in the ACC can also be disruptive to effective behaviour since the ACC signals a loss of reward. The cingulum bundle has been the target for neurosurgery (cingulotomy) to alleviate chronic pain, anxiety, depression and obsessive-compulsive disorder (OCD) (Hutchison et al, 1999). For example, OCD sufferers have greater sensitivity (higher affective response) to errors as evident in a larger hemodynamic signal. Hyperactivity of the ACC in OCD may be related to error processing abnormalities, more precisely, preoccupation with correcting or preventing errors which seems to normalise with successful treatment (Fitzgerald et al, 2005).

One of the most direct links between the ACC, self regulation and errors is the negative deflection or error related negativity (ERN or N_e) in the event related potential (ERP) to error responses which peaks ~80 - 150 ms after an error in responding to stimuli in visual, auditory or somatosensory modalities. This implies that the cognitive system eventually realises (consciously or not) that a mistake has been made. The amplitude of

ERN increases with the importance of the error and ERN can even be produced by the absence of an expected reward. Some studies report that brain lesions in the ACC can preclude or decrease the development of the ERN after errors (Swick & Turken, 2002), while OCD sufferers produce an abnormally large ERN (Holroyd et al, 2004). However, ERN can also be triggered for correct responses or it may be absent for errors (Botvinick et al, 2001). It is, however, unclear whether ERN is produced by errors as such (mismatch between executed and representation of correct response) or conflict between correct and incorrect response representations.

Error detection depends on continuous information processing after an initial error when the correct response representation is eventually activated resulting in conflict (Yeung et al, 2004b), and can be compromised even in healthy people. Alcohol, even in moderate doses, reduces ERN amplitude (and not just the overall EEG amplitude) associated with errors, suggesting impairment in performance monitoring, stimulus-response processing and quality of information upon which the monitoring system is dependent. Alcohol may reduce correct response activation and related conflict activation and subsequently amplitude of ERN, in turn compromising such complex behaviours as driving (Ridderinkhof et al, 2002).

The above evidence demonstrates the critical importance of cognitive conflict detection which acts like a warning system signalling that improvement in performance is needed to avoid further aversive outcomes, losses of reward, or to produce positive outcomes. The ACC appears to be one of the most important cortical regions involved in conflict detection. Detection of conflict often leads to increased attentional focus and the ACC appears to achieve this by summoning further responses from one of the largest, most complex and most advanced cortical regions – the PFC.

The PFC comprises 30% of the cortical mass and is larger and has more complex folding in the human brain compared with great apes such as gorilla, orangutan and chimpanzee. The PFC receives projections from visual, auditory and somatosensory cortices and has connections with the premotor area, which in turn sends projections to the primary motor cortex and spinal cord. The PFC is thought to have significant neuronal and functional connectivity and organisation and, hence, an enhanced ability to inhibit automatic responses, form symbolic representations of objects, goal maintenance,

performance monitoring and planning, and selecting actions (Miller & Cohen, 2001). Virtually all complex behaviours involve constructing relationships between diverse, arbitrary pieces of information which may have no obvious, intrinsic connections unlike rigid, reflexive, stereotypical stimulus-response (S-R) chains. Hence, the PFC with its sophisticated neuronal and functional connectivity and organisation provides infrastructure for combining a diverse range of information to produce complex forms of intelligent behaviour (Miller, 2000) such as resisting inappropriate automatic responses. People with PFC lesions, for example, do indeed have deficient response inhibition (Brunia & Van Boxtel, 2000).

The role of the PFC is vital when top down processing is needed; that is when behaviour has to be guided by goals and intentions and when mapping between stimulus features and correct actions is weak compared with habitual, but incorrect responses. Selective attention and intentional behaviour depend on task and goal representations which are thought to be reflected in the form of activity patterns in the PFC. Cues in the environment activate multiple internal representations which compete for behavioural expression and hence the PFC may play a vital part in selecting the most appropriate action guided by activated goal representations. For example, damage to the PFC in humans causes such symptoms as perseveration, evident in inappropriately repetitive behaviour and distractibility which is in effect an inability to maintain goals (Miller & Cohen, 2001). The PFC is assumed to be modulatory not merely transmissive; that is, information is not just passively transmitted, but is instead strategically guided and altered in the process. For example, for weaker, but correct targets or responses the PFC may provide support by biasing processing in sensory or motor regions to guide the flow of activity through these neural pathways as a strategic adjustment to counteract competing, more automatic, but incorrect responses. How this strategic adjustment is achieved during cognitive conflict is the focus of the following four experiments.

The PFC is thought to provide both inhibitory and excitatory inputs to distributed neural networks to support performance in a range of diverse tasks. For example, in monkeys, damage to the frontal lobe, which is analogous to the human PFC, severely impaired their performance in remembering the location of a baited well and this impairment was not related to a simple memory problem, but rather the problem with

inhibitory inputs towards sensory distracters. Hence, it is thought that PFC sculpts and organises behaviour through both inhibitory and excitatory regulation in neural networks (Knight et al, 1999).

It appears that attentional and motor networks are under the control of the PFC which is responsible for organising complex behaviour and preparing for upcoming events at least in part by priming relevant perceptual systems and motor structures (Brunia & Van Boxtel, 2000; Pessoa & Ungerleider, 2004). The PFC is thought to achieve this through top down signalling while remaining responsive to bottom up inputs (Cohen et al, 1998). Top down signals modulate sensitivity of neural information and improve signal to noise ratio (Knudsen, 2007). Hence, in order to produce effective and appropriate behaviour the PFC remains open to a constant (most likely selected) flow of sensory information processing of which is iteratively guided top down to produce goal intended behaviour.

It is clear then, why during cognitive conflict, which signals a high possibility of negative outcomes unless improvement in performance is achieved, the ACC summons the PFC. It is the PFC that not only has access to up to date inflowing sensory information, but also has a controlling influence over perceptual systems and motor regions because of its sophisticated extensive neuronal and functional organisation. Much of the above discussed evidence has been obtained using ingenious human and animal behavioural experiments, but is also the product of recent advances in psychophysiological methods which allow the noninvasive imaging of functional activity inside the living human brain such as functional magnetic resonance imaging (fMRI). fMRI (Bandettini, 2006) is an indirect measure of brain activity which can use either change in blood flow, blood volume or blood oxygenation level-dependent (BOLD) signals. The BOLD signal is generated by veins or capillaries and is triggered by increased neuronal activity that results in metabolic demands for increased oxygen consumption. BOLD measurement is one the most commonly used brain imaging measures because of its high functional contrast. The temporal resolution of fMRI is estimated to be between 4 – 8 s (limited by the hemodynamic of the BOLD response itself) with a spatial resolution of 3 mm² and even down to 1 mm² depending on the strength of the applied magnetic fields. Traditionally, fMRI studies present experimental

stimuli in blocks which are then compared with a block of baseline or reference condition stimuli (Reiman et al, 2000). Blocked paradigms require participants to perform tasks in a predictable and repeatable manner, the aim of which is to generate stable and clear hemodynamic signals. This does, however, limit the type of questions that can be answered using fMRI. For example, questions involving measuring the timing of brief changes related to one type of stimulus are not best suited to the fMRI technique. However, blocked designs maximise the signal to noise ratio in brain imaging data and continue to be widely used.

The neurophysiological meaning of fMRI signals is, unfortunately, not straightforward either. The fMRI signal may reflect changed firing rates of a local neuronal population, subthreshold activity and activity in both excitatory and inhibitory neurons (Heeger & Ress, 2002). The BOLD effect may become saturated at high levels of blood flow because further increases in flow would cause a negligible decrease in the concentration of deoxyhaemoglobin. Hence, a moderately strong stimulus may evoke a near maximal fMRI response leaving very little room to reveal any further changes in fMRI signal in response to a stronger stimulus (Heeger & Ress, 2002). Thus, while fMRI demonstrates excellent spatial resolution which is ideal for measuring sustained hemodynamic activity, its temporal resolution is poor, limiting its usefulness in studying the temporal dynamics of brief events.

Scalp electroencephalogram (EEG), on the other hand is a direct measure of electrical activity generated by the brain. Scalp EEG is the product of summated, cortical postsynaptic potentials. Postsynaptic potentials or voltages arise when ion channels open or close leading to a change in the potential across the receptor cell membrane of a postsynaptic cell where neurotransmitters bind for periods of tens to hundreds of milliseconds (Luck, 2005). The source of the EEG is the current flow in the apical dendrites of pyramidal cells (the largest neurons) in the gray matter, perpendicular to the cerebral cortex (Rippon, 2006). Thus, EEG allows the measuring of dynamic changes over very brief periods of time. However, even with high density electrode arrays (e.g., 128 channels) spatial resolution of scalp EEG is poor. Firstly, the signal at each electrode is thought to be influenced by a cortical area of approximately 6 cm^2 . Even with a dense electrode array the average distance between electrodes on an adult's head would be

approximately 2.25 – 2.50 cm, a poor spatial resolution compared with fMRI (Davidson et al, 2000). Secondly, the skull acts as a low pass filter (passing slower frequencies, but eliminating higher frequency components) and smears electrical activity over large regions of the scalp. Thirdly, there are many possible configurations of sources which will generate the same pattern of scalp electrical activity (i.e. the inverse problem); thus, uncertainty exists between scalp measured electrical activity and its inferred neuroanatomical source/s (Davidson et al, 2000).

From the above evidence it is clear that fMRI and EEG are best suited to measure rather different aspects of neuronal activity. In the case of fMRI, it takes seconds for neurons to change their blood supply, while EEG reflects millisecond electrical changes. EEG and fMRI measures can be integrated and can inform each other; for example, hemodynamic results may be used to guide which aspects of or how EEG data are best analysed (Hopfinger et al, 2005).

This brief Introduction provides the broad context which influenced the design and interpretation of the following four experiments. Effective behaviour is assumed to depend on the ability and flexibility to resist automatic responses when circumstances require this, and instead to perform less practised, weaker, but correct responses or behaviour. Cognitive conflict driven activation is theorised to serve the role of signalling when automatic responses have to be managed. In this model, conflict signal is proposed to originate in the dACC which then increases activity in the relevant PFC task set and goal representations, which, in turn, modulate competing lower level sensory, motor processes to resolve cognitive processing conflict, that is, to implement cognitive control. How this top down modulation or cognitive control is implemented in the brain is the focus of all the four following experiments using EEG. This Introduction has highlighted the importance of the choice of psychophysiological method depending on the experimental aims. The following four experiments are, hence, primarily focused on temporal EEG effects related to conflict resolution and these are investigated by tracking *the same dependent variables using different variants of the same task.*

**Paper 1: Facilitation and Inhibition Modulate Cognitive Conflict in Blocked Design
Face/Name Stroop Task: EEG Evidence**

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2.1 Abstract

The current experiment investigated the results of Egner and Hirsch's (2005) blocked fMRI face/name Stroop task study. They found that facilitation alone, without any input from inhibitory effects, resolved cognitive conflict by amplifying activity in processing pathways of to-be-responded-to stimulus attributes as compared to to-be-ignored stimulus attributes. The current EEG experiment employed an analogous blocked design face/name Stroop task to that used in Egner and Hirsch's (2005) fMRI study, but instead used EEG derived measures of facilitation and inhibition. A behavioural Stroop interference effect was observed for both face targets and face distracters (name targets), while the Gratton or conflict adaptation effect was observed for face targets, but not for face distracters (name targets). EEG results indicated that both facilitation and inhibition modulated cognitive conflict. Enhanced post-stimulus inhibition was observed in high control trials compared with low control trials at channels Pz and P4 for face targets and this effect disappeared for face distracters. Enhanced post-stimulus inhibition was observed in high control compared with low control trials at channel T6 for face distracters and this relationship disappeared for face targets. A non-significant drop in the mean negative value at T6 in high control compared with low control trials for face targets was interpreted as pointing to the presence of relative facilitatory effects. Subsequent analyses revealed enhanced significant facilitatory pre-stimulus effects in high compared with low control trials at T6 for face targets. This effect was eliminated for face distracters.

Preliminary source localisation sLORETA results suggested that the right superior temporal gyrus extending to the right FFA was the likely source of facilitatory effects for face targets, while inferior parietal lobule and cingulate gyrus were the likely sources of inhibitory effects for face distracters. Hence, the results suggested the right FFA to be the source of facilitatory control activity for face targets, but not the source of inhibitory control activity for face distracters. Results also suggested the parietal lobule next to the FFA, which is involved in motor planning, to be the source of inhibitory control signals for face distracters. The current blocked study showed that both facilitation and inhibition temporally modulate cognitive conflict as evident in inverse evoked upper alpha ERD and ERS patterns depending on whether face served as a target or as a distracter.

Key words: conflict, cognitive control, Stroop, Gratton effect, facilitation, inhibition, blocked design, fMRI, EEG, evoked upper alpha, ERD, ERS, FFA

2.2 Introduction

One of the most advanced human achievements manifests in the human ability to perform any arbitrary, novel or difficult cognitive task after only brief instructions and little practice, often with a high degree of accuracy and speed (Braver & Barch, 2006). The flexibility, complexity and innovation of human behaviour appear to be infinite. A homunculus, that is, a clever little man in the head, a ghost-in-the-machine, or the more modern executive controller were, and often still are, used to account for this complex behaviour providing unavoidably circular accounts leading to an infinite regress of explanations (Driver, 1998). A central goal of neuroscience is to explain how behaviour and psychological processes including complex cognition emerge from neural mechanisms (Schall et al, 2002). The aim of the current experiment is to investigate the neural basis of cognitive control, conceived of as a strategic adjustment in behaviour to respond to task relevant information while avoiding the influence of prepotent distracters.

2.2.1 Cognitive Control and Associated Neural Structures

Self-regulation refers to the way more complex, advanced functions manage more basic mental operations, that is, how top down mechanisms manage bottom up operations. Cognitive control is an umbrella term for a set of mechanisms that manage thoughts and responses in accordance with goals as required during such demanding tasks as problem solving, decision making, avoiding errors, learning novel behaviours, and in dual tasks such as those in task switching, control of relevant retrieval from memory, selection of appropriate responses, inhibition of inappropriate responses, monitoring performance, and resolving interference. The issue of cognitive control is relatively uncontroversial as a majority of authors agree that cognitive control refers to the advanced ability to coordinate thought and action to obtain goals and manage more elementary mental operations such as planning, error corrections, novel actions and inhibition of automatic behaviour to produce coherent, effective and adaptive behaviour (Wagner et al, 2004; Cohen et al, 2004).

Cognitive control as proposed here refers not to an almighty clever homunculus residing in a specific cortical region which then appears like *deus ex machina* to save the day, but rather to a set of mechanisms or more precisely a set of cortical networks and

processes that are triggered during difficult tasks. Any task beyond simple reflex or simple S-R chains is thought to involve varying levels of cognitive control. Cognitive control is thought to involve frontal lobes (dorsolateral PFC (DLPFC) and ventromedial PFC (VMPFC)), dACC, supplementary motor area (SMA) which is involved in the planning and execution of actions and subcortical structures such as the basal ganglia. The PFC is thought to represent and actively maintain task demands (Brass & von Cramon, 2004) while the dACC monitors for the presence of processing or response conflict, for example, that arising when automatic responses have to be inhibited or during errors (i.e. by monitoring *when* an increase in cognitive control is necessary). The frontal lobes are thought to regulate action or response selection in posterior parietal and occipital regions involved in perceptual processing and basal ganglia which is part of the motor control system (Cohen et al, 2004; Clark et al, 2005).

The environment affords a variety of different behavioural options and only some are adaptive at a given time (Brass & von Cramon, 2004), hence, cognitive control network/s, through the PFC, maintain task or behavioural goals and control response selection and production (Cohen et al, 2004). The PFC is interconnected with regions responsible for processing external information such as sensory and motor regions and internal information such as memory and reward related processing from limbic and midbrain regions. Hence, the PFC is thought to combine diverse external and internal information sources to produce goal directed behaviour which depends on the capacity to evaluate action consequences. The PFC is essential in enabling control of behaviour by abstract, high level rules which acquire and represent goals and means to goals (rules) which prevent the system from being at the mercy of the environment ruled by whatever sensory input happens to be active (Miller & Wallis, 2009). This is illustrated, for example, by a failure to maintain goals in schizophrenia or impulsive, S-R trigger-like behaviour in children suffering from ADHD (Driver, 1998).

Cognitive control is required when task demands change unpredictably, when the stimulus is ambiguous, changing or novel, for inhibiting automatic responses, setting S-R mappings, timing responses and switching tasks. Cognitive control is thought to be implemented through biasing, that is, by further exciting relevant and/or inhibiting irrelevant information pathways through top down signals which emerge from the PFC

task set and goal representations which then constitute the source of control (Kouneiher et al, 2009). Maintenance of activation and manipulation of representations are forms of control and neuroimaging studies of working memory (e.g., encoding and maintaining visually presented words) suggest that the ventrolateral PFC (VLPFC) among other regions maintains, and retrieves task-relevant representations, while the DLPFC manipulates these representations (Wagner et al, 2004). Control relies on appropriate representations (task demands, rules, intentions, goals) which direct behaviour to produce desired outcomes by biasing processing and guiding the activity along relevant processing pathways. Thus cognitive control is exercised by biasing activation in basic systems such as sensory or motor networks by cognitive control networks towards, for example, one stimulus over another (Cohen et al, 2004). Cognitive control and its networks manage task and behavioural goals, manage conflict, modulate perceptual processing of stimuli and regulate responding. Since goal directed behaviour is likely to be sculpted via top down modulation of more reflexive circuitry, eventual outcomes reflect combined influences.

The neural expression or signature of cognitive control is currently one of the most researched areas in cognitive neuroscience. Brain activation studies measuring cognitive control can be divided into three broad categories. The first group contains tasks which measure how predominant or prepotent, but task irrelevant information is overridden, for example, the word/colour (Stroop, 1935) or face/name (Egner & Hirsch, 2005) Stroop task where one dimension of the stimulus interferes with another. The second group contains tasks which present stimuli and a set of responses, none of which is more obvious than the other as measured by such tasks as letter fluency, where participants are asked to generate words starting with a particular letter or are given stem completion tasks (Frith et al, 1991; Barch et al, 2000). The third group of tasks uses speeded responses and measure commissions of errors as measured by such paradigms as go/no-go, where, depending on the instructions, participants have to make or withhold a response (Scheffers et al, 1996). All these 3 task categories measuring cognitive control generate cognitive conflict stemming from the need to override habitual, but incorrect response in favour of a weaker, but correct one, from uncertainty or errors or from the need to terminate initiated responses all requiring control to resolve it.

It has become clear that there is no single central controller or control mechanism, but rather different networks (Dosenbach et al, 2008; Badre, 2008) through which cognitive processing can be reconfigured, prepared or modulated in accordance with goals and specific task demands (Yeung et al, 2006; Braver et al, 2003). Cognitive control is a dynamic process implemented by a distributed network of closely interacting, but anatomically and functionally dissociable components focused on accommodating and guiding flexible behaviour to meet rapidly changing or complex environmental demands. For example, there is uncertainty whether interference in the Stroop task is generated at semantic processing or response selection levels. In one study, authors (van Veen & Carter, 2005) used colour/word Stroop and found that semantic and response conflicts both contributed to the overall Stroop interference effect. Furthermore, these effects elicited nonoverlapping regions of activation in the ACC, prefrontal and parietal regions; hence, the brain may have distinct, but parallel mechanisms for resolving different types of interference. Response conflict may also activate larger areas which also encompass semantic conflict areas. Van Veen and Carter proposed that conflict occurs at both semantic or conceptual encoding and response selection stages and can be elucidated by manipulating response eligibility, for example, whether a response is part of the response set or not. However, they conceded that ineligible stimuli may be processed differently and concluded that the brain is likely to have a distinct but analogous mechanism to deal with semantic and response conflict allocating resources depending on the nature of the conflict. For example, separate regions of the PFC, such as the superior DLPFC for semantic conflict and more inferior for response conflict can resolve semantic and response conflict, while separate regions in the ACC, for example, more posterior for semantic and more anterior, consistent with activation by errors, for response conflict. Hence, different types of conflict may trigger the PFC to make a control response specific to that particular type of conflict (van Veen & Carter, 2005). Nelson and colleagues (2003) used fMRI and a verbal working memory task (item recognition) to examine brain activity related to different types of conflict. Results indicated double dissociation with stimulus related conflict resulting in left PFC (inferior frontal gyrus or IFG, BA 45) activation, but not ACC and reverse pattern for response

related conflict. They interpreted this as pointing to differing contributions to cognitive control of specific cortical regions depending on the source of conflict.

The PFC certainly plays a critical role in cognitive control, but its contribution is neither unitary, since different regions within the PFC play different roles, nor exclusive, since posterior cortical and subcortical regions also make their own distinctive contributions (Driver, 1998). However, the PFC is central to the network of brain regions supporting cognitive control; hence, investigating functional organisation of the PFC may help clarify the architecture of cognitive control.

2.2.2 Cognitive Conflict, Control and Parallel Distributed Processing (PDP) Model

One of the leading theories of cognitive control proposes that flexible control is the outcome of a (series of) feedback mechanism/s primarily guided by the detection of cognitive conflict at various levels of information processing, for example, perceptual, stimulus categorisation or response selection. It assumes that the ACC monitors for conflict between information processing pathways and then signals the PFC to increase the allocation of attentional resources, for example perceptual selection, to cope with (increases in) task difficulty (Cohen et al, 2004). According to this conflict monitoring hypothesis conflict occurs when there is crosstalk or interference between coactive processing pathways. For example, the ACC may be triggered when two stimuli activate parallel multiple incompatible response pathways resulting in crosstalk (Botvinick et al, 2001). Conflict monitoring theory is based on connectionist or parallel distributed processing (PDP) models and was proposed almost two decades ago based on computer simulation models (Cohen et al, 1990; Botvinick et al, 2004).

Processing in PDP models occurs in a system of connected components, each component containing elementary processing units which accumulate inputs from other units and adjust their output in response to these inputs (Cohen et al, 1990; Botvinick et al, 2001). Information is thought to be represented as a pattern of activation, maximum or minimum, over units in a component which can accumulate and dissipate with time. Connections are thought to exist between the units in different components. Processing of information in PDP models occurs via a sequence of connected components that form a pathway. The speed and accuracy of the task processing depends on the speed and

accuracy with which information flows along the processing pathway which depends on the units which make components along the pathway. Components are thought to be able to participate in different pathways and interactions, but crosstalk occurs when processes depend on a common component. Pathways which intersect with similar activation patterns result in facilitation as target information (e.g., stimulus, response) representations overlap, while dissimilar activation patterns result in interference as target information representations compete with each other. Intersection between pathways can occur at any stage, but particularly at the response stage. Information flow in pathways may be modulated by attention which alters the responsiveness of the processing units. Hence, attention is an additional source of input to support the processing of signals within a selected pathway and is not otherwise given a special status. Each pathway is considered to consist of input, intermediate and output units. A response occurs when sufficient activation has accumulated to exceed a response threshold and RT depends on the number of processing cycles necessary for the threshold to be exceeded. Processing component pathways are like sets of resources and are therefore limited and cannot process two signals at once (Cohen et al, 1990; Botvinick et al, 2001).

Thus, in PDP models processing occurs by the propagation of activation among the units through weighted connections which store knowledge and can be modulated by practice and attention which is a pattern of activation over units. As activation spreads it leads to the corresponding response and RT are linearly related to the number of cycles taken for response units to reach activation threshold. Competition arises when two different sources of information compete for representation within a component and stronger, more automatic processes are less affected than the less practised, weaker ones. Attention is comprised of top down signals which allow execution of weaker, less practised tasks by biasing activation towards its pathways (Cohen et al, 1992).

In this PDP model, conflict is defined as the simultaneous activation of incompatible representations or mutually inhibiting units and can occur at any stage of information processing including stimulus evaluation and response selection. Conflict monitoring is an ongoing process, evidenced, for example, by the ERN which emerges when the correct response is activated rapidly after an error. Hence, it is likely that conflict occurring at any stage of information processing is likely to be reflected at

response selection stage when independent processing pathways meet at the final response selection level and evident in RT latency (Gratton et al, 1992). Conflict activates the ACC which indicates that a shift in attentional control is needed to prevent negative outcomes. The ACC evaluates both environmental inputs and internal conflict to assess how the system is dealing with them (Botvinick et al, 2001).

According to this PDP model, the Stroop task consists of two pathways, one for colour naming and one for word reading, with both converging on the same response mechanism. Activation of the task representation engages attention or cognitive control manifesting as a changed pattern of activation and can selectively facilitate processing in either pathway. However, reading through practice acquires larger connection weights and consequently more rapid spread of activation with a corresponding decrease in RT (and SD and errors) (Cohen et al, 1992).

The connectionist model has its critics (Kanne et al, 1998). Some authors argue that the model incorrectly predicts lack of interference for processes of comparable strength and implies that the *standard* Stroop task interference pattern can be reversed by extensive training of the weaker pathway, but training colour naming to the extent that it becomes faster than reading may be empirically impossible (Roelofs, 2003). However, compared to other available theories of the Stroop effect, for example the “horse race” account which suggests that word processing is simply faster and hence beats responding to colour in the race for motor control, the PDP account explains the widest range of empirically observed phenomena including interference, facilitation and the role of attention which can accommodate execution of weaker task by enhancing activation in its processing pathways (MacLeod & MacDonald, 2000).

Whether conflict detection is really necessary to trigger changes in control is also questioned by some authors (Mansouri et al, 2009). In one study, which examined if conflict on a preceding trial triggers higher levels of control on the following trial, the trials were sorted on the amount of conflict as measured by electromyographic (EMG) muscle activity involved in response selection and ERN/N_e and it was found that conflict did not trigger changes in control (Burle et al, 2005). However, the majority of studies provide evidence contrary to this finding (Hester et al, 2005; Carter et al, 1998; Kerns et al, 2004; van Veen & Carter, 2005) with the detection of stimulus processing or response

conflict acting as a catalyst for the involvement of cognitive control networks and processes. Signals about processing conflict, production of errors and delivery of reinforcement allow an organism to act in accordance with regularities in the environment through sensory and motor neural pathways that bias for or against previously repeated responses. Conflict signals may originate from mismatch detection between intended and actual behaviourally contingent rewards or reinforcers (Schall et al, 2002) acting as a “regroup” command. Since attentional limitations often stem from conflict, competition between or within processing pathways and hence conflict reduction may be a central function of the control system (Kerns et al, 2004). If there are many different types of conflicts and subsequent control loops, a more appropriate question may be not whether conflict is necessary, but whether ACC and PFC involvement is preserved across different types of conflict (Egner, 2007).

PDP models offer explanatory neurobiological mapping as information processing is interpreted as computation with relevant processing units, graded flow of activation, and modifiable connection weights. Units representing task bias earlier processing pathways placing them in sensitive range of their activations and hence making them more sensitive to inputs which allow selective responding (Cohen et al, 2004).

2.2.3 Conflict Adaptation or Gratton effect

Once the ACC conflict monitoring system detects conflict in information processing it appears to signal regions within the PFC to modulate top down control in order to resolve it. The PFC consequently seems to implement a strategic adjustment in performance as a reaction to difficult or changing environmental demands. About two decades ago, Gratton and colleagues (1992) noticed in their behavioural experiments that congruent and incongruent trials had sequence effects and participants’ behaviour appeared to change from trial to trial with less interference evident in trials that followed incongruent compared with congruent trials. This has become widely known as the conflict adaptation or Gratton effect. The Gratton effect in behavioural data obtained using Stroop and flanker tasks (Egner & Hirsh, 2005; Mayr et al, 2003) among others is evident in shorter RT on incongruent (I) trials that followed incongruent rather than congruent (C) trials or $II < CI$, while congruent trials are shorter if they follow congruent rather than incongruent

CC < IC. Faster RT for II than CI is thought to result from reduced interference from incongruent distracters because of an increase in control, while slower RT for IC than CC trials results because greater control on the previous trial led to focus on colour and hence reduction of facilitation from congruent distracters (Egner, 2007; Kerns et al, 2004).

Gratton et al (1992) explained that, given sufficient time, people can extract relevant information from a noisy environment; however, under time pressure processing becomes more strategic, that is, it is under the person's control and focused, hence affecting the way target and distracting information is processed. This may not necessarily be a conscious, deliberate decision. Participants' behaviour changes from trial to trial depending on the speed at which they extract the relevant information. Hence, if information extraction is difficult as is expected in, for example, incongruent trials, participants may increase the deployment of cognitive resources such as perceptual focus to cope with it. Strategies such as this behavioural adjustment to manage increased interference or conflict are primarily driven by the need to organise cognitive resources most efficiently to achieve goals. In the PDP Stroop processing model this behavioural adjustment may be achieved by weakening or strengthening processing links through attentional inputs biasing activation in competing pathways (Gratton et al, 1992). This attentional input is, in other words, the top down control signal found to originate from regions within the PFC in numerous neuroimaging studies. For example, this top down control signal was found to be evident in higher fMRI BOLD activity in the right DLPFC in II than CI trials (Egner & Hirsch, 2005).

However, the top down control account of the Gratton effect has been challenged by Mayr et al (2003) who argued that it was not a conflict adaptation effect, but rather a consequence of stimulus repetition priming. Many tasks such as the Stroop or flanker tasks have limited stimulus sets; for example, a typical colour/word Stroop task used in imaging studies may have two or three colour names and two or three ink colours requiring many repetitions during experimental testing. Conflict adaptation effects and may, therefore, be caused by stimulus repetition priming effects, since 50% of the CC and II transitions but none of the IC and CI transitions involve an exact target with flanker repetitions in, for example, flanker tasks. Hence RT in II and CC trials may be faster because of repetition priming that is absent from CI or IC trials. Since, in their

study, conflict adaptation pattern was present only for repetition trials and not for target/response change, Mayr et al (2003) concluded that repetition priming can account for conflict adaptation effects and the degree of conflict per se may not determine the subsequent levels of control (Mayr et al, 2003). In other words, it is bottom up, perceptual processes rather than top down, control effects that account for the Gratton effect. In a later study using EMG and ERN Burle et al (2005) also failed to find evidence that conflict triggers increased level of control.

In lieu of the findings of Mayr et al (2003) that a conflict adaptation pattern was present only for repetition trials and not for target/response change, Ullsperger and colleagues (2005) pointed out that, firstly, Mayr et al used an unspeeded version of the flanker task since stimuli remained on the screen until participants responded. Lack of pressure for speeded responses may have resulted in a decreased need to use conflict triggered strategic adjustments in performance. Secondly, Mayr et al presented results of two studies to claim that Gratton effect is accounted for by bottom up, perceptual rather than top down, control signals. In their first study Mayr et al used left and right facing arrows (< >), while the second experiment also used upward and downward facing arrows ($\wedge \vee$). This can be interpreted as two different tasks and hence, task switch which in turn involves complex cognitive control effects. Ullsperger et al (2005) concluded that the findings of Mayr et al (2003) may not be generally applicable and their theoretical implications may be limited. Egnér & Hirsch (2005) controlled for repetition priming effects by excluding direct stimulus repetitions and found a robust Gratton effect which could not be attributed to repetition priming effects and most likely related to conflict related adjustments in cognitive control. Nevertheless, the findings of Mayr et al (2003) are important, since they demonstrate that the Gratton effect does not necessarily emerge in every task.

Congruency effects arise when different dimensions of stimuli or responses overlap perceptually, conceptually or structurally. Conflict monitoring theory assumes that in incongruent trials increased conflict leads to an increase in control as the ACC triggers PFC task set and/or goal representations to increase activation to cope with increasing difficulty and hence leads to higher levels of control (e. g., the Gratton effect) (Kerns et al, 2004). After congruent trials, control is relatively lax, hence conflict should be high on

subsequent incongruent trials (Botvinick et al, 2001; Botvinick et al, 1999). An alternative account is that this results from a stimulus and response repetition effect which is a bottom up process. This may be particularly important if response-stimulus interval (RSI) is very short, since it is assumed that top down control needs time to develop (Notebaert et al, 2006; Egner, 2007). Bottom up processes may, therefore, be especially important when RSI are short, since it is assumed that top down effects emerge only for RSI >500 ms, since they need time to develop. This suggests that different mechanisms may affect short RSI. However, there may also be common mechanisms such as response conflict monitoring, control adjustments (Jentsch & Leuthold, 2005).

It requires great care to tease apart the contribution of top down and bottom up processes to the Gratton effect. There are two general approaches. The first is to use larger stimulus sets. The second relates to data exclusion at the analysis stage. However, data exclusion such as exclusion of complete or partial repetitions or target to distracter transitions leads to loss of statistical power because of data reduction. The types of trials included in analyses represent only a certain type of transitions where no feature is repeated from the previous trial, meaning that conflict adaptation is investigated on one particular type of transition only. Certain statistical techniques such as multiple regression (MR) can test all effects, and all factors are tested on a complete data set, but it also has its disadvantages since the effect of a given factor depends on the inclusion of other correlated factors, making interpretations complex (Notebaert & Verguts, 2007).

Conflict paradigms such as the Stroop task also lead to arousal and noradrenalin release throughout the brain (Verguts & Notebaert, 2009). The Gratton effect is thought to reflect an increase in cognitive control. However, it may instead be the result of an interaction between arousal and learning facilitated by conflict detection in the ACC which has projections to brainstem nuclei involved in autonomic responses or arousal processes and these may play a role in adaptation to task demands. The detection of perceptual interference and/or response conflict may lead to increased arousal which in turn may lead to a stronger focus on task relevant stimuli, thus generating a Gratton type effect. Cognitive control may be an instance of the more general interaction between learning and arousal and all connections between representations active during the arousal signal may be strengthened regardless of their relevance to the task (Verguts &

Notebaert, 2009). The claim that arousal plays a part in generating the Gratton effect does indeed make good sense considering that the conflict detection signal must act to marshal all potentially relevant brain resources if an adaptive response is to be made. The question remains as to exactly how computationally such strategic adjustments to conflict detection are achieved.

2.2.4 Conflict Modulating Excitatory and Inhibitory Effects

Key functional and anatomical components of brain networks implementing cognitive control have now been mapped. Principal nodes of this network (or family of networks) include regions for monitoring and resolving processing conflicts located within the ACC and PFC respectively. The PFC is thought to be the source of top down, control signals, and in the context of current PDP models the PFC resolves conflict by biasing information processing pathways in accordance with goal or task set representations. The Gratton effect demonstrates that increased levels of conflict may result in increased levels of control as evident in improved behavioural performance such as shorter RT and lower error rates, illustrating strategic adjustment of processing as a response to task difficulty. Facilitation of relevant and/or inhibition of irrelevant information processing pathways may be the main mechanisms through which strategic adjustment in performance is achieved, but this is highly disputed. Both generally and in specific instances it is unclear whether facilitation, inhibition or both forms of top down control are employed to modulate processing conflicts.

The functional role of facilitation (definable as cellular excitability) on amplification of target processing pathways and increased focus on task relevant information is well established (Egner & Hirsch, 2005). Note that approximately 85% of cortical neurons are excitatory or glutamatergic (Pfurtscheller & Lopes da Silva, 2005). The DLPFC is thought to regulate posterior association cortex through mostly excitatory connections (Beer et al, 2004). Task relevant information has to be maintained through excitatory activation and DLPFC lesions are known to impair this (Knight et al, 1999).

However the role of (cognitive) inhibition in the modulation of cognitive conflict is strongly disputed by some theorists (MacLeod et al, 2003). Note that approximately 15 – 20% of cortical neurons are inhibitory and use primary inhibitory neurotransmitter

gamma-aminobutyric acid (GABA) and are known as GABAergic interneurons (Buzsáki et al, 2007). Arguments in support of cognitive inhibition propose that without inhibition conscious awareness would be swamped with distracters, visual stimuli would invoke actions without intending to and attention would be captured haphazardly (Aron, 2007). Cognitive inhibition is conceptualised as a process which acts to suppress previously activated, but now irrelevant cognitive contents, while behavioural inhibition is thought to manage overt behaviour. For example, sufferers of prefrontal lobe damage often impulsively perform affordances provided by the objects (e.g., a plate of food triggers eating), while children, as demonstrated on the A-not-B task, keep searching for an object in an inappropriate location. Inhibition is believed to be required when responding to the Stroop task in order to inhibit irrelevant, distracting stimulus' attributes (Aron, 2007).

Inhibition is thought to come in at least three types. First, neural inhibition refers to some neurons inhibiting each other and is not disputed since it can be directly observed. For example, GABAergic interneurons releasing GABA neurotransmitter across synaptic cleft can induce inhibition in target neurons in the form of inhibitory postsynaptic potential (IPSP) (Aron, 2007). Second, physical, behavioural inhibition refers to the situation in which actions are initiated but then inhibited. This is not disputed either. However, the third possible form, cognitive inhibition, which refers to the inhibition of mental processes and representations, is highly contentious, since it is much more difficult to gather unambiguous empirical evidence of its operations (MacLeod, 2007).

Critics argue that cognitive inhibition holds an intuitive, even seductive appeal because of its neural analogy, and has been indiscriminately applied to developmental, social, clinical, personality psychology, cognitive activities, language, meaning, memory, perception, responding, thought and working memory, resulting in the absence of meaningful operational definitions or measures (MacLeod, 2007). MacLeod (2007) argues that there may not necessarily be a relation between neural and cognitive inhibition as they belong to different levels of analyses. In this view, cognitive inhibition cannot be inferred from neural activity as electrochemical impulses do not (indeed may not be able to) explain the nature of a thought even if they provide the means by which thoughts can occur. Hence, it should not be expected that mechanisms required to

understand mind and brain are necessarily similar, since psychological elements represent while neural mechanisms merely implement them (MacLeod et al, 2003).

In PDP models of processing responses to Stroop stimuli the word and colour dimensions are processed in parallel and the processing influence of one dimension on the other is restricted to the (later) response units. Hence, processing of the word does not slow processing of the colour, but rather it inhibits response execution. Thus, what this PDP model refers to as inhibition is a type of response competition realised via inhibitory links. However, inhibitory links may not be necessary. For example, Roelofs' (2003) model can account for Stroop task without inhibition as control is achieved not by inhibiting the irrelevant attribute, but because it takes longer to excite relevant attribute or information. PFC damage may also result in poor amplification of relevant processing rather than impaired inhibition. Children may perform poorly on an A-not-B search task because of poor amplification of relevant information or immature working memory (Aron, 2007).

Interference and inhibition are often inferred from slowing in performance, but if inhibition means only slowing then the term has no theoretical value and is simply a synonym for interference. This highlights the problem of circularity in operationalising the concept of inhibition as, for example, deviation from the baseline manifesting, for instance, in RT latency, is often used as evidence for inhibition, while non inhibitory mechanisms may explain cognitive performance (MacLeod et al, 2003).

Echoing similar sentiments, other authors agree that the term inhibition has been overextended and requires more specificity. Inhibition has been defined as reducing targeted neural, mental or behavioural activity. Typically, a set of tasks thought to measure inhibitory processes are selected and correlations between them or group differences in performance on them are measured. However, the construct validity of some of the tasks used to measure inhibition is not well established which may explain poor, even negligible correlations between them. They also often have poor reliability since executive tasks are difficult, but with practice get easier and they may also have high measurement error. Impurity is another problem as a range of other task demands, not just inhibition, are involved and inhibition (at best) accounts for just a small proportion of variance (Friedman & Miyake, 2004).

Thus, theoretical opposition to cognitive inhibition is based on four broad types of arguments of: i) circular definition of inhibition, ii) inappropriateness of analogy between neural and cognitive inhibition, iii) non inhibitory mechanisms may account for observed cognitive performance decrements and iv) the poor psychometric properties of the tasks used to measure inhibition. Each argument warrants careful consideration and response by experimenters who choose to investigate the construct.

Firstly, undoubtedly the operational definition of inhibition is a difficult task for the experimenter. For the behavioural scientist, inhibition is conceived of as an *absence* or *lack of* certain behaviours which cannot be verified by simple observation. There is a logical gap between absence of evidence and evidence of absence, and behavioural observations alone can only inform the former. However, in an appropriate experimental context, behavioural/response inhibition can be studied through (and is implemented by) psychophysiological inhibition, for example, through lateralised readiness potential (LRP) in the EEG. LRP, a measure of motor activation, can be used to inquire activation of correct and incorrect responses (Eimer, 1999; Eimer & Schlaghecken, 1998).

Measuring inhibition is also a complex task as the relationship between inhibition and imaging techniques is not simple. A significant reduction in BOLD signal in some task irrelevant cortical areas (Egner & Hirsch, 2005) using fMRI may reasonably be taken to indicate a task related drop in processing activity within that region. However, there is a lot of uncertainty about the relationship between fMRI signal and neural activity in the region of interest since both a decrease in (physiologically) excitatory inputs and an increase in inhibitory inputs to a target region may lead to a decrease in BOLD signal. Conversely, both an increase in excitatory outputs or an increase in inhibitory inputs from a target region may lead to an increase in BOLD signal. Waldvogel and colleagues (2000) examined the relationship between neural inhibition and fMRI signal in the motor cortex using a go/no-go task and transcranial magnetic stimulation (TMS). TMS showed there was increased inhibition in no-go trials establishing that no-go trials produced increased GABA mediated neural inhibition in the motor cortex; however, fMRI signal for no-go trials in the motor cortex was negligible (Aron, 2007), indicative of that inhibition is less metabolically demanding. Hence, fMRI

signal in a given region may not change even when a different technique unequivocally shows an increase in GABA mediated neural inhibition (Aron, 2007).

Hershey and colleagues (2003) used positron emission tomography (PET) and deep brain stimulated subthalamic nucleus (STN) which sends excitatory inputs to the pallidum which in turn has inhibitory functional projection to the thalamus. They found that STN stimulation increased blood flow not only in both the STN and globus pallidus, but also in the thalamus. Hence, despite inhibitory projection from the pallidum to thalamus, blood flow in the thalamus actually increased. Hence both excitatory and inhibitory input to a target region can result in increased measured blood flow (Aron, 2007). There are also doubts as to whether GABA mediated inhibition can be reflected in fMRI BOLD changes because it is related to astrocytes (as distinct from neurons) differing reactions when exposed to glutamate and GABA (Buzsáki et al, 2007).

Secondly, the practice of interpreting deflection below baseline as evidence for inhibition has been criticised as circular (MacLeod, 2007). However, this criticism was without specific examples, hence it is difficult to meaningfully address it, but it is important to note that a similar approach is also applied to excitatory effects where an increase above baseline is interpreted as evidence for excitation and this has not received such criticism. For example, in one such study both amplification (above) and inhibition (below) were defined and interpreted relative to a perceptual baseline depending on the instructions, and measured in cortical regions of interest (Gazzaley et al, 2005).

Thirdly, it is unclear how there can possibly be complete independence between neural (physiological) inhibition and psychological processes implemented in the brain. In particular, neural inhibition does play a role in behavioural inhibition and at least suggests the possibility of cognitive inhibition as a psychological process worthy of serious investigation. The brain has inhibitory as well as excitatory neural connections. Approximately 20% of cortical synapses use gamma-aminobutyric acid (GABA) which is nearly always inhibitory. Some modulatory transmitters (e.g., dopamine, serotonin) have also been found to be inhibitory at some synapses. If facilitation were the only physiological signal in neural networks, they would rapidly escalate to excessive levels of electrical activity (Levine & Brown, 2007) disabling the functional activity of the network, as evident, for example, in epileptic seizures.

Neural inhibition is thought to optimise energy demands and to control excitation (Pfurtscheller & Lopes da Silva, 2005). Inhibitory neurons are more diverse in morphology and function and the dynamic partnership between excitatory and inhibitory neurons ensures homeostatic regulation while also allowing dramatic changes in excitability in narrow time intervals. Inhibitory neurons assure that excitatory trajectories are effectively routed and competing cell assemblies segregated. Response to the same input can produce different responses depending on inhibitory activity (Buzsáki et al, 2007). Much of the incoming information about the environment is behaviourally irrelevant. If the nervous system could not control the flow of information, only a fraction of available resources could be devoted to analysing crucial aspects of incoming information (Treue, 2001).

Excitatory networks are inherently unstable and without inhibition any external input would generate more or less the same one-way pattern, an avalanche of excitation involving the whole population. Inhibitory networks are fundamentally different and produce nonlinear effects depending on the fine details of connections and synaptic weights. Neural inhibition is a necessary condition permitting the emergence of functional complexity amongst cortical neurons as it ensures that excitation recruits the right number of neurons at the required time and that it spreads in the right direction. There may be fewer inhibitory neurons, but they have stronger than usual synaptic connections and are strategically positioned to control action potentials. Inhibitory neurons alone cannot maintain an activity, but they provide the basis for temporal coordination of activity (Buzsáki, 2006). It is almost inconceivable that higher level cognitive organisation of neural activity would not share these basic organisational principles related to the interplay of physiological excitatory and inhibitory processes.

Fourthly, there may be conceivable alternative mechanisms, which employ excitation alone, but the inclusion of inhibition often provides a simpler and more elegant model to account for data. Noninhibitory account of conflict resolution in the Stroop task may suggest that slowing on incongruent trials occurs because it takes longer to activate correct dimension, but they do not explain how irrelevant, prepotent, distracting dimensions are managed once an incorrect response has actually begun especially

considering the brief time window in which interference must be resolved in many real world cognitive and motor tasks.

Inhibition is a fundamental aspect of information processing in the nervous system. It is therefore plausible that inhibitory control mechanisms may play a direct role in down regulating or disengaging task inappropriate pathways (Faust & Balota, 2007). For example, successful inhibition may not be evident in fMRI hemodynamic effects if task irrelevant regions were successfully disengaged. Inhibition may also control timing of neuronal activity and hence shape the temporal flow of information processing. Different neural populations may be activated during stimulus processing and inhibition may shape the temporal pattern of this activation sculpting interactions between cells activated at different phases of the trial, typically at transition points coincident with the next step in the processing sequence (Constantinidis et al, 2002).

To improve research on the functional role of inhibition the definition or concept of inhibition under investigation must be clearly defined in each particular instance. Different operational and conceptual definitions of inhibition must be acknowledged and the relationships between them carefully established. If there is a role for inhibition in cognitive control, the goal for experimenters is to define and measure it in such a way that separates it from facilitation. Alternative mechanisms to inhibition should be considered and where possible tested against hypothesised inhibitory mechanisms in the same design (MacLeod, 2007). Choice of baseline is also critical to establish criteria for their occurrence and non occurrence of inhibitory processes (MacLeod et al, 2003).

Cognitive inhibition must be grounded in actual brain mechanisms. Contrary to some criticisms behavioural and cognitive inhibition must be shown to be functional instances of physiological/neural inhibition. This may be done, firstly, by studying a system (e.g., fronto-thalamic circuitry) with a known anatomical connectivity between source and target region and, secondly, by using unambiguous methods (e.g., TMS) to manipulate and measure inhibition in the target region. Behavioural inhibition is relatively unambiguous as inhibition applies at the level of physical response and the target of inhibition is motor cortex, but it is functionally and anatomically (motor cortex) distinct from cognitive inhibition. However, behavioural inhibition may help to provide a model for cognitive inhibition (Aron, 2007).

Since excitation only theories cannot solely account for such effects, for example, how initiated incorrect responses can be halted in very brief time intervals, it is assumed that inhibition is a necessary complementary process at neural, behavioural and cognitive levels of information/response processing. The dynamic partnership between excitatory and inhibitory neurons ensures homeostatic regulation while also allowing dramatic changes in excitability in narrow time intervals (Buzsáki et al, 2007). There is no reason to believe that the mind, including cognitive processing, is separate from the brain; hence, inhibition, like excitation, is, and can be evident, at both neural and cognitive analysis levels, but measuring it requires skilful experimental and task designs.

2.2.5 EEG Measures of Facilitation and Inhibition: Alpha ERD and ERS

The brain represents about 2% of the adult human body weight, but accounts for 20% of all energy consumed with up to 80% of the brain's energy spent on neuronal communication. The majority of the brain's energy budget is devoted to ongoing rather than evoked changes (Buzsáki et al, 2007). The most notable examples of EEG measures of stimulus evoked changes in neural activity are ERP. ERP are a summary measure of the brain's electrical activity obtained by time locked averaging of EEG epochs defined around some specific experimental event over a large number of trials. ERP are assumed to be generated by a set of event (stimulus or response)-evoked, fixed-latency and fixed-polarity brain events (Penny et al, 2002). The signal averaging approach used in calculating ERP assumes that ERP waveforms reflect neural activity which is uncorrelated with ongoing EEG. ERP are voltage changes time locked to stimuli or responses which consist of positive and negative peaks which are assumed to reflect phasic activity in particular cortical regions. Hence, the classical view holds that ERP reflect phasic activity time-locked to the events in particular brain regions and are embedded in ongoing, background EEG activity which in turn is otherwise uncorrelated with these events (Yeung et al, 2004a).

An alternative view suggests that uncertainty exists in the relationship between ERP and rhythmic ongoing EEG. ERP are extracted by averaging which may result in loss of information such as inter-trial variability amongst single evoked potentials as in averaged ERP only consistent activity across trials is considered important, and “noise”

or background activity is averaged to zero. Many researchers are considering the possibility that ERP peaks may in fact be generated by reorganisation in the timing (i.e. the phase) of ongoing cortical oscillations through phase resetting of specific frequency (Yeung et al, 2004a). Hence, at least some ERP components may be produced by stimulus induced changes in ongoing brain dynamics by phase synchronisation of ongoing rhythms meaning that after stimulus presentation the phase of ongoing rhythm may be shifted towards a particular value or weighted towards dominant phase or *phase resetting* (Makeig et al, 2002) in relation to the stimulus (Penny et al, 2002; Klimesch et al, 2007b).

If the brain invests so much energy in ongoing cortical oscillations then it is reasonable to assume that these dynamics are significant for complex information processing. The primary task of the brain's neocortex is to accurately and quickly perceive and respond to stimuli by interacting with the world through the motor system. This is achieved through a system of simple and complex brain rhythms. Synchronised cortical oscillations create a temporal ordering within and across neuronal networks. Paradoxically the largest amplitude and most regular spontaneous oscillations occur during sleep, when the brain is disengaged from the environment or during epileptic discharges. In contrast, during cognitively demanding activities such as decision making, the brain appears to be desynchronised (Buzsáki, 2006; Buzsáki & Draguhn, 2004). Hence, rhythmic activity is organised in complex patterns depending on the state (e.g., awake, asleep, epileptic) of the brain and current task (Thut & Miniussi, 2009). Rhythms of different frequency are thought to reflect coordination in networks with different spatial scales with higher frequencies coordinating local networks being in centimetre range, and slower frequencies coordinating networks across distances between lobes and even hemispheres (Varela et al, 2001; Sauseng & Klimesch, 2008).

Event related desynchronisation (ERD) and event related synchronisation (ERS) reflect ongoing (oscillatory) EEG activity, a decrease and increase in power within a certain frequency band relative to a baseline. ERD/S is always time locked to an event, but can either be phase locked (evoked) or not phase locked (induced) (Pfurtscheller, 2003), while ERP is both phase and time locked to the events. The difference between ERP and evoked ERD/S is that evoked ERD/S are frequency band specific. ERP are

derived from time domain averaging while ERD/S are extracted from frequency analysis in a sliding time window, thus giving a combined time-frequency domain analysis and representing percentage of frequency changes (increase, decrease) relative to the reference interval in ongoing EEG. Because ERD/S in ongoing EEG needs time to develop and recover, intervals between consecutive events should last seconds (Pfurtscheller & Lopes da Silva, 1999). ERD predicts the onset of change in oscillation amplitude with an error margin of only 10 – 30 ms (Knösche & Bastiaansen, 2002).

It has been argued extensively by Klimesch and colleagues (2007a) that functional (event related) changes in EEG desynchronisation and synchronisation within alpha frequency band provide an index of recruitment and inhibition respectively of neural networks underlying processing. Alpha (α) oscillations or alpha rhythm is referred to as a waking or background, sinusoidal parieto-occipital pattern in the range of 8 to 13 seconds per cycle or Hz (Rippon, 2006; Herrmann et al, 2005), the dominant oscillation in the human scalp EEG, is believed to be strongly influenced by thalamic nuclei and the thalamus plays an important role in selectively processing and relaying sensory (bottom up) information to the cerebral cortex (top down effects) through reciprocal connections (Klimesch et al, 2007a). Attention is closely associated with alpha, for example, alpha power increases as children mature and may be related to the general increase in cognitive competence with maturation (Ward, 2003), while the opposite pattern occurs in the latter part of lifespan (Klimesch, 1999). However, the distribution of energy (amplitude or power) across the different alpha rhythms tends to exhibit large fluctuations over time even when measured within the same individual (van der Stelt, 2008). It has been argued that there are several independent rhythms in the alpha band with different functional properties (Niedermeyer, 1999). For example, alpha rhythm at supplementary motor area (SMA) is called mu (μ) or Rolandic mu rhythm which has the same frequency range as alpha but is topographically and reactively different; for instance, it is not blocked by eye opening (Niedermeyer, 2005). Alpha is the most prominent cerebral rhythm of the awake, healthy human brain and two main hypotheses suggest that alpha either arises from cortical or thalamic neurons, or that it emerges from the synaptic coupling of distributed network of neurons and, hence, no one group is responsible (Buzsáki, 2006; Niedermeyer, 2005).

Alpha oscillations are assumed to reflect reverberating loops of activity in thalamic, thalamo-cortical and cortico-cortical circuits (Buzsáki, 2006). Strong alpha activity is associated with behavioural deactivation or inhibition and alpha usually shows a reduction in amplitude (or desynchronisation in the activity of these underlying networks) during active cognitive processing seen for example in alpha blocking (Sauseng & Klimesch, 2008). Therefore, alpha ERS is believed to reflect inhibition, interruption of thalamocortical information transfer and thus the reduction in activity of task-irrelevant networks (Rippon, 2006; Klimesch et al, 2007a), while alpha ERD is a reliable correlate of the increased cellular excitability in thalamocortical information processing (Pfurtscheller & Lopes da Silva, 2005; Penny et al, 2002).

Hence, alpha ERD and ERS reflect aspects of the interaction between the thalamus and cortical areas. Alpha ERD may involve activated cortical networks (open thalamic gate) and readiness for in/output information processing. Alpha ERS, in contrast, may indicate that thalamo-cortical information transfer is disengaged (thalamic gate closed) and cortical neuronal networks are inhibited. Changes in oscillatory activity also reflect changes (increase, decrease) in energy demands which may also be expressed in changes in blood flow and glucose metabolism (Neuper & Pfurtscheller, 2001).

Alpha ERD can be seen as a correlate of activated cortical areas with increased cellular excitability in thalamo-cortical systems, a correlate of activated cortical areas involved in processing cognitive information and producing motor responses, and vice versa for alpha ERS. Alpha, however, is not a unitary phenomenon. For example, lower alpha (8 – 10 Hz) ERD is obtained in response to almost any type of task, is topographically widespread over the scalp and is likely to reflect general task demands and attentional processes. More widespread, increased ERD could also be the result of larger neural networks, more cell assemblies influenced by task complexity, more efficient performance or the need for more attention and effort, reflecting the allocation of attentional resources, arousal and effort in cognitively demanding tasks. Upper alpha (10 – 12 Hz) ERD is topographically restricted and more task-specific. More intelligent people also demonstrate less ERD, alpha ERD more focused over task-specific cortical regions. This finding has been replicated using different tasks modalities (verbal, numeric) and complexity (Pfurtscheller & Lopes da Silva, 2005). ERS between 10 – 13

Hz is thought to represent inhibited cortical areas or networks. For example, more intelligent participants exhibit larger upper alpha ERS over task irrelevant cortical regions, and instruction not to execute a learned response is associated with ERS over motor cortex. ERS is likely to reflect top down control to inhibit processes (Freunberger et al, 2008).

Movement related ERD over sensorimotor areas involves a frequency range of 8 – 13 Hz (i.e. the mu rhythm) and premovement ERD in the lower (8 – 10) alpha is evident over sensorimotor regions, while upper (10 – 13 Hz) alpha ERD is restricted to somatotopic representation areas (hand area to support specific movement) (Neuper & Pfurtscheller, 2001; Pfurtscheller, 2003). It is known that quantification of movement related ERD can improve the diagnosis of functional deficits in neurological disorders such as Parkinson's disease (PD) where ERD may be reduced or abolished over affected hemispheres, the premovement ERD may be less lateralised and start later while ERS may be of smaller magnitude and delayed compared with controls. ERD measurements during voluntary movements may differentiate between superficial and deep vascular lesions (Pfurtscheller & Lopes da Silva, 1999).

Anticipatory behaviour can also be researched using ERD. Anticipatory behaviour is directed at upcoming events and serves to generate faster and more efficient information processing, for example, by pre-setting necessary physiological processes. Anticipatory behaviour may be accommodated through a thalamo-cortical gating mechanism (opens sensory gate to cortex) which also forms the neural basis of alpha ERD; hence, pre-stimulus ERD may be a true index of anticipatory attention (Bastiaansen et al, 2002). If relevant stimuli appear in a predictable pattern, neuronal oscillations may entrain (phase-lock) to the temporal structure of the attended stimulus stream (changing response gain and amplifying neuronal responses to it) and hence serve as an instrument of sensory selection. When a stimulus is predictable it is more likely to be detected, while a random or unpredictable stimulus (Lakatos et al, 2008) may not be processed as efficiently.

It is unclear whether certain oscillatory effects are causative or merely correlative. Psychopharmacological and neurostimulation such as TMS techniques can help to evaluate, for example, their temporary or disruptive impact on cognitive behaviour

(Sauseng & Klimesch, 2008). For example, abnormalities in GABAergic inhibitory neurons and N-Methyl-D-Aspartic acid (NMDA, which binds with glutamate receptors) receptor dysregulation have been found in schizophrenia sufferers. Acute effects of NMDA antagonist ketamine doses produced acute psychosis symptoms in healthy volunteers (Uhlhaas & Singer, 2006). Alpha has been demonstrated to play an active and causal role in information processing. For example, in one experiment only upper alpha TMS pulses improved performance and not control condition of lower alpha or beta TMS pulses (Klimesch et al, 2007a). If synchrony is the basis for normal brain functioning, then its disruption should cause functional abnormalities (Varela et al, 2001). Diminished alpha power in schizophrenia sufferers may also reflect a dysfunction in thalamo-cortical circuits associated with poor inhibition of irrelevant information (gating of sensory information is impaired) (Klimesch et al, 2007a).

Alpha ERS plays an active role in inhibitory control, while alpha ERD reflects release of inhibition or engagement of activation. Alpha power suppression during eye opening suggests that light stimulation (bottom up) is responsible for decreasing amplitude, but just opening eyes in a darkened room with no visual stimulation can also suppress alpha, hence alpha suppression can also be triggered by top down processes (Klimesch et al, 2007a). Alpha ERS can be selectively observed in tasks in which a well learned response must be withheld and over task irrelevant cortical regions. For example, ERS in the upper alpha was observed when motor response had to be inhibited. Control of attention, especially when sensory information must not be processed, is associated with an increase in alpha activity. Therefore, inhibition may operate like a filter to reach a high signal to noise ratio by allowing only a small, excitatory subset of cells to selectively process information and silencing the rest (Klimesch et al, 2007a).

Single neurons have an intrinsic ability to oscillate at multiple frequencies and precise timing of their activity within neural networks itself may represent discrete informational states. Hence, it is no surprise that perception, memory and consciousness are closely related to the synchronisation of neural networks. Higher frequency oscillations (e.g., gamma) are usually confined to a small cortical volume, while slow oscillations (e.g., theta) recruit much larger networks. Information in the brain is processed, transferred and stored by neural networks that are transiently synchronised by

dynamic connections. For example, different stimulus's attributes might be processed separately in distributed networks and linked by (e.g., alpha) frequency oscillations which may also even be responsible for binding feature representations into cognitive percepts. Synchrony from oscillations is the most energy efficient means of establishing temporal coordination allowing synchrony to be sustained even if synaptic links are weak. Different (e.g., slow versus fast) oscillations may be responsible for different dimensions of brain integration (Buzsáki & Draguhn, 2004). Hence, oscillations control timing of neural activity since neurons fire during excitatory phase and thus target cells receive neural activity synchronously. Timing of neural processes is involved in long term learning as learning related changes are not induced in a continuous manner, but rather in narrow time windows (Klimesch et al, 2007a).

In modular models of the brain, anatomical connections and individual cortical regions are traditionally studied in isolation. On the other hand, the network oscillation model of information processing in the brain requires studies of how widespread cortical networks and regions are coordinated through changing synchronisation of cortical oscillations. Communications between areas may be regulated depending on how the phase (timing) of their oscillations match up, for example, changes in phase offsets may weigh the strength of connections between cortical regions resulting in an effective interaction pattern. Such a mechanism would be dynamic, connectionist and self organising (Miller & Wilson, 2008; Womelsdorf et al, 2007). Take for example processing in the fusiform face area (FFA) which is a pea sized region and a plausible localised processing module for those favouring the modular view of neural function. The FFA responds strongly to faces (Grill-Spector et al, 2006). The FFA specialisation for faces may be the neurobiological solution to the perceptual challenge to identify individual faces from other similar faces that differ only in subtle configurations and share the same basic structure. Hence, specialisation of the FFA may optimise the capacity to store many thousands of visual categories. According to the modular view, deficits in face perception such as congenital prosopagnosia may mean deficits in the actual FFA cortical region itself. However, this may not necessarily be the case. Rather than reflecting deficits in functional region, prosopagnosia may reflect deficits in a wider face processing network (Baker, 2008).

In a particular context, specific cortical areas perform unique functions (although the functional role of a specific region may vary in different contexts); nonetheless, complex cognitive functions require the integrated action of many distributed areas (Bressler, 1995). Particular dedicated networks are defined by unique anatomical sets of interconnecting pathways with modulatory control of processes configuring the implementation of those functions. This of course means that network interactions are constrained by anatomical connectivity and modulatory control processes. Distributed processing is an efficient way of managing alternative communication routes and broad access to information in high demand tasks. Control processes are necessary to modulate the network by dynamically selecting cortical areas to process complex stimuli through input gating (by priming excitability of the cells by lowering their firing thresholds), operational control and output gating (by eliminating response conflict) (Bressler, 1995).

Thus elementary functions may be localised in discrete cortical regions, but complex functions are processed in networks which are dynamically organised and regulated by control processes. In interactions with the environment, the cortex must process time-varying sensory patterns and generate time-varying motor patterns on time scales from milliseconds to seconds. Hence, the cortex must flexibly and rapidly process a wide range of complex patterns. A mechanism must exist for the selection of processing in relevant cortical regions and synchronised cortical oscillations are a likely candidate for this mechanism (Bressler, 1995; Fries, 2005). Alpha ERD and ERS is one of the EEG mechanisms through which effective processing is achieved by engaging (alpha ERD) task relevant or inhibiting (alpha ERS) task irrelevant, interfering information processing network/s (Klimesch et al, 2007a).

2.2.6 Egner and Hirsch (2005) Study and Current Study

This elegant and innovative Stroop task study was designed to find behavioural and neural evidence using fMRI of whether cognitive control resolves conflict through amplification of relevant information, inhibition of distracters or both. Participants were presented with faces and superimposed names of famous politicians and actors. Stimuli were presented in two blocks, one requiring responding to faces (face-target) and another to names (face-distracter), grouped in a classic blocked fMRI design aimed at increasing

signal to noise ratio. Faces and superimposed names were either congruent (e.g., actor's face with actor's name) or incongruent (e.g., politician's face with actor's name) and arranged to manipulate conflict and control levels by contrasting high control trials (an incongruent stimulus following an incongruent stimulus) and low control trials (an incongruent stimulus following a congruent stimulus) thus utilising the Gratton effect.

The authors theorised that unintended processing of the irrelevant (e.g., face) attribute would activate the same response required for the relevant (e.g., name) attribute in the congruent condition, but in the incongruent condition it would activate the incorrect response as a result producing response conflict. Control levels were manipulated by trial sequences which could be incongruent following incongruent (II: high control) or incongruent following congruent (CI: low control).

The authors measured BOLD signal in the FFA which is known to be selectively and sensitively activated by faces. Cognitive conflict and control levels were manipulated through congruent and incongruent trial sequences and BOLD levels in the FFA were interpreted as a cortical measurement of attended (FFA in face target block) and ignored (FFA in face distracter block) information. Thus, the authors chose the face/name Stroop task and measured activity in the FFA which, in turn, gives a well defined region of interest for contrasting control related changes in activation when the face was a target versus when the face was a distracter.

Behavioural results demonstrated both Stroop and Gratton effects. This meant that cognitive control successfully modulated conflict. BOLD results demonstrated that activity in the FFA was enhanced in face target block in the high control (II) relative to the low control (CI) condition indicating amplification of activity in this region of task relevant processing, but remained unchanged in this contrast in face distracter block. Inhibitory effects of cognitive control should have been expressed as a decrease in activation in the FFA in the high control condition relative to the low control condition when the face was a distracter. Hence, fMRI evidence demonstrated that amplification of task relevant information in the FFA, but not inhibition of task distracters, modulated the resolution of this cognitive conflict.

Nieuwenhuis and Yeung (2005), reviewing the above study, suggested that given the massive range of potential perceptual distracters it may be impractical to predict and

inhibit all of them. The question thus is whether amplification and/or inhibition is more important in response than perceptual selection since the range of competing responses is usually limited and, hence, inhibiting competing responses may be a more feasible strategy.

In reviewing the Egner and Hirsch (2005) study, Aron (2007) concluded that a failure to identify fMRI signal change (increase or decrease) in the posterior FFA in relation to inhibition is not definitive evidence that such inhibition was not present at the neural level in the structure, especially considering that fMRI may not be suitable to detect such differences given the sometimes complex effects of inhibition on BOLD response. The fMRI go/no-go study of Waldvogel et al (2000) indicated that the fMRI signal in a given region may not change even when a different technique unequivocally shows an increase in neural inhibition (Aron, 2007). Hershey et al (2003) showed that functional projection from the pallidum to the thalamus is inhibitory, yet the measured blood flow in the thalamus can actually increase from deep brain stimulation of the pallidus. The relationship between imaging techniques and inhibition often is very complex.

Current Study

Cognitive inhibition like behavioural inhibition may be a functional application of physiological inhibition. Indeed, if cognitive functions are implemented in neural networks and if inhibition alongside facilitation is a common property of the connections within and between various functionally specialised neural networks then the phenomena such as behavioural inhibition and cognitive inhibition should be observed in the functions implemented by neural networks subject to inhibitory inputs. It would be extraordinary if such phenomena did not exist.

Like Egner and Hirsch (2005), the current study was designed to examine responses to face stimuli in blocks where the face is the target and in block where it is a distracter. Egner and Hirsch used fMRI BOLD response in the FFA while the current study examines the difference in topographic patterns of ERD/ERS in evoked upper alpha between high control (II) versus low control (CI) conditions. These topographic patterns should be generated by the neural, in this case face processing network/s modulated by

the facilitatory and/or inhibitory cognitive control influences. Following Klimesch and colleagues (2007a), this is because evoked upper alpha ERD should show activation/facilitation of information processing while evoked upper alpha ERS should show suppression/inhibition of information processing.

Another critical issue was that many tasks require processing of input and output cognitive and motor patterns in millisecond or second range, hence, the excitatory/inhibitory system must be swift and flexible yet stable. If inhibitory control is implemented through evoked alpha oscillations as Klimesch and colleagues (2007a) proposed then such signals would be exceedingly brief and their immediate effects would be resolved within hundredths of milliseconds, well below the 4 – 6 second temporal resolution of fMRI. As EEG has excellent temporal resolution down to 5 milliseconds, it is the most suitable tool for investigating the presence of brief inhibitory modulation in cognitive control and was the method utilised in the current study.

A further related issue was whether cognitive control is comprised of a single central mechanism or whether it is implemented through multiple networks and mechanisms. Potentially cognitive control could be implemented at multiple points in task related processing pathways such as at stimulus processing or response selection. In each case it remains to be determined whether control is achieved by facilitation, inhibition alone or some combination of both.

If the face processing network/s is inhibited in the high (II) compared to low (CI) control in face distracter condition, which is yet to be determined, but is facilitated in the case of the high (II) compared to the low (CI) control in face target condition, successfully demonstrated by Egner and Hirsch (2005), then the results such as topographic maps and area reports obtained in the former case should be the inverse of those obtained in the latter case for those regions adjacent the FFA.

All paradigms in the current project use the face/name Stroop task pioneered by Egner and Hirsch (2005) and aim to provide EEG evidence to clarify some of these issues.

2.3 Method

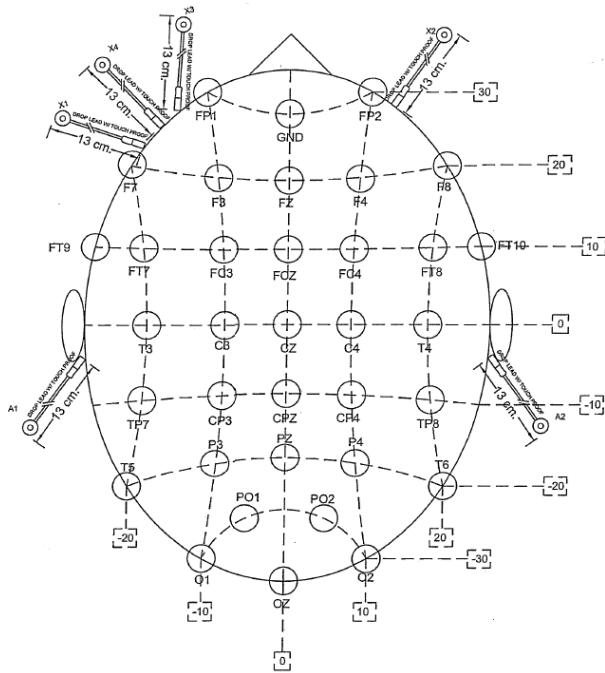
2.3.1 Participants

Twenty six naïve participants (16 males and 10 females) aged between 18 and 49 years ($M = 26$, $SD = 9$) took part in this experiment. All of the participants were University of New England (UNE) volunteers who were paid \$10 for their participation. Participants were right handed, not taking any psychoactive medication and had normal or corrected-to-normal vision. The experiment consisted of a single 1½ - 2 hour session.

2.3.2 Data Acquisition

EEG data was collected using an elastic Compumedics NeuroScan Quik-Cap using small (48 – 54 cm), medium (54 – 62 cm) and large (62 – 68 cm) sizes to accommodate variability in head circumference. EEG recordings were taken from an array of 40 silver/silver-chloride (Ag/AgCl) coated electrodes arranged according to the international 10 – 20 system montage using nasion and inion landmarks and referenced to right ear (A2). VEOL and VEOU (vertical electro-oculogram: below (L) and above (U) left eyes), HEOL and HEOR (horizontal electro-oculogram: Left and Right outer canthi), Fp1, Ground (anterior to Fz), Fp2, F7, F3, Fz, F4, F8, FT9, FT7, FC3, FCz, FC4, FT8, FT10, A1, T3, C3, Cz, C4, T4, A2, TP7, CP3, CPz, CP4, TP8, T5, P3, Pz, P4, T6, O1, PO1, PO2, O2 and Oz channels were recorded (Figure 2.1a). During recordings all electrode impedances were maintained below 30 kΩ. Topographic map colour key in Figure 2.1b.

a



b

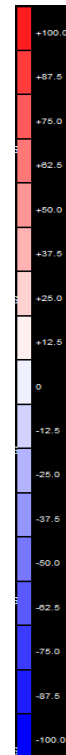


Figure 2.1. Panel a) Forty channel 10 – 20 system NeuroScan Quik-Cap[®] montage, Compumedics Ltd. Image reprinted with permission. Panel b) Colour key (see Appendix B).

EEG signals were amplified with 0 – 100 Hz (48dB/octave rolloff) bandpass and digitized with a 32-bit A/D converter at a rate of 500 Hz per channel using a NuAmps 7181 amplifier and ACQUIRE 4.3.1 software (both by Compumedics NeuroScan, 2003). Participants' responses were recorded with ACQUIRE 4.3.1. Analyses were conducted offline with EDIT 4.3.1 (Compumedics NeuroScan, 2003).

Prior to the experiment all participants completed an eye-movement-artifact correction calibration task (Croft & Barry, 2000; Croft et al, 2005) while their ocular potentials were recorded at VEOL, VEOU HEOL and HEOR electrodes. This task required participants to follow with their eyes-only on screen changes in stimulus position; first vertical changes (40 each up-to-down and down-to-up) and then horizontal changes (40 each left-to-right and right-to-left) to a moving brown square on a black background. The stimulus was presented for 800 ms with 200 ms inter stimulus interval (ISI). Participants were then asked to blink whenever a centrally-presented square

changed colour from brown to blue and from blue to brown (Figure 2.2). This stimulus was presented for 1 000 ms with 200 ms ISI. In total the eye-movement-artifact calibration task lasted approximately 3 minutes.

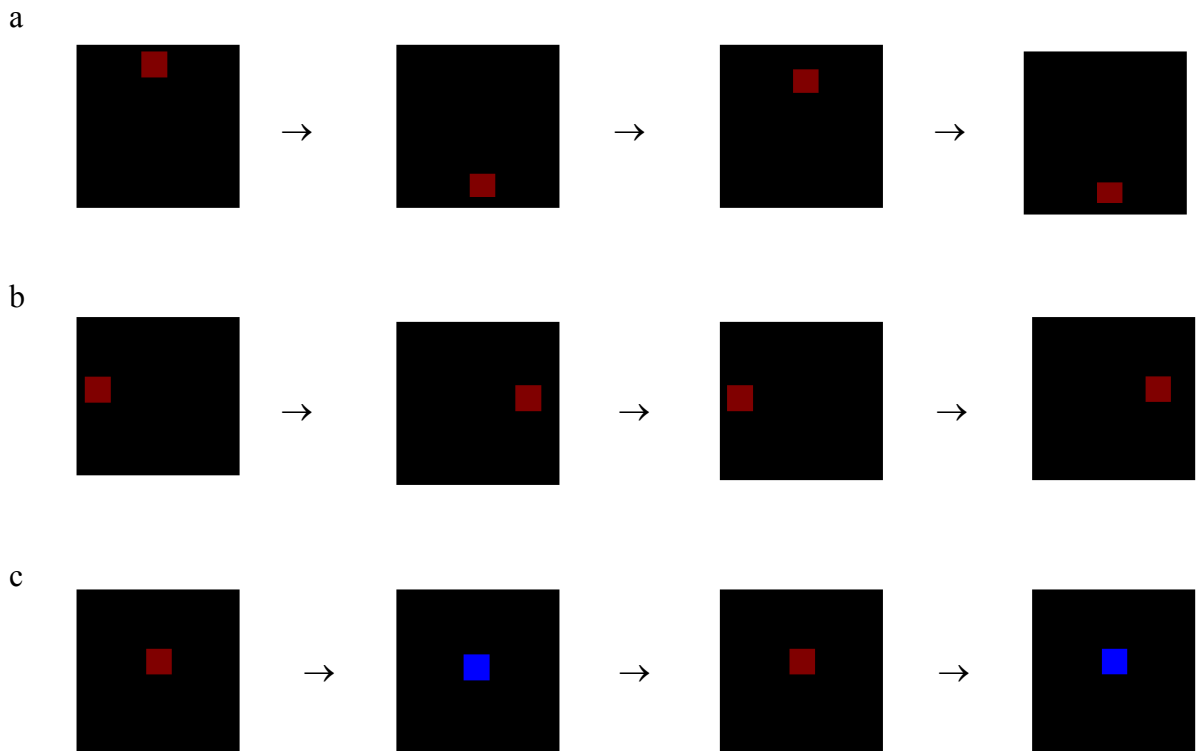


Figure 2.2. Eye-movement-artifact correction task required participants to follow with their eyes-only: a) vertically moving square, b) horizontally moving square and c) to blink when square changed colour from brown to blue and from blue to brown.

The purpose of this task was to record and calculate ocular potentials and then subtract them using an algorithm from the participants' experimental recordings. This approach allows the reduction of ocular potentials without the need to discard data related to eye movements (Croft & Barry, 2000).

2.3.3 Stimuli

Stimuli were created using CANVAS 9.0.4 (ACD Systems, 2004) and presented with STIM² (Compumedics NeuroScan, 2003) software and displayed on a 41 cm DELL computer monitor with participants seated approximately 130 cm away. Stimuli consisted

of 6 black and white 80 x 80 mm (226 x 226 pixel, 152 kilobytes) photographs and names of famous actors (Jack Nicholson, Russell Crowe and Tom Cruise) and politicians (John Howard, Kevin Rudd and Winston Churchill). Participants readily recognised the identity of actors and politicians in both photographs and written names before the experiment.

Each photograph had a name written across it in red letters. The response related category (politician or actor) of names were either congruent or incongruent (Figure 2.3) with that of the photograph. Photographs were never paired with their own name (e. g., a photograph of Winston Churchill was never paired with the name “Winston Churchill”). Neither negative priming, when a distracter on a current trial turns into a target in the subsequent trial, nor immediate stimulus repetitions were included in the sequence of stimuli. There were in total 30 stimuli comprised of 12 congruent and 18 incongruent stimuli.

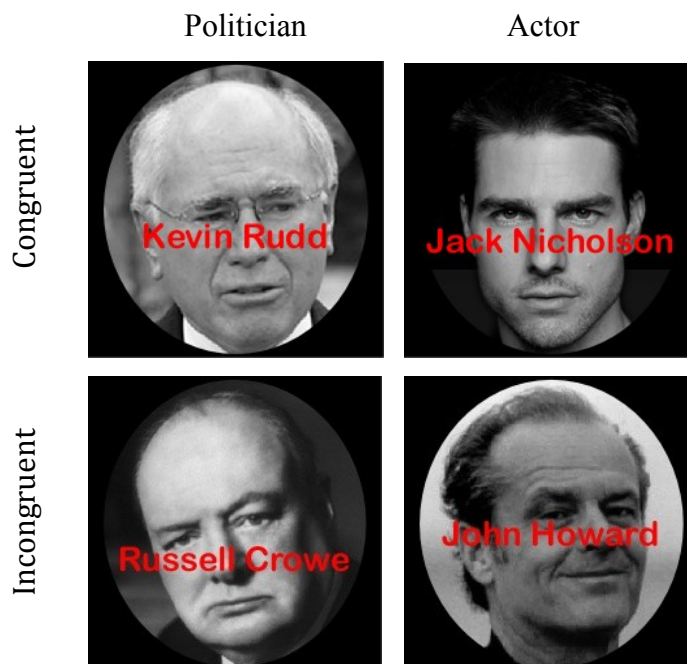


Figure 2.3. Stimuli were either congruent (e.g., actor’s face with actor’s name) or incongruent (e.g., politician’s face with actor’s name). Adapted with permission from Egner and Hirsch (2005).

Trial sequences were created in regard to current-trial and previous-trial congruency (congruent-congruent (CC), incongruent-congruent (IC), congruent-

incongruent (CI), incongruent-incongruent (II)) (Figure 2.4a). Participants had to respond to either name or face and to classify whether this person was “a politician” or “an actor”. Photographs were presented on black background centrally on the monitor for 1 000 ms. The size of the photographs and written names required no scanning in order to reduce eye movement artifacts. Participants responded to photographs which disappeared as soon as the response was made or when 1 000 ms terminated. A fixation point was 1 300 ms ISI between the pictures (Figure 2.4b).

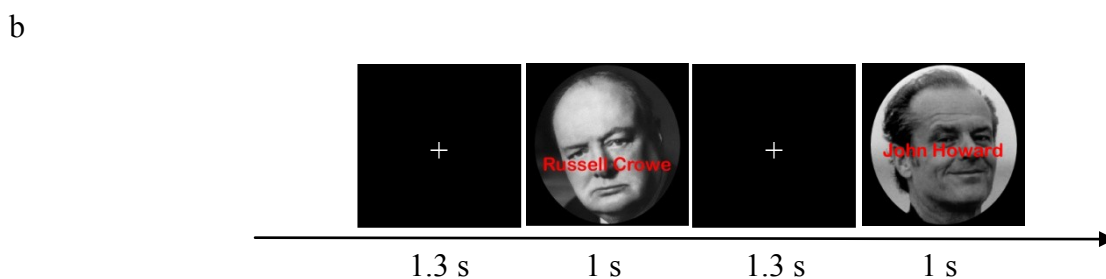
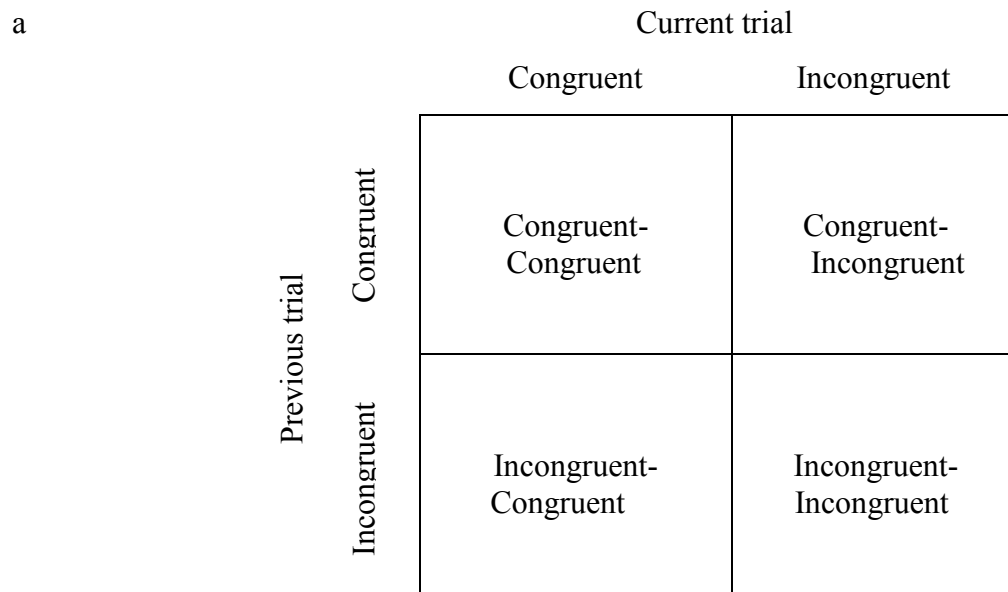


Figure 2.4. Panel a) Trial sequences were created with respect to current- and previous-trial congruency. Panel b) Participants had to respond to faces and names classifying whether the person was “an actor” or “a politician”. Adapted with permission from Egner and Hirsch (2005).

Stimuli were presented in two blocks. In one block participants were instructed to respond to faces and in the other block to respond to names. In the face target block, the names acted as distracters and in the name target block the faces acted as distracters. There were near/equal numbers of all trial sequences presented in pseudo-random order in the face target (CI = 37, II = 38, IC = 37, CC = 35) and in the face distracter (name target) (CI = 37, II = 38, IC = 38, CC = 34) blocks.

Each participant completed 296 trials in total, consisting of 148 trials in face target and 148 trials in name target blocks. Predictability of the on-coming stimulus and the required response was reduced by varying the type of the on-coming stimulus. For example, sometimes a photograph of an actor followed a photograph of a politician, but on other occasions an actor followed an actor or a politician followed a politician.

2.3.4 Procedure

Prior to the commencement of the experiment a pilot study was conducted to refine procedures. Before coming to the laboratory participants were asked to wash their hair with shampoo, but not to use any other cosmetic products such as 2-in-1 shampoos, hair conditioners, gels or make-up as these coat the skin or the scalp and make it more difficult to obtain low impedances.

Each participant signed a consent form and completed the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) where scores ≥ 50 were interpreted as indicating right-handedness, between 50 and -50 ambidextrousness and ≤ -50 left-handedness following Hervé et al (2005). After completing the forms participants were given a small round brush with stiff plastic bristles to vigorously brush their scalp for 2 - 3 minutes to exfoliate the scalp and to remove any debris such as dandruff. The cap was placed around each participant's head and secured with a chinstrap. The skin surface for drop-down electrodes (HEOL, VEOL, VEOU, HEOR, A1, A2) was first vigorously cleaned with a cotton swab dipped in isopropal-alcohol and then cleaned with abrasive EEG prepping gel until the skin looked pink and flushed with blood.

QuikCell System electrodes were activated by injecting sponge disks inside them with 130 μ l saline solution comprised of deionised water, electrolytes and a drop of "Amphoteric Surfactant Baby Shampoo" using an electronic micropipette (Research Pro

Eppendorf Pipetter). Drop-down electrodes were then attached to the skin using electrode collars and surgical tape. A 10 – 15 cm segment of surgical gauze (Livingstone Tubular Net Bandage; Size 6 – Pelvic region) was placed on most participants' heads horizontally over the forehead and back of the head (avoiding frontopolar electrodes) or/and vertically under the chin and over the top of the head to provide more uniform electrode (especially ground) pressure and thus lower impedances.

Once the EEG signal was established, participants were shown their incoming EEG on the computer monitor and were encouraged to grind and tap their teeth, talk, move their neck or body and observe the impact of these movements on their EEG. Consequently, participants were instructed to make minimum unnecessary body movement (e.g., looking at the keyboard) during the experiment.

Participants were given detailed written and verbal instructions including visual illustrations (e.g., of a trial structure and what was required of them) to ensure a high level of understanding of the demands of the experimental task. Participants were instructed to respond as quickly and as accurately as they could. Participants responded with left and right hand index finger button presses on the computer keyboard. Half of the participants responded with a right (m) button press for politicians and a left (z) for actors and the other half responded with a right (m) button press for actors and a left (z) for politicians. Response types (i.e. “an actor” or “a politician”) were kept to ≤ 4 in a row. Half of the participants first completed the face target block followed by the face distracter (name target) block, while the other half first completed the face distracter block followed by the face target block. The experiment lasted approximately 13 minutes and participants could rest during the experiment.

During preparation and testing the researcher kept participants as comfortable as possible by regularly inquiring about their physical and emotional comfort. At the conclusion of the experiment participants were asked for their informal verbal feedback on the difficulty of the task and any strategies they had devised to manage those difficulties. Those who requested it (following an invitation) were further debriefed. All participants were provided with an information sheet regarding the research background and the researcher's contact details should they have wished to find out the results when these became available.

2.3.5 EEG Analysis

The effects of ocular potentials for each participant were calculated using the eye-movement calibration file and then subtracted from individual experimental EEG recordings using the Croft and Barry (2000) algorithm. Each experimental EEG recording was visually inspected and contaminated segments including gross motion artifacts and noisy data channels were marked for rejection. One corrupt recording (participant 42) was permanently discarded and excluded from the main analyses.

EEG data were re-referenced to the common average and a global field power (GFP) channel was added (Skrandies, 1990). Epochs for face targets and face distracters (name targets) in CI and II trials were extracted from unfiltered EEG files with epoch intervals defined from -1 500 ms prestimulus and +1 500 ms poststimulus. Epochs which overlapped rejected blocks were excluded from further analyses. Remaining epochs were then baseline corrected over the entire epoch length and set aside.

Eye-movement -artifact corrected, cleaned and re-referenced EEG recordings were then filtered using 1 – 30 Hz bandpass with 48 dB/oct with zero phase shift for all channels. Then CI and II face target and face distracter epochs were again created as for above unfiltered files. These epochs were then baseline corrected over the entire epoch and criteria-based artifact rejection in time-domain (rejection criteria set to minimum -50 and maximum 50 μ V) applied to all channels except GFP, VEOU, VEOL, HEOR, HEOL, A1 and A2. The specific epochs rejected this way were then identified by epoch number (their sequence in the file of epochs). For one participant (38) all epochs were rejected and this recording was also permanently discarded.

Epochs created from *filtered* EEG recordings which were consequently rejected were used as an objective criteria based upon which contaminated epochs created from *unfiltered* files were rejected. Only uncontaminated epochs extracted from unfiltered EEG recordings were used in the subsequent event-related band power (ERBP) analyses. ERBP was calculated as a percentage change in band amplitude in a sliding time window of 125 ms relative to the reference interval. ERBP analyses employed a bandpass filter zero phase shift, reference interval -1 000 to 1 000 ms (with control related effects expected to be evident at both pre and post stimulus time intervals), epochs were trimmed 500 ms on both left and right. ERBP was performed separately for 9 Hz (low alpha) and

11 Hz (high alpha) centre frequency with 1 Hz half bandwidth and 48dB/octave rolloff. These analyses were conducted separately for both induced (non phase locked) and evoked (phase locked) components of the EEG signal. This set of analyses was performed separately on CI and II trials for face target and face distracter conditions.

Source localisation for evoked ERBP effects was performed using standardised low resolution electromagnetic source tomography (sLORETA) (Pasqual-Marqui et al, 1994; Sekihara et al, 2005) a free functional imaging technique which computes and estimates the point source or generator of neuronal activity in 3D using real scalp electric potentials. ERP were first calculated by averaging unfiltered and uncontaminated epochs in the time domain. ERP were then processed in as similar a manner as possible to ERBP analyses by filtering ERPs with bandpass filter zero phase shift, 10 Hz to 12 Hz with 48dB/octave rolloff for both. Hence, high evoked alpha ERP for CI and II trials for face target and face distracter trials were used in sLORETA. Based on previous investigations the time interval for source localisation of these ERP was chosen at 170 ms post-stimulus. The negative ERP component peaking at 170 ms (i.e. N170) has been identified as relating to processing of faces (Luck, 2005).

2.4 Results

2.4.1 Edinburgh Handedness Inventory Scores

Twenty four participants scored >50 and 2 scored between 33 and 45 points on EHI respectively, hence most participants were evidently right handed (Figure 2.5).



Figure 2.5. Participants' scores on Edinburgh Handedness Inventory.

2.4.2 Behavioural Stroop Effect and Gratton Effect and Preliminary EEG Results

Behavioural Stroop Effect and Gratton Effect Results

Mean RT (ms) and accuracy rates (%) were calculated for all correct trials. There was strong evidence of a classic Stroop interference effect from incongruent distracters for both face target incongruent ($M = 605$ ms) compared with congruent ($M = 597$ ms) trials, $t_{24} = 3.13$, $p = .005$ and face distracter (name target) incongruent ($M = 748$ ms) compared with congruent ($M = 700$ ms) trials, $t_{24} = 9.05$, $p < .001$. Congruent RT were significantly shorter than incongruent RT in both cases.

The Gratton or conflict adaptation effect was only significant for face target trials, but not for face distracter trials (Table 2.1; Figure 2.6). As expected, for face targets RT were significantly shorter on high control incongruent trials than on low control incongruent trials ($II < CI$), $t_{24} = 2.22$, $p = .04$ (Figure 2.6a) indicative of Gratton effect. This resulted in a significant previous x current trial interaction, $F_{1, 24} = 15.29$, $p = .001$, $\eta^2 = .39$ as current-trial conflict under low control ($CC < CI$), $t_{24} = 5.34$, $p < .001$ was eliminated under high control ($II = IC$), $t_{24} = .06$, $p > .05$.

Contrary to expectations, for face distracter RT were not significantly shorter on high control incongruent trials than on low control incongruent trials ($II \approx CI$), $t_{24} = .05$, $p > .05$ (Figure 2.6b) failing to reveal Gratton or conflict adaptation effect. Interaction between previous x current trials was marginally not significant, $F_{1, 24} = 3.76$, $p = .07$, $\eta^2 = .14$. Current-trial conflict under low control ($CC < CI$), $t_{24} = 8.01$, $p < .001$ was not eliminated under high control ($II > IC$), $t_{24} = 5.74$, $p < .001$.

Accuracy rates for face targets indicated no significant differences between low and high control trials ($II = CI$), $t_{24} = .43$, $p > .05$, but significantly higher accuracy rate in low control congruent trials compared with incongruent trials ($CC > CI$), $t_{24} = 3.49$, $p = .002$ with an identical pattern in high control congruent trials compared with high control incongruent trials ($IC > II$), $t_{24} = 3.09$, $p = .005$.

Accuracy rates for face distracters reflected the same pattern as for face targets. No significant difference in accuracy was found between low and high control ($II \approx CI$), $t_{24} = 1.74$, $p > .05$, but significantly higher accuracy rate was found in low control congruent trials compared with low control incongruent ($CC > CI$) trials, $t_{24} = 5.49$, $p < .001$ with

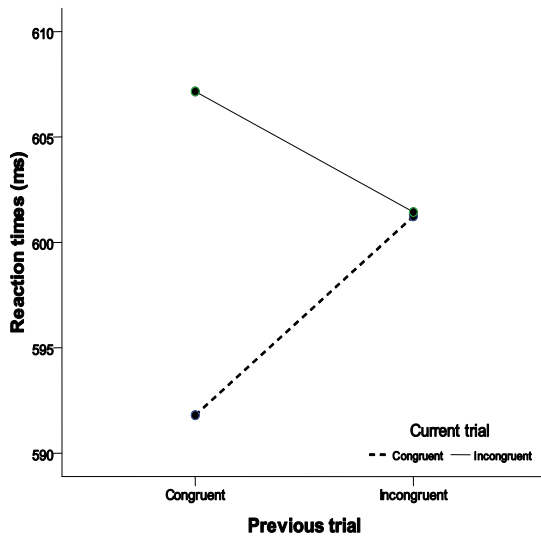
identical pattern in high control congruent trials compared with high control incongruent (IC > II) trials, $t_{24} = 5.36$, $p < .001$.

Table 2.1

Reaction Times (ms) and Accuracy (%) for Face Target and Face Distracter in CC, CI, IC and II Trials.

	Face Target		Face Distracter	
	RT (SD)	Accuracy (SD)	RT (SD)	Accuracy (SD)
Congruent – congruent	592 (45)	94% (6)	692 (39)	75% (17)
Congruent – incongruent	607 (46)	90% (7)	748 (33)	65% (19)
Incongruent – congruent	602 (47)	93% (9)	709 (36)	75% (15)
Incongruent – incongruent	602 (46)	90% (8)	747 (34)	60% (19)

a



b

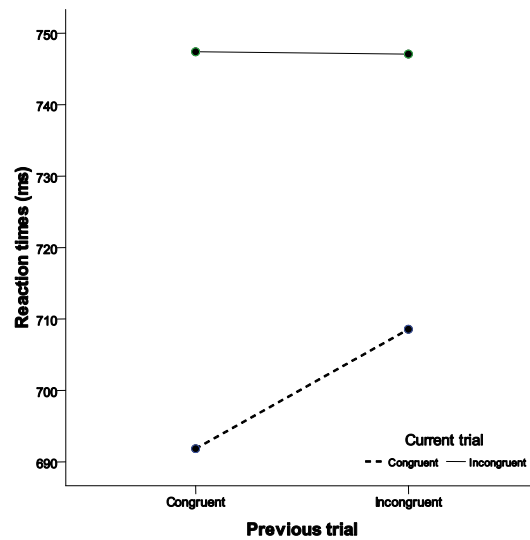


Figure 2.6. Mean group reaction times (ms) in CC, CI, IC and II trials. Panel a) face target, b) face distracter.

The absence of a Gratton effect for face distracter trials may be explained by the overall low accuracy/high error rate in CI and II trials (Table 2.1). High control II trials had more errors overall compared with low control CI trials (16 versus 14), $t_{24} = 2.1$, $p =$

.05 and more time-outs, $t_{24} = 2.93$, $p = .007$ (Table 2.2). A higher degree of time-outs in II than in CI trials indicated that participants were slowing down to avoid errors due to the difficulty of the face distracter condition suggesting a control effect. Mean reaction times for errors were not significantly different between low and high control groups, $t_{17} = .75$, $p > .05$ even though error RT were longer in II than CI and neither did the percentage for which incorrect responses accounted for the overall error rate, $t_{24} = 1.00$, $p > .05$.

Table 2.2

Mean Error Reaction Times (ms), Mean Number of Time-Outs and Their Respective Percentages (%) from Total Errors in CI and II Trials in Face Distracter Trials.

	Error RT (SD)	Total error % (SD)	Time-outs (SD)	Total error % (SD)
Congruent – Incongruent	672 (79)	24% (24)	11 (7)	76% (24)
Incongruent – Incongruent	687 (54)	20% (19)	13 (8)	80% (19)

Time-outs accounted for a significantly larger percentage of the overall errors compared with actual mistakes in both low control CI, $t_{24} = 5.58$, $p < .001$ and high control II, $t_{24} = 7.92$, $p < .001$ trials.

Preliminary EEG Results

Grand average waveforms for induced and evoked, high and low alpha, CI and II, face target and face distracter (name target) trials (total: 16) were calculated. Average waveforms were calculated as voltage changes from baseline after stimulus onset, thus providing a stimulus-locked, evoked signal and averaged across all participants. High minus low control (II – CI) condition grand average difference waveforms were calculated for the trials.

Voltage distribution topographic maps for the II – CI average waveforms were created from -300 to 600 ms at 24 ms intervals. Following theoretical predictions analyses focused on high evoked alpha and are reported below. In order to test the specificity of predictions, and thus the theoretical framework, regarding evoked upper alpha, parallel analyses were conducted using induced upper alpha and induced and

evoked lower alpha, but, as expected, these failed to show similar effects. They are therefore not reported here.

Electrode channels used for the analyses were chosen firstly by priori selection of occipital/posterior site following Gazzaley et al (2005) and secondly, visual examination of the two main conditions (II – CI face target and II – CI face distracter) which revealed inverse evoked upper alpha ERD and ERS patterns (Figure 2.7a, b) in the areas of T6 (e.g., ERD for face targets and ERS for face distracters) and P_{PZ, P4} (e.g. ERS for face targets and ERD for face distracters) electrodes which overly the FFA and nearby occipital regions (Gazzaley et al, 2005) in the present montage. These electrodes were therefore chosen for the subsequent analyses (in both current and following papers).

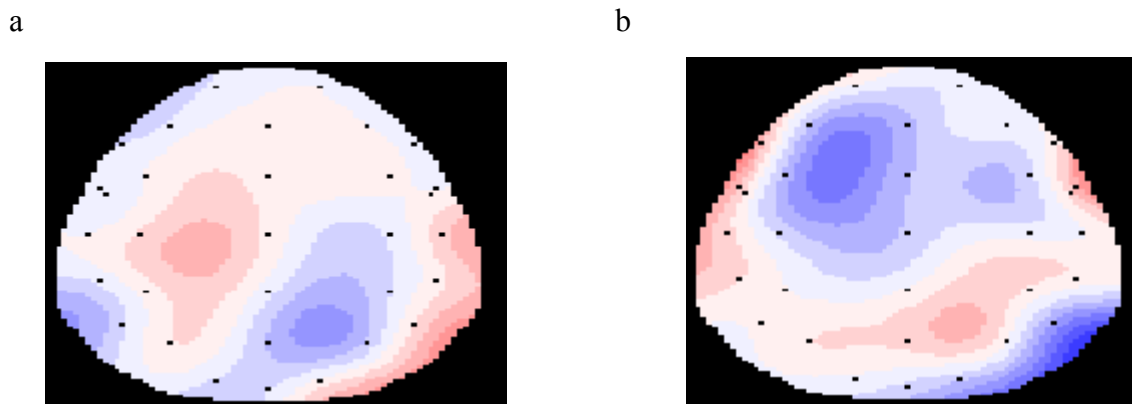


Figure 2.7. Topographic maps of ERS (blue) and ERD (red) pattern of grand average difference waveforms at 168 ms of stimulus onset. Panel a) II minus CI face target, b) II minus CI face distracter trials. Colour key Figure 2.1b (p. 43).

2.4.3 Main ERD and ERS Results

Area reports were calculated for high evoked alpha for face target and face distracter (name target) trials in CI (high conflict/low control) and II (high conflict/high control) conditions for 0 - 250 ms post-stimulus interval as this time interval corresponds to 170ms (N170) which has been found to be related to the processing of faces (Luck, 2005). Electrodes P (comprised of summed Pz and P4 channels) and T6 which is on the immediate boarder of occipital electrode category, as guided by topographic maps, were the focus of the main analyses even though it is difficult to determine the location of the

neural generator source/s simply by looking at the voltage distribution over the scalp (Luck, 2005).

Conflict adaptation effects in target (face target versus face distracter) and control (II versus CI) trials were analysed separately for $P_{PZ, P4}$ and T6 channels with 2 x 2 repeated measures ANOVAs and planned comparison t-tests. Main effects will not be reported since the primary interest was in the interactions. All ANOVA results are reported with Greenhouse-Geisser adjustment.

Conflict adaptation ERS effects were evident in the $P_{PZ, P4}$ region (Figure 2.8a) with an inverse pattern for face targets and face distracters. When face served as a target, conflict adaptation effects were evident in enhanced inhibition (ERS) in high control II ($M = -31.51$) compared with low control CI ($M = 9.59$) trials, $t_{24} = 2.33$, $p = .03$ resulting in a significant target x control interaction effect $F_{1, 24} = 6.53$, $p = .02$, $\eta^2 = .22$. This ERS effect in the $P_{PZ, P4}$ region disappeared in face distracter trials in high control II ($M = -13.90$) compared with low control CI ($M = -30.56$) trials, $t_{24} = .81$, $p > .05$ as indicated by the (non significant) drop in the mean negative value in II compared with CI, possible expression of relative facilitatory effects.

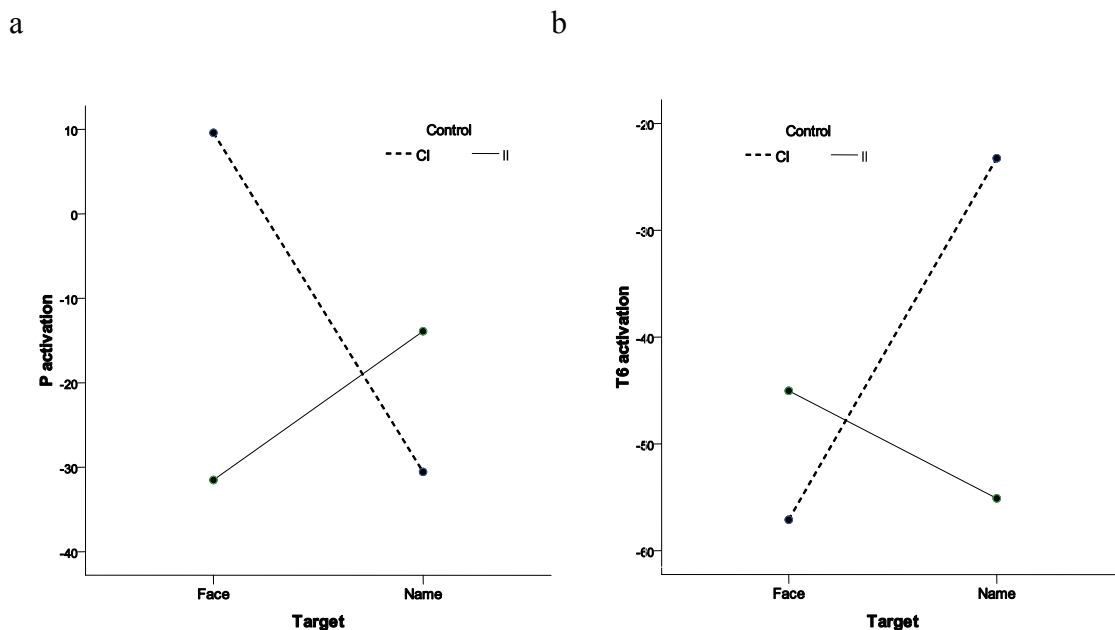


Figure 2.8. Conflict adaptation effects in high II and low CI control trials at 0 – 250 ms post-stimulus interval in face target and face distracter (name target) trials. Panel a) $P_{PZ, P4}$, b) T6 channel.

Conflict adaptation effects were assessed at channel T6 (Figure 2.8b) where an inverse pattern for face targets and face distracters was again observed. When face served as a distracter, conflict adaptation effects were evident in enhanced inhibition (ERS) in the high control II ($M = -55.10$) trials compared with the low control CI ($M = -23.26$) trials, $t_{24} = 2.42$, $p = .03$ resulting in a significant target x control interaction effect, $F_{1, 24} = 4.65$, $p = .04$, $\eta^2 = .16$. This effect disappeared for face targets in the high control II ($M = -45.03$) trials compared with the low control CI ($M = -57.09$) trials, $t_{24} = 1.14$, $p > .05$ where a drop in the mean negative value in II trials consisted with facilitatory effect even though the difference was non significant.

Area reports were calculated for high evoked alpha for face target and face distracter in II and CI trials in -500 – 0 ms pre-stimulus interval at T6 electrode. Clear absolute facilitatory ERD effects were demonstrated for face target trials (Figure 2.9). When face served as a target, facilitation (ERD) was evident in enhanced activity in the high control II ($M = 9.73$) trials compared with the low control CI ($M = -13.59$) trials, $t_{24} = 3.31$, $p = .003$, resulting in a significant target x control interaction effect $F_{1, 24} = 4.95$, $p = .04$, $\eta^2 = .17$. This effect disappeared for face distracter trials in the high control II ($M = -.37$) trials compared with the low control CI ($M = -2.76$) trials, $t_{24} = .33$, $p > .05$.

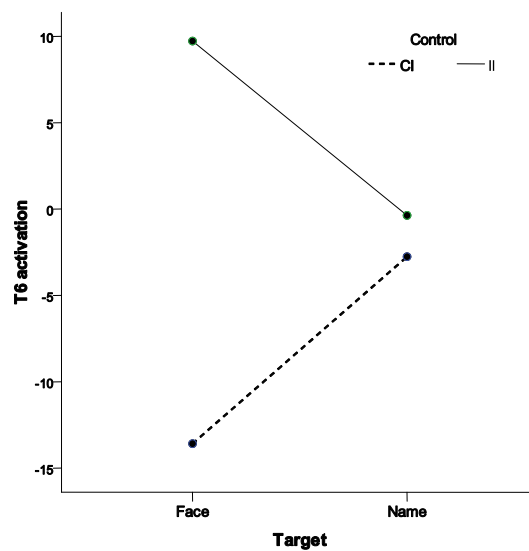


Figure 2.9. Conflict adaptation effects in high II and low CI control trials at -500 – 0 ms pre-stimulus interval in face target and face distracter (name target) trials at channel T6.

Area reports for high evoked alpha for face target and face distracter in II and CI trials for -500 – 0 ms pre-stimulus interval were also calculated for P_{PZ}, P₄, but no significant effects were found.

2.4.4 sLORETA Results

EEG files of four participants contained marked and excluded noisy channels (one each) and in order to comply with the stringent criteria for the uniformity of available channels, these participants' data were excluded from sLORETA analyses. Thus, the following results are based on the upper alpha ERP obtained from 21 participants. sLORETA was performed on II and CI trial evoked upper alpha (10 – 12 Hz) ERP at 170 ms post-stimulus for face target and face distracter (name target) conditions (Figures 2.10 & 2.11). Note that blue denotes a drop in evoked upper alpha in II trials (high control) relative to CI trials (low control), and red indicates the reverse. Following the inhibition timing interpretation of evoked upper alpha (Klimesch et al, 2007a), voxels indicated in blue show a facilitatory control effect, while those in red show an inhibitory control effect.

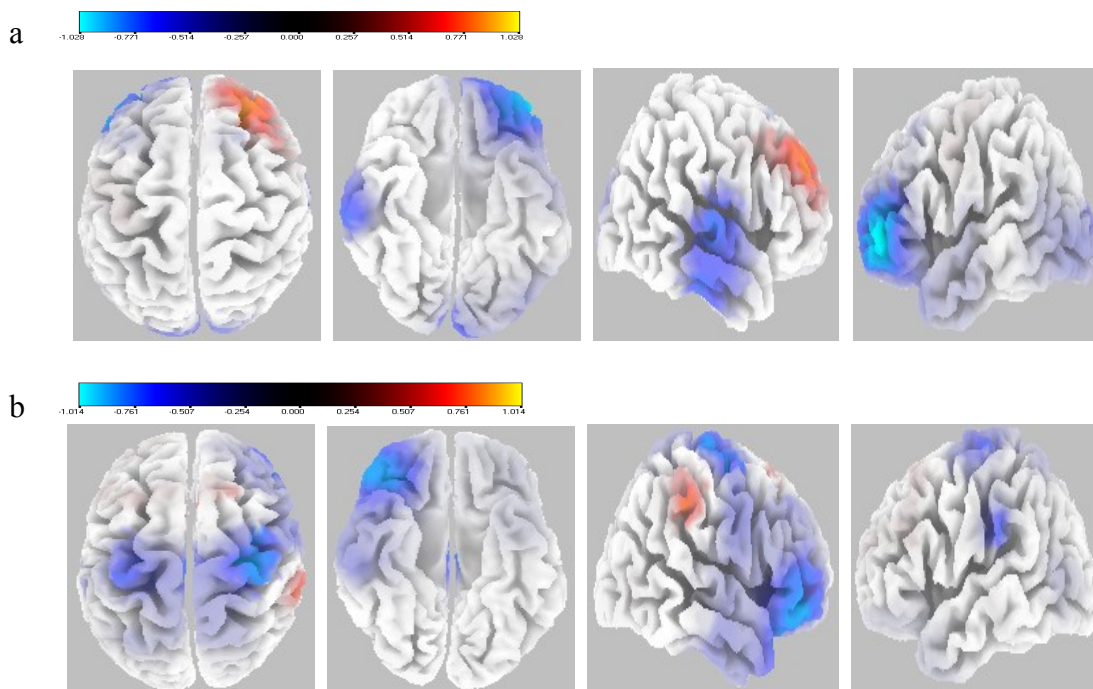


Figure 2.10. From left to right: top and bottom views, right and left hemisphere. Panel a) face targets, b) face distracters.

For face targets, sLORETA maximum solution values between II and CI trials were in the right middle frontal gyrus (BA 10) indicating the most likely source of inhibitory control related activity, and minimum solution values indicating the most likely source of facilitatory control related activity in the left middle frontal gyrus (BA 10) and the right superior temporal gyrus (BA 22) (Figure 2.11a).

For face distracters, (name targets) sLORETA maximum solution values between II and CI trials were for voxels in the right inferior parietal lobule (BA 40) and the bilateral cingulate gyrus (BA 32) indicating the most likely sources of inhibitory control related activity, and minimum solution values indicating the most likely source of facilitatory control related activity in the bilateral (more on the right) precentral gyrus (BA 6) (Figure 2.11b).

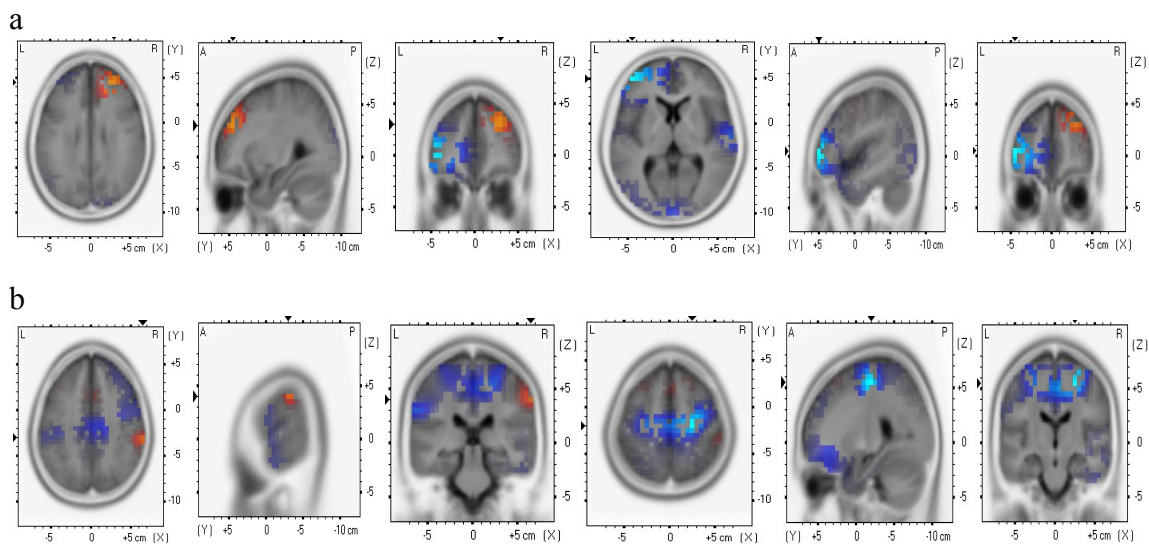


Figure 2.11. Panel a) face target: MNI xyz = 30, 45, 30 ($t = .89$, $p > .05$) maximum and MNI xyz = -45, 50, 5 ($t = -1.03$, $p > .05$) minimum solution value. Panel b) face distracter MNI xyz = 65, -30, 40 ($t = .81$, $p > .05$) maximum and MNI xyz = 25, -20, 55 ($t = -1.01$, $p > .05$) minimum solution value.

All sLORETA solutions failed to reach significance. Considering that analyses used 6 239 voxels at 5 mm resolution for the whole head, this was not surprising. The use of sLORETA was exploratory and aimed to identify potential voxels in networks associated

with cognitive control in the face/name Stroop task. However, it did indicate voxels which were most likely to implement control. At this stage, sLORETA served as a heuristic tool to identify regions of interest (ROI) which may be tested in further studies. It nonetheless pointed to relative changes in control related facilitation and inhibition in specific regions engaged in processing responses to face stimuli depending on whether the face served as a target or distracter for required responses.

2.4.5 Results Summary

Behavioural data demonstrated the classic Stroop distracter interference effect in both face target and face distracter (name target) trials with mean reaction times in incongruent trials significantly longer than in congruent trials. Face target trials demonstrated a Gratton effect where RT were faster in high (II) control trials compared with low (CI) control trials. The Gratton effect was not observed in face distracter trials for RT possibly due to the fact that face was a very potent distracter. The higher degree of time-outs in II than CI trials indicated that participants were slowing down to avoid errors due to the difficulty of the face distracter condition indicating a Gratton type control effect. Accuracy rates were not significantly different between high and low control trials for both face target and face distracter, but congruent trials had significantly higher accuracy rates than incongruent in both low and high control trials.

EEG demonstrated clear electrophysiological control related effects elicited for both face target and face distracter (name target) trials. Event related bandpower analysis of evoked upper alpha indicated an inverse facilitatory and inhibitory pattern of desynchronisation and synchronisation (interpreted as facilitatory and inhibitory effects respectively) at the P_{PZ, P4} and T6 electrodes which overlie the region of the FFA and immediate associated areas in face target and face distracter trials.

Consequent analyses revealed enhanced post-stimulus inhibition in high control compared with low control trials at channel P_{PZ, P4} when face served as a target and this effect disappeared when face served as a distracter.

Enhanced post-stimulus inhibition was observed in high control compared with low control trials at channel T6 when face served as a distracter and this relationship disappeared for face target. A non-significant drop in the mean negative value (increased

upper alpha desynchronisation) at T6 in high control compared with low control trials for face targets was nonetheless consistent with the presence of relative facilitatory effects. Subsequent analyses revealed enhanced significant facilitatory pre-stimulus effects in high compared with low control trials at T6 when face served as a target. This effect was eliminated when face served as a distracter.

sLORETA solutions served a heuristic purpose to identify the most probable cortical sources of control related effects and could not reach significance due possibly to the whole head analyses (6 239 voxels). However, exploratory results indicated that the right superior temporal gyrus extending to the FFA was the likely source of facilitatory effects and the middle frontal gyrus of inhibitory effects for face targets, while the inferior parietal lobule and the cingulate gyrus were the likely sources of inhibitory effects and the precentral gyrus of facilitatory effects for face distracters.

2.5 Discussion

The current experiment aimed to critically examine the fMRI study results of Egner and Hirsch (2005) which indicated that facilitation alone without any inhibitory effects resolves cognitive conflict. Results of the current blocked EEG study convincingly demonstrated that inhibitory processes play an important part in the implementation of cognitive control. The current study's behavioural results were comparable to those of Egner and Hirsch (2005) finding Stroop interference effects for both face target and face distracter (name target), a Gratton effect for face target RT. Overall, the pattern of behavioural results was very similar. The differences were in the absence of Gratton effect for face distracter RT (however, a Gratton type effect was found for face distracter time-outs) and the fact that reaction times in the current study for both face targets and face distracters were somewhat shorter compared with those recorded by Egner and Hirsch (2005). All average RT for face targets and face distracters were between 705 – 732 ms and 859 – 915 ms respectively in Egner and Hirsch's study, while in the current study they were between 592 – 607 ms and 692 – 748 ms respectively.

Average accuracy rates for all trials were lower in the current study, especially for the face distracters where they were noticeably lower. Accuracy and RT are thought to stem from different sources, from perceptual and response selection respectively

(Lindsay & Jacoby, 1994), hence suggesting that specific manipulations in the current experiment may have affected them. One of the most obvious differences in experimental manipulation between Egner and Hirsch (2005) and the current study was the ISI of 3 – 5 seconds and 1.3 seconds respectively which may have affected preparation processes and may have impaired perceptual selection of the stimulus. This study had twice even thrice temporally denser stimulus presentation (Egner and Hirsch ISI of 3 – 4 s versus 1.3 s in the current study) making the current task more difficult as indicated by a relatively low accuracy rate especially for face distracters. At the same time, RT for face distracters remained relatively shorter compared with the Egner and Hirsch (2005) study.

It is unclear why there was no Gratton effect detected in behavioural data for face distracter RT in the current study even though high control II trials had more time-outs and longer error RT compared with low control CI trials, suggesting a Gratton type effect. Participants appeared to slow down in II compared with the CI face distracter (name target) trials as, for example, evident in longer error RT in II trials and to the point of timing out. One strong possibility is that faces were very powerful distracters requiring much greater levels of control to inhibit them compared with inhibiting name distracters in face target trials. This may have been influenced and/or further exacerbated by the short ISI.

Another possibility is that temporally denser presentation (short ISI) of stimuli in the current study may have precluded the emergence of a behavioural Gratton effect for face distracter RT by impeding extraction of relevant stimulus information from name targets within short (1.3 s) periods of time between stimulus presentations. Names are more abstract than faces, hence they are assumed to require additional processing and reading names is assumed to be more perceptually difficult than scanning faces.

Short ISI may also have affected both preparatory processes and actual conflict resolution. For example, assuming that top down modulation was required to manage bottom up circuits for sensory processing (LaBerge, 1995) a short preparation period in combination with the reasonable assumption that names are more abstract than faces and require additional processing than faces may have prevented effective conflict resolution and, hence, absence of behavioural a Gratton effect for face distracter RT. One of those preparatory processes is expectancy which is known to modulate the Stroop interference

effect, possibly through strategic preparation of sensory processes (Gratton et al, 1992; Egner, 2007). In addition, during difficult tasks people may adopt particular strategies to cope and block presentation such as in the current task may the encourage adoption of a particular strategy. Short ISI may have affected expectancy and precluded effective strategies from developing for responding to face distracters (name targets).

The classic Gratton effect of shorter RT in II than in CI trials was detected for face targets, but not detected for face distracter RT. However, a Gratton type effect was assumed to be evident for face distracters in more time-outs (and longer error RT) in II than CI trials. This was interpreted as being evident in elicited control in II versus CI condition. This may be accounted for by the potency and effectiveness of the face as distracter. RT for face targets in all four trial types (CC, CI, IC, II) were on average at least 100 ms shorter than for face distracters (name targets), this effect is also evident in Egner and Hirsh's (2005) study, and accuracy rates were lower for face distracters compared with face targets. Certainly it may be more difficult perceptually to extract information from names compared with faces especially if the ISI is short, but there is an equal possibility that faces are stronger distracters than names and hence require greater control levels to inhibit them. Face distracters had longer RT and lower accuracy rates compared with face targets. Considering 1.3 s ISI and the fact that name targets had a more powerful distracter, it seems also plausible that in the name target (face distracter) block, participants reached a ceiling effect as their performance was stretched to the limit.

Temporal density did not seem to affect the Gratton effect in RT or high accuracy rates in face target trials in this blocked design study because it was somehow easier to extract information from face targets compared with name targets (face distracters) even under pressure of time. Another possibility is that face targets had a weaker distracter (i.e. names) while name targets (face distracters) had a more powerful one (i.e. faces).

fMRI data in Egner and Hirsch (2005) study demonstrated the effect only of facilitatory processes with enhanced FFA activity in high compared with low control trials when face served as a target, but absence of inhibitory effects in FFA in high control trials when face served as a distracter. Evoked upper alpha results in the current study revealed inverse patterns of desynchronisation and synchronisation, that is, of facilitation and inhibition in the right temporoparietal region depending on whether face

acted as a target or distracter. Post-stimulus inhibition (ERS) was evident at channel P_{PZ}, P₄ for face targets in high control trials, but this effect disappeared for face distracters, while post-stimulus ERS was evident at channel T6 for face distracters in high control, but disappeared for face targets where relative ERD effects were observed. Absolute facilitatory effect was evident at T6 in the pre-stimulus interval for face targets in the high control condition. This effect disappeared for face distracters. Hence results clearly demonstrated that conflict induced modulation of cognitive control on the face/name Stroop task was implemented by both facilitatory and inhibitory processes which temporally excited (switch on) or inhibited (switch off) task related activity in particular cortical regions and networks depending on whether the face attribute was the target or the distracter. These effects were indeed remarkably brief, occurring in under 250 milliseconds and thus much more readily detectable by the EEG which can detect dynamic temporal activity more or less synchronously with its occurrences in the brain.

Exploratory sLORETA results suggested the right middle frontal gyrus was the most likely source of inhibitory effects and the left middle frontal gyrus along with the right superior temporal gyrus which extends into the right FFA were found to be the most likely sources of facilitatory effects for face targets. The right inferior parietal lobule and the bilateral cingulate gyrus were suggested as possible sources of inhibitory control and the bilateral (more on the right) precentral gyrus for facilitatory effects for face distracters (name targets). These results suggest that the right superior temporal gyrus which extends into the right FFA was not the source of inhibitory signals when names were targets and faces served as distracters, in effect replicating the Egner and Hirsch (2005) fMRI finding that the FFA demonstrated no inhibition of activity when faces were distracters. This was a remarkable replication which suggested one of two possibilities. Firstly, inhibition may not be involved in resolving conflict when faces are distracters; however, current evoked upper alpha ERS results provided evidence against this proposition. Secondly, it suggested that there is something exceptional about the FFA and/or processing of faces.

In their study, Gazzaley and colleagues (2005) researched facilitatory and inhibitory effects with both event related fMRI and ERP. Participants viewed scenes and faces and were instructed to remember, ignore or passively view them. Activity in the right FFA (left FFA was not consistently identifiable across participants and hence

excluded) for faces and both right and left parahippocampal place area (PPA) for scenes were measured. Scenes produced significantly higher and lower activity compared with passive viewing baseline in PPA in the remember and ignore conditions respectively. Thus, both amplification and inhibition were observed in PPA for scenes. For faces, only amplification was demonstrated in the right FFA in the remember faces condition compared with the passive viewing baseline. Inhibition effects in the FFA did not reach significance. Hence, only amplification and not inhibition was observed in the FFA for faces. However, ERP data of N170 latency (in PO8 electrode) showed both amplification and inhibition of processing speed in remember and ignore trials respectively for faces. The authors concluded that both enhancement and suppression sculpt neural processes (Gazzaley et al, 2005).

Thus, in line with Egner and Hirsch's (2005) findings, Gazzaley and colleagues (2005) also failed to detect fMRI inhibitory effects in the FFA even though ERP data showed evidence of electroencephalographic inhibition. Considering the importance of information that faces carry, the FFA may indeed be a highly specialised region so intrinsically primed to perceive faces that it may fail to be inhibited (even under explicit instructions to inhibit) to such an extent that hemodynamic effects fall below baseline. Face perception is a common ability amongst primates and so must have a much longer history of natural selection than reading which has only become species wide in the last 100 years or so. Because face perception is likely to be strongly biologically prepared direct inhibition may be particularly difficult. This would also indirectly support the above claim that faces are also more powerful distracters compared with names.

Preliminary sLORETA analysis of evoked upper alpha ERS and ERD suggested that the locus of inhibitory control effects in the face distracter condition lay not in the right FFA, but in an immediately adjacent region in the right inferior parietal lobule (in addition to the cingulate gyrus) which takes part in language processing and motor planning. The right inferior parietal lobule may be engaged to load the outcome of perceptual/semantic processing to guide motor response preparation. It would suggest that it was here (on the right) the next step on from the FFA rather than the FFA itself (which *was* the site of control related facilitation; Figure 2.11) which was the site of control related inhibition in the current data set. This suggested that cognitive control is

not a single, central mechanism, but can be implemented by multiple regions, networks, mechanisms and stages including the stage where perceptual/semantic processing is loaded into motor preparation.

All discussions related to possible generators, their relationships and implications of observed evoked upper alpha ERD and ERS results cannot be viewed as anything more than preliminary since sLORETA source solutions failed to reach significance. This can be no doubt largely explained by the highly conservative and unfocused (e.g., use of >6 000 voxels at 5 mm for the whole head) approach to analyses. sLORETA analyses were only aimed to be provisional and limits attached to the scope of this project prohibited further detailed and more focused analyses. The existence of strict localised generators is not a general property of EEG data which are a mixture of local, regional and global sources especially in complex cognitive processes such as the Stroop task.

sLORETA, like all localisation techniques, has its limitations, fundamental to which is the broad question of whether *any* localisation technique can find an accurate neural source from a potentially infinite number of neural generator/s (Luck, 2005). Nonetheless, sLORETA is a robust and reliable neural source localisation technique (Sekihara et al, 2005) meaning that, if a simple point source/s exists and can be located, sLORETA will accurately locate it. Hence, even though sLORETA results failed to reach significance, these results will accurately identify the most probable location of neural source/s generating observed evoked upper alpha ERD and ERS effects.

Current results indicated that cognitive conflict in the face/name Stroop task is modulated by both facilitation and inhibition. Evoked upper alpha ERS and ERD results indicated that in less than 250 milliseconds the brain appeared to switch on or off (or at least modulate) activity in the regions related to the current task demands to effectively process relevant information while limiting the interference of irrelevant or distracting information. Evoked upper alpha ERD and ERS results suggested that control can be implemented at different stages during information processing. For example, anticipation of prepotent and predictable stimuli such as faces was preceded by facilitatory bursts of activation in some cortical regions (as recorded at T6), while inhibitory bursts occurred in other regions (as recorded at P_{Pz}, P₄) after face stimulus was presented. This suggested that irrelevant cortical regions, networks had their activity dampened and relevant regions,

networks were enhanced before the stimulus was even presented. These effects may be dependent on blocked design paradigm which has a very high level of predictability and may promote development of strategies (and expectancies) to improve performance.

Preliminary source localisation results suggested that cognitive control is not a unitary mechanism and that multiple cortical regions and networks are involved in temporally modulating cognitive conflict such as motor regions which may become more active (and perhaps more sensitive to signals from ACC and PFC). An array of control mechanisms, as opposed to a single central mechanism, may be necessary. For example, if distracters are highly prepotent, such as faces, under demanding task conditions, it may be ineffective to aim to inhibit biologically prepared (e.g., the FFA) cortical regions. Instead control may be applied at the next processing stage where perceptual processing is loaded into motor system coordinates for the production of responses (Nieuwenhuis & Yeung, 2005).

The FFA may be a specialist region intrinsically primed to respond to faces with fMRI unsuitable to detect millisecond electrophysiological changes in its functional interaction with surrounding regions. Hence, the fMRI finding that facilitation alone without inhibition resolves conflict (Egner & Hirsch, 2005) may not be representative of how complex, demanding tasks are temporally accomplished. Cognitive control is likely to be a multistage process from stimulus processing to response production. It may use ERD and ERS in evoked upper alpha among other processes as a vehicle through which it temporally engages relevant and disengages irrelevant cortical regions and this may not always be readily detectable in hemodynamic changes.

Thus, current study showed inverse evoked upper alpha ERD and ERS patterns reflecting facilitation and inhibition between high and low control conditions at temporoparietal regions and networks depending on whether face served as a target or as a distracter. Both inhibition and facilitation modulated resolution of cognitive conflict and these effects were exceedingly brief with their immediate effects manifesting in under 250 milliseconds. EEG evidence in the current study suggested that cognitive control is not a single, unitary mechanism, but rather involves the implementation of multiple networks and stages including at the stimulus processing and motor preparation stages.

STATEMENT OF ORIGINALITY

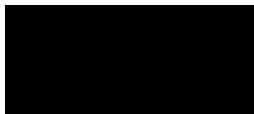
We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Figures	43, 44, 45*, 46*, 50
	52, 54, 55, 56, 57, 58
Tables	52, 53

* Adapted from Egner & Hirsch (2005), with permission.

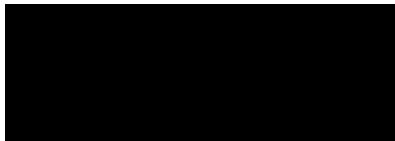
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



Candidate

April 2010



Principal Supervisor

April 2010

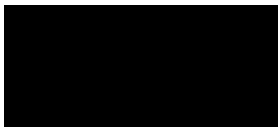
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	% of contribution
Candidate	Daiva Newby	70
Other Authors	Graham Jamieson	30

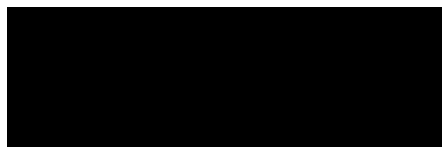
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



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April 2010



Principal Supervisor

April 2010

**Paper 2: Facilitation and Inhibition Modulate Cognitive Conflict: EEG Evidence
from Event Related Design Face/Name Stroop Task**

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3.1 Abstract

The current experiment attempted to replicate Paper 1 blocked design evoked upper alpha ERD and ERS results by using the same face/name Stroop stimuli as in Paper 1, but this time arranged in an event related paradigm. The blocked design task in Paper 1 presented stimuli in blocks; in the face target block, participants responded to faces, and to names in the name target (face distracter) block. The current event related paradigm required unpredictable and continuous switching between responding to face and name targets as indicated by preceding cues. The behavioural Stroop interference effect was not detected for face targets since incongruent trials were faster than congruent, but was observed for face distracters (name targets). The Gratton or conflict adaptation effect was not detected neither for face targets nor face distracters. Preliminary EEG topographic map displays failed to reveal expected facilitatory and inhibitory effects at P_{PZ, P4}, T6 and T5 electrodes for either face targets or face distracters. For face targets, no enhanced post-stimulus inhibition was observed in high compared with low control trials at channel P_{PZ, P4}, contrary to findings in Paper 1. For face distracters, there was relative enhanced post-stimulus inhibition in high control compared with low control trials at channel T6, but, unlike in Paper 1, it did not reach significance level. A higher negative mean value at T6 was observed in high compared with low control trials for face targets; again contrary to findings in Paper 1. Subsequent pre-stimulus interval analyses failed to reveal the expected facilitation in high compared with low control trials for face targets at channel T6. Control effects were assessed at T5 channel for face targets revealing higher inhibitory values in high compared with low control trials. For face distracters, high control trials had somewhat (not significantly) lower negative values than low control suggesting the presence of relative facilitation at channel T5. Topographic map displays of cue “face” and “name” epochs revealed that actual cues in the event related paradigm may exhibit 3 distinct phases with dynamically shifting inhibitory and facilitatory effects. Thus, most of the behavioural and alpha ERD and ERS findings obtained using a blocked paradigm in Paper 1 were not replicated by the current event related paradigm. Current task switching results suggest the existence of multiple control mechanisms operating to regulate control both *within a task set* and *between task sets* (task switching).

Key words: conflict, cognitive control, Stroop, Gratton effect, facilitation, inhibition, event related design, blocked design, task set, task switch, switch costs, evoked upper alpha ERD, ERS

3.2 Introduction

One of the most obvious characteristics of blocked paradigms is that they are repetitive and have a very high level of predictability, for example, about the nature of upcoming stimulus. In the blocked fMRI study of Egner and Hirsch (2005), for example, or in the blocked EEG study in Paper 1, participants knew that in the face target block the upcoming response would be to faces and to names in the name target (face distracter) block. Predictability of the impending stimulus would have made the task easier by allowing preparation and expectancy effects which may, in turn, have been reflected in the high accuracy rate and RT. Blocked designs are likely to encourage the adoption of particular strategies and these strategies may depend on the speed and accuracy of the responses they yield. A practical reason for using blocked designs in fMRI research is, of course, to produce robust changes in hemodynamic signal (i.e. increase signal to noise ratio) since event related design induced signal changes are weak compared with the 2 - 5% signal change induced in blocked designs (Bullmore & Suckling, 2001). Event related designs are more traditional to EEG experiments.

3.2.1 Event Related and Blocked Designs

Event related designs usually present at least two, often unpredictably, alternating tasks with cues specifying whether the current trial requires response to one or other task. Event related designs measure a particular stimulus's neural activation patterns which can then be averaged across trial types which allows measuring of very brief events in EEG.

Event related designs differ fundamentally from blocked designs in that they require switching between two or more tasks. On their own, such tasks are relatively easy, but when combined they become more difficult. In event related paradigms stimuli are not presented in blocks as in blocked design, but instead a preceding or simultaneous cue indicates what stimulus dimension requires response, that is, the cue specifies which task should be executed. Often a stimulus may contain information relevant to both tasks. For example, face/name Stroop stimuli in Paper 1 contained both tasks (i.e. faces with superimposed names). This requires selecting the relevant task on each trial which in turn relies on top down control. Switching between the tasks may be predictable (e.g., every 5 trials) or unpredictable. Recovery after random switches appears to be more gradual than

with predictable switching, perhaps because participants adjust their task readiness, prepare as a function of the probability that the following trial will require another switch (Monsell & Mizon, 2006). However, cues, themselves, are also likely to add another dimension to the task set and cue change may be as demanding as task change (Monsell, 2003). Thus, event related designs allow the measurement of very brief events, but are more difficult than blocked design because they combine multiple tasks, and switching between them relies heavily on top down control. Cue change further increases task difficulty demanding more top down control.

Blocked designs average neural activity over events, hence results may potentially be confounded by state or ongoing task demands, slow, phasic signal change and transient or specific trial demands, rapid or tonic signal change. Event related designs have higher working memory demands for stimulus response, higher attentional demands for cues and, hence transient effects are superimposed on state and focus solely on transient effects, temporal profile of activity. Sustained or state activity may be enhanced during the processing of an easy task (for example, in a blocked paradigm) while a similar task in an event related design may be more difficult (for example, event related task with random switching) and elicit more transient effects (Scheibe et al, 2006).

It is known that anticipatory behaviour is directed at upcoming events and serves for faster and more efficient information processing, for example, by pre-setting necessary physiological processes, preparing perceptual processes such as focus towards relevant features of the stimulus and hence filtering out irrelevant information. Anticipatory behaviour may be accommodated through the thalamo-cortical gating mechanism (opens sensory gate to cortex) (Bastiaansen et al, 2002). If relevant stimuli appear in a predictable pattern, for example, as in a blocked task, neuronal oscillations may entrain (phase-lock) to the structure of the attended stimulus stream and hence serve as an instrument of sensory selection. Predictable stimulus, for example, an impending target type in a blocked paradigm, is more likely to be detected, while a random or unpredictable stimulus, for example, in an event related task, may arrive at a low-excitability phase (Lakatos et al, 2008) or a low point in the amplitude of relevant oscillations occurring by chance just prior to stimulus onset, and may not be processed as efficiently.

Task switching, especially random, produces low predictability about the nature of the upcoming stimulus, requires activation of criteria for what is currently relevant or intentional retrieval of task goals, inhibiting previous task carryover effects. Event related designs, by their very nature, require higher levels of top down control compared with blocked designs and are hence more vulnerable. For example, if long term conflict is low, as evident, for example, in a high level of performance such as high accuracy rates, occasional lapses are managed by an increase in control, however high level of constant conflict may result in withdrawal of control (Cohen et al, 2004) possibly related to such affective effects as frustration or because it is too taxing to maintain a constant high level of control.

In Paper 1, which used a blocked design, the evoked upper alpha ERD and ERS results indicated that, for example, for face targets, facilitatory ERD bursts were evident in certain cortical regions at pre-stimulus interval. However, the same regions at post-stimulus interval showed a drop in the mean negative value, interpreted as relative facilitatory effects, while opposite effects were found for name targets (face distracters) producing systematic patterns. Predictability and repetitive presentation of stimuli, despite a large stimulus set, in blocked design may promote sensory or perceptual strategies to optimise performance and demand less intense top down control and effort, potentially affecting psychophysiological processes. This raises the question of whether results obtained from the blocked paradigm in Paper 1 generalise to event related designs. The current event related task was designed to attempt to replicate the evoked upper alpha ERD and ERS effects in the blocked design task in Paper 1. It was designed this way due to the expectation of more pronounced, sharper effects in the event related paradigm resulting from the additional demands for cognitive control imposed by an event related design. Nonetheless, blocked and event related paradigms cannot be considered to be equivalent because of their unequal complexity and processing demands.

3.2.2 Task Set and Associated Cortical Regions

Task set is an abstract form of actively maintained configuration or rule of perceptual, attentional and motor processes necessary for consequent task performance. In other words, task set is an assembly of elementary processes configured to deal with specific

tasks such as input-output transformations, and enabling and disabling of inter-module connections for effective flow of information (De Jong et al, 1999). Representations in the PFC are believed to maintain task set and different representations may be activated for task demands depending on stimulus. For example, the right ventrolateral PFC (VLPFC) may be active when participants respond on the basis of the gender of a face and left VLPFC on the basis of number of syllables in a word (Sakai, 2008).

Establishing task set is time consuming as it requires higher-order neural interactions between regions in the prefrontal and posterior association cortices which represent task set. Inefficient preparation may not recruit relevant neural structures (Sakai, 2008). In event, compared with blocked paradigm, participants are required to maintain larger task sets, to maintain, not only the response set, but also what is the current target as indicated by a cue (Barch et al, 2009) and task sets may compete with each other. Furthermore, because of task alternations or switching and, hence, lack of predictability about upcoming task, preparatory processes would not be expected to be accomplished in the event related design to the same extent as in blocked designs.

Internal representations are required to identify an incoming stimulus and if the signal is repeated several times the representations of this signal are sharpened, while alternating signal representations are blurred. Consequently, constant task set reconfiguration may impair early perceptual processing from being implemented (Jentsch & Leuthold, 2005) in event related compared with blocked designs. Preparation would have to be done after stimulus onset either before task specific processes such as stimulus classification or response selection, thus, postponing them or in parallel, thus, prolonging them and they are likely to be less thorough (Monsell & Mizon, 2006) often leading to slow and/or inaccurate responses in event related compared with blocked paradigms. In summary, cognitive control during task switch fluctuates from trial to trial and is mediated by the fluctuating activity of discrete brain regions, hence successful behavioural performance in task switching may depend on whether a specific brain region can be differentially activated to a sufficient degree (Braver et al, 2003).

3.2.3 Task Switching and Control Related Facilitatory and Inhibitory Activity

Task switching often results in switch cost. This refers to slower, less accurate performance in tasks involving switching compared with tasks with no switching or repetition trials. Switch cost may stem from shifting attention between stimulus attributes, retrieving goals, action rules, and enabling response sets. Switch cost that persists residually even with long preparation time is called residual switch cost. Residual switch cost may be the time needed to reconfigure the system, and this cannot be completed until the target stimuli appear (Brown et al, 2007).

Preparation can halve switch cost, but after ~500 ms spent preparing, no further benefits may be obtained. Preparation does not appear to affect interference or crosstalk, prompting some authors to suggest that control may be purely reactive rather than proactive as it may only be triggered after a conflict signal has been generated (Monsell et al, 2003; Sakai, 2008). Nonetheless, there is evidence that long preparation intervals can eliminate switch cost, hence prompting suggestion that there is no limit on ability to prepare, but rather failure to make effective use of preparation interval (Gilbert & Shallice, 2002). Preparation may not be completed because of lack of motivation, not understanding its benefits and because preparation requires effort (Monsell et al, 2000).

Switch cost may originate from associative strengthening between task-related stimuli and internal representations of the task set with which they were paired on a previous trial, and in the current trial stimuli may re-evoked the previous task set which may be different from the current one leading to interference evident in longer RT. Hence, switch cost may be related to residual activity in the task set. Furthermore, some portion of switch cost may also be related to cues (Brown et al, 2007). With predictable switching, switch cost may be limited to the first trial, while random switching may produce a more gradual approach to asymptotic performance. Since cues in unpredictable switching require more attention, interpreting them can interfere with the stimuli and may constitute a distinct task in itself, generating further demands for top down control.

There is still intense debate about the causes of switch and residual switch costs. The causes can be generally classified into those reflecting delays in reconfiguring the new task set and those managing interference effects stemming from the previous task set. Left frontal lesion patients in one study had difficulties activating a currently relevant

task set while right frontal lesion patients showed difficulties inhibiting an old task set (Mayr et al, 2006). A weakened task goal might be insufficient to enable or facilitate a strong and fully configured task set, goals may be inherently incapable of activating task set and there may be failure in inhibiting competing task sets. Residual switch cost may reflect interference from a previous, now irrelevant task set with preparation only capable to partially configure the task set while exogenous, actual stimulus completes this reconfiguration or there may be complete failure to engage in advance preparation (De Jong et al, 1999).

The PDP model of task switching assumes that switch trials are slowed down by an extended response selection process which results from persistent inappropriate activation and inhibition of task controlling representations and associative learning which allows stimuli to evoke task sets with which they have been recently associated. Switch cost indexes interference caused by active carryover of the previous task set into switch trials. For example, this is demonstrated by asymmetrical switch costs which result in increased RT for a switch into a more automatic, stronger task, as it was previously inhibited with higher degrees of inhibition (Yeung & Monsell, 2003). However, the opposite pattern of switch cost, that is, higher from a stronger to a weaker task, has also been demonstrated. Without top down control, switching would be impossible, but task reconfiguration may not be completed until the arrival of the stimulus (i.e. bottom up processes), hence explaining insensitivity to the preparation interval (Gilbert & Shallice, 2002).

In summary, task switch requires an active, top down process that changes the current task set. Task switch costs can be reduced but not eliminated by longer preparation intervals as the task set from the previous trial remains somewhat active. Hence, no amount of top down task preparation can provide benefits as strong as the bottom up effects of having just performed the task on the previous trial. Residual switch cost may be explained by the fact that top down attempts at reconfiguring the task set are inherently incomplete and full reconfiguration can only be triggered exogenously by the appearance of the actual stimulus and hence no amount of preparation can eliminate residual switch cost. Top down goal driven processes aim to ensure that the task is in place, but may have limited direct influence over elementary cognitive processes (Pashler

et al, 2001). Task set configuration may not be fully achieved until the appearance of the stimulus when stimulus response rules are loaded into working memory (Monsell, 2003).

Thus switch costs are assumed to stem either from problems activating, facilitating the current task set, or carryover effects, interference, poor inhibition of the previous task set. The question now is how control is implemented. For example, does control manifest only in increased focus on activating the current task set, inhibiting the irrelevant one or both, especially considering that the human brain is not like a computer operating system which can switch tasks/programs without interference (Driver, 1998). Top down control of task readiness should be relatively conservative as it requires effort, while excessive amounts of control may lead to inflexibility compromising the ability to change rapidly if an unexpected problem or opportunity arises (Monsell et al, 2003).

Control Related Facilitatory and Inhibitory Activity

Control effects are assumed to be much more complex in event related compared with blocked design (Ullsperger et al, 2005). Control may exert protracted and persistent effects on performance and may manifest in relatively persistent slowing in response time possibly reflecting both top down and bottom up effects. If the required response changes frequently, then it is difficult to predict where to focus attention and conflict between expected and actual response may be effectively addressed by general slowing of responses to prevent premature and erroneous responses from being generated before stimuli are adequately processed, hence more involvement from inhibitory processes. If the task requirements change little, but strong task irrelevant conflicting stimuli appear, then performance may be best served by increasing attention to the relevant stimuli, hence more involvement from facilitatory effects. If there were a single control mechanism, it would not be effective to specific task situations since a non-specific response slowing mechanism would not increase attention to relevant stimuli and away from irrelevant stimuli. An attention focusing mechanism would be ineffective in responding to unexpected changes in task requirements. Hence there are likely to be multiple conflict control loop mechanisms associated with adjusting specific forms of control. Multiple cognitive mechanisms dynamically modulate behaviour in a continuous

manner especially in rapidly changing circumstances (Brown et al, 2007) as would be required in an event related task.

Performance demands in an event related task are indeed very high, requiring multiple control mechanisms capable of both facilitatory and inhibitory effects, for example, facilitating new tasks set, while also inhibiting previous ones. In the face of interference, strongly activated task sets are needed; however, they may be difficult to get rid of. Evidence for inhibition comes in the form of a change in performance usually a decrement to a stimulus that previously was targeted by inhibition. Task switching requires inhibition of the old set which in turn will be less available for some time as demonstrated by slowing of RT on switching compared with repeat trials suggesting problems with access to a previously inhibited task set. It is not clear how representation sets are less accessible, if it was only facilitation modulating conflict (Mayr, 2007).

Inhibition is used to suppress irrelevant and distracting representations of stimuli, goals or motor responses. However, processes attributed to inhibition may be explained by facilitation. For example, during interference facilitation may eventually win over rather than distracters being inhibited. Facilitation and inhibition affects can be assessed on the grounds of difference between activation levels (meaning that there is no inhibition, but only varying facilitation levels) or accessibility (meaning that inhibition is involved as demonstrated by blocked access to a previous task set). Inhibition is assumed to be necessary in difficult conflict situations when distracters compete with targets and can lead performance astray. Evidence for inhibition is thought to manifest in blocked access to competing information and is behaviourally evident in backward inhibition. In switching tasks, switch cost (longer RT, lower accuracy) occurs for switching, but not for repetition trials. Backward inhibition in task set switching manifests in the magnitude of the switch cost which is greater if the new task has recently been switched away from and now has to be performed than when it has not been performed for several trials. This is evidence of reduced accessibility since inhibition dissipates slowly (Dagenbach et al, 2007) and cognitive control configures resources to perform goal directed task rather than currently competing, in such paradigms, most recent or most frequent, tasks.

The fundamental aim of the current event related study was to investigate whether the blocked design behavioural and evoked upper alpha ERD and ERS results from Paper

1 would be replicated using an event related design. Event related design requires constant and unpredictable switching between two tasks and, hence relies more heavily on top down control. The aim of the current event related paradigm was to track and measure exactly the same dependent variables as in Paper 1 including evoked upper alpha ERD and ERS patterns in topographic maps and area reports in the high (II) compared to low (CI) control in face target and face distracter conditions. It was expected that facilitatory and inhibitory effects observed in the Paper 1 blocked paradigm would be more pronounced and sharper in the event related paradigm because of increased demands for top down control even though blocked and event related paradigms were not assumed to be equivalent because of their unequal complexity and processing demands.

3.3 Method

3.3.1 Participants

Twenty seven naïve participants (12 males and 15 females) aged between 18 and 55 years ($M = 23$, $SD = 9$) took part in this experiment. The majority of the participants were first year psychology students at UNE and took part in this experiment for a course credit. Those who participated in this study not for a course credit were paid \$10 for their time and effort. The majority of participants were right handed, not taking any psychoactive medication and had normal or corrected-to-normal vision. The experiment consisted of a single 1½ - 2 hour session.

3.3.2 Data Acquisition

Data acquisition was identical to that in Paper 1 (Chapter 2).

3.3.3 Stimuli

Stimuli were identical to those in Paper 1 (Chapter 2) except for the following. Practice was included consisting of a photo of one politician (Bill Clinton) and one actor (Hugh Jackman). Hence, there were in total 32 stimuli with 2 (both incongruent) used in practice and 30 (12 congruent and 18 incongruent) experimental stimuli.

As in Paper 1, participants had to respond to either face or name, classifying the person as “a politician” or “an actor”. However, this time a cue preceded each photograph

specifying whether the response was needed to a face or a name (Figure 3.1) rather than photographs being presented in blocks. The cue (ISI) consisted of a word “face” or “name” written in white font and presented on black background centrally on the monitor for 1 300 ms. Participants responded when they were presented with a photograph which disappeared as soon as the response was made or when 1 000 ms terminated. Thus, the current experiment was event related rather than blocked as in Paper 1.

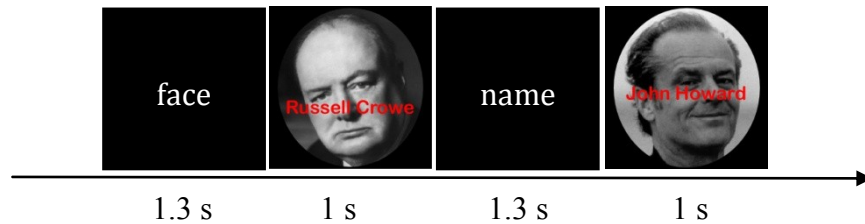
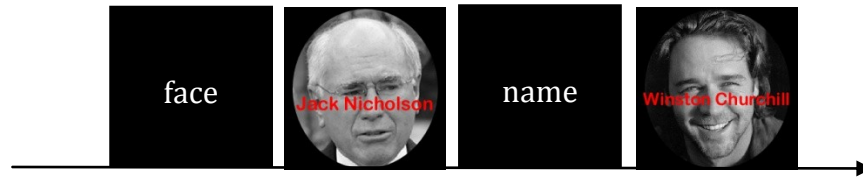


Figure 3.1. Participants had to respond to either face or name as specified by a preceding cue and classify whether person was “an actor” or “a politician”.

There were 64 fixed trial sequences created (Figure 3.2) comprised of 16 trial sequences in each of the four conditions in regard to the current and the previous trial congruency (CC, IC, CI, II). There was an equal number (8 in each 16 trial sequences, hence 32 in total for each) of cue (“face”, “name”) and stimuli (“actor”, “politician”) trial sequences. Again, the predictability of the upcoming stimulus and the required response was reduced by varying the type of the upcoming stimulus and cue. For example, sometimes a photograph of an actor followed a photograph of a politician, but other times an actor followed an actor and so on. Similarly the “face” and “name” cues were randomised.

a

Fixed trial sequence 38 (II)



b

Fixed trial sequence 60 (CI)

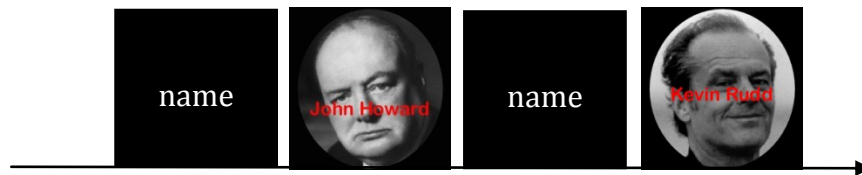


Figure 3.2. Examples of fixed trial sequences. Panel a) Trial sequence 38: II trial; b) Trial sequence 60: CI trial.

Each participant was presented with 192 trials (64 x 3) of 384 (192 x 2) photographic stimuli in total. Fixed trial sequences were presented in pseudo-random order. Paper 1 employed blocked design where current stimulus played a critical role forming the type of the upcoming trial. For example, current incongruent (I) stimulus could subsequently form only either II or IC trial, but not CI or CC trial (and C could only form CI or CC), hence such design by its nature has a certain order effect (e.g., CI can never be immediately followed by CC only by IC or II) and may increase carryover effects. In this study, such possible order effects were controlled by analysing only the second stimulus in each fixed sequence. As a result, there were fewer trials left for analyses, but they were assumed to be free of any possible order effects. Again, as in Paper 1, participants completed an eye-movement-artifact correction task.

3.3.4 Procedure

Experimental procedure was identical to that in Paper 1 (Chapter 2) except for the following. Participants were given a short practice (20 trials) before the experiment to familiarise them with the demands of the experimental task. Participants were presented with 3 experimental runs each lasting approximately 5 - 6 minutes with two rest periods, one after the first run and another after the second run. Participants could rest as little or

as long as they wanted and they were asked to press the spacebar when ready to continue. The experiment lasted approximately 17 minutes.

3.3.5 EEG Analysis

Two corrupt recordings (participants 1 and 7) were permanently discarded. Processing of EEG files was identical to that in Paper 1. EEG recordings were also ocular-artifact corrected and visually inspected. Epochs created for face and face distracters (name targets) in CI and II trials from unfiltered files were compared to those created from filtered and rejected accordingly as in Paper 1 and then ERBP analyses were performed.

3.4 Results

3.4.1 Edinburgh Handedness Inventory Scores

Twenty two participants scored >50 and 5 scored between 22 - 46 points on EHI, hence most, if not all, participants were right handers (Figure 3.3).



Figure 3.3. Participants' scores on Edinburgh Handedness Inventory.

3.4.2 Behavioural Stroop Effect and Gratton Effect and Preliminary EEG Results

Behavioural Stroop Effect and Gratton Effect Results

Mean reaction times (ms) and accuracy rates (%) were calculated for all correct trials. Contrary to expectations for face targets, incongruent (M = 604 ms) trials were significantly shorter than congruent (M = 621 ms), $t_{24} = 2.69$, $p = .02$. In effect congruent trials for faces behaved as if they were more difficult than incongruent. For face

distracters (name targets), as expected, incongruent ($M = 724$ ms) trials were significantly longer than congruent ($M = 679$ ms), $t_{24} = 7.26$, $p < .001$. Hence, the Stroop interference effect was behaviourally detected only for face distracters, but was reversed for face targets.

The expected Gratton or conflict adaptation effect was obtained neither for face target nor distracter trials (Table 3.1; Figure 3.4). Contrary to expectations, for face targets, the RT were longer to distracters in what were expected to be high compared with low control trials ($II \geq CI$) even though this difference was not significant, $t_{24} = 1.26$, $p > .05$ (Figure 3.4a) indicating absence of the classic Gratton effect. There was no significant interaction between previous x current trials, $F_{1,24} = 3.22$, $p > .05$. Neither was the Gratton effect obtained for face distracters as RT were not shorter to distracters in high compared with low control trials ($II \approx CI$), $t_{24} = .22$, $p > .05$ (Figure 3.4b). The interaction between previous x current trials was again not significant, $F_{1,24} = .23$, $p > .05$, $\eta^2 = .01$.

Comprehensive analyses of behavioural data were performed aiming to better understand unexpected Stroop and Gratton effect related results. Accuracy rates for face targets indicated no significant differences between expected low and high control trials ($II = CI$), $t_{24} = .25$, $p > .05$, but there was a significantly higher accuracy rate in the expected low control congruent trials compared with incongruent ($CC > CI$), $t_{24} = 2.64$, $p = .02$ with a similar trend, but not significant difference in the expected high control congruent trials compared with the incongruent trials ($IC \geq II$), $t_{24} = 1.23$, $p > .05$.

Accuracy rates for face distracters reflected a similar pattern to face targets. No significant differences in accuracy were found between expected low and high control trials ($II \approx CI$), $t_{24} = .91$, $p > .05$, but there was a significantly higher accuracy rate in the expected low control congruent trials compared with incongruent trials ($CC > CI$), $t_{24} = 4.51$, $p < .001$, with an identical pattern in the expected high control congruent trials compared with the incongruent trials ($IC > II$), $t_{24} = 4.82$, $p < .001$.

Table 3.1

Reaction Times (ms) and Accuracy (%) for Face Target and Face Distracter in CC, CI, IC and II Trials.

	Face Target		Face Distracter	
	RT (SD)	Accuracy (SD)	RT (SD)	Accuracy (SD)
Congruent – congruent	625 (53)	78% (13)	675 (60)	67% (18)
Congruent – incongruent	600 (62)	71% (14)	722 (49)	52% (18)
Incongruent – congruent	616 (61)	75% (14)	683 (44)	67% (19)
Incongruent – incongruent	608 (59)	72% (13)	725 (43)	54% (16)

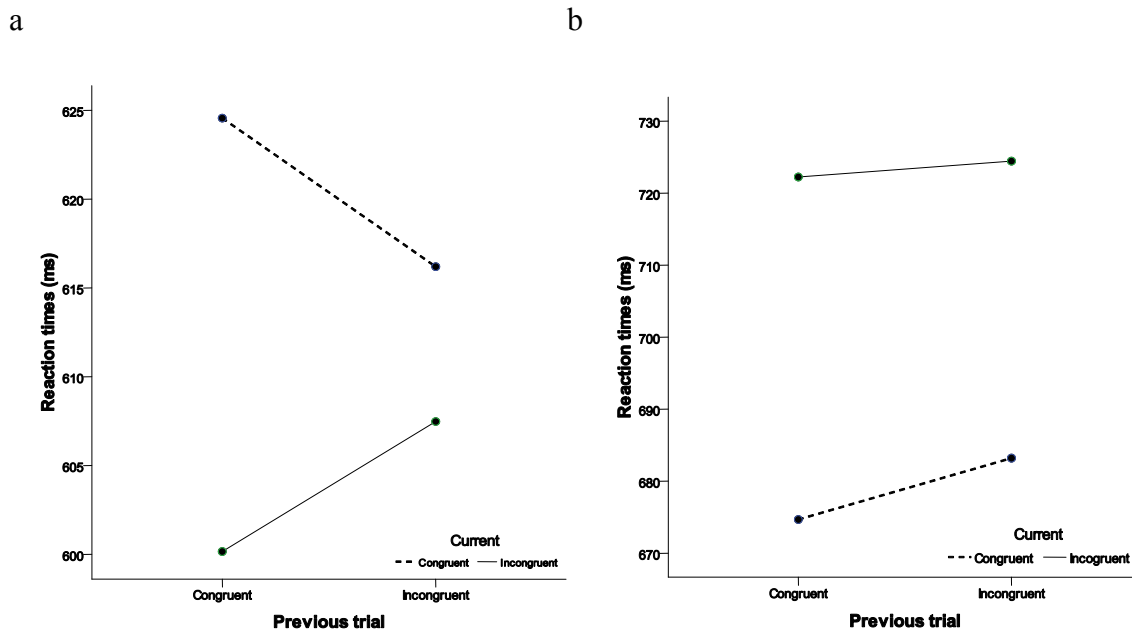


Figure 3.4. Mean group reaction times (ms) in CC, CI, IC and II trials. Panel a) face targets, b) face distracters.

Overall accuracy rates for face targets were significantly higher than face distracters in all trial types comprised of CC, $t_{24} = 3.79$, $p = .001$, CI, $t_{24} = 5.77$, $p < .001$, IC, $t_{24} = 2.53$, $p = .02$ and II, $t_{24} = 5.16$, $p < .001$ trials (Table 3.1). Total number of errors comprised of both time-outs and actual mistakes was significantly higher for face distracters compared with face targets across all trial types comprised of CC, $t_{24} = 5.68$, $p < .001$, CI, $t_{24} = 3.14$, $p = .005$, IC, $t_{24} = 4.38$, $p < .001$ and II, $t_{24} = 2.54$, $p = .018$.

For face targets, expected high control trials did not have fewer overall errors compared with low control trials (II = CI), $t_{24} = .20$, $p > .05$ and an identical result was found for face distracters (name targets) (II \approx CI), $t_{24} = .89$, $p > .05$. Overall errors for face targets were higher in incongruent compared with congruent trials in both the expected low control (CI > CC), $t_{24} = 5.08$, $p < .001$ and high control trials (II > IC), $t_{24} = 3.56$, $p = .002$. Overall errors for face distracters were not significantly different between congruent and incongruent trials in both expected low control (CI \approx CC), $t_{24} = 1.30$, $p > .05$ and high control (II \approx IC), $t_{24} = 1.01$, $p > .05$ trials.

Average RT were calculated for actual mistakes; however, there were greatly varying numbers (ranging from 8 to 22) to make valid comparisons between trial types. Percentage from total errors was calculated to assess the percentage for which actual mistakes were responsible in all conditions (Table 3.2).

Table 3.2

Mean (SD) Number of Total Errors (Actual Mistakes and Time-Outs), Percentage (SD) of Actual Mistakes and Time-Outs Accounting for Total Errors in CC, CI, IC and II Trials for Face Targets and Face Distracters.

	Face Target			Face Distracter		
	Total	Mistakes %	Time-outs %	Total	Mistakes %	Time-outs %
Congruent - Congruent	5 (3)	25% (31)	71% (35)	9 (5)	30% (26)	71% (26)
Congruent - Incongruent	8 (4)	22% (21)	75% (26)	11 (4)	44% (29)	57% (29)
Incongruent - Congruent	6 (3)	17% (20)	76% (30)	9 (5)	19% (24)	81% (24)
Incongruent - Incongruent	8 (4)	27% (23)	72% (25)	10 (4)	34% (23)	67% (23)

For face targets, CI trials did not account for a larger percentage of actual mistakes from total errors compared with II (CI \approx II), $t_{24} = 1.08$, $p > .05$. Incongruent trials were not accounting for more total errors with mistakes in the expected low control trials (CI \approx CC), $t_{24} = .46$, $p > .05$, but they were in high control trials (II > IC), $t_{24} = 2.36$, $p = .03$. For face distracters, low control trials accounted for a significantly higher percentage of mistakes from total errors compared with the expected high control (CI > II), $t_{24} = 2.61$, $p = .02$. Incongruent trials were not accounting for more total errors with mistakes in low

control trials ($CI \approx CC$), $t_{24} = 1.27$, $p > .05$, but they were in high control ($II > IC$) trials, $t_{24} = 3.39$, $p = .002$.

There was no significant difference in the number of time-outs for face targets in high compared with low control trials ($II \approx CI$), $t_{24} = .97$, $p > .05$. There were significantly more time-outs in incongruent trials compared with congruent in the expected low control trials ($CI > CC$), $t_{24} = 5.39$, $p < .001$ and in the high control trials ($II > IC$), $t_{24} = 2.38$, $p = .03$. There was no significant difference in the number of time-outs for face distracters in high compared with low control trials ($II \approx CI$), $t_{24} = .25$, $p > .05$. There were not significantly more time-outs in incongruent trials compared with congruent trials in low control ($CI \approx CC$), $t_{24} = .67$, $p > .05$ and high control trials ($II \approx IC$), $t_{24} = 1.72$, $p > .05$.

The percentage of total errors was calculated to assess the percentage for which time-outs were responsible. For face targets, low control trial time-outs did not account for a higher percentage of total errors compared with high control ($II \approx CI$) trials, $t_{24} = .67$, $p > .05$. Incongruent trials did not account for a higher percentage of time-outs from total errors compared with congruent trials in either the expected low ($CI \approx CC$), $t_{24} = .72$, $p > .05$ or high ($II \approx IC$), $t_{24} = .58$, $p > .05$ control trials. For face distracters, high control trial time-outs accounted for a significantly higher percentage of total errors compared with low control ($II > CI$) trials, $t_{24} = 2.63$, $p = .02$. Congruent trials accounted for more total errors with time-outs in the expected low control ($CI < CC$), $t_{24} = 3.16$, $p = .004$ and high control trials ($II < IC$), $t_{24} = 3.38$, $p = .003$.

Time-outs accounted for a significantly higher percentage of the overall errors compared with actual mistakes in almost all trials for both face target trials CC , $t_{24} = 3.67$, $p = .001$, CI , $t_{24} = 6.34$, $p < .001$, IC , $t_{24} = 6.99$, $p < .001$ and II , $t_{24} = 4.99$, $p < .001$ and face distracter trials CC , $t_{24} = 3.95$, $p = .001$, IC , $t_{24} = 6.47$, $p < .001$ and II , $t_{24} = 3.70$, $p < .001$, but this difference was not significant in CI , $t_{24} = 1.09$, $p > .05$ trials.

The mean number of mistakes in expected high compared with low control trials did not differ ($II = CI$) for face targets, $t_{24} = .20$, $p > .05$ or face distracters, $t_{24} = .90$, $p > .05$. The mean number of time-outs in expected high compared low control trials did not differ ($II = CI$) for face targets, $t_{24} = .97$, $p > .05$ or face distracters, $t_{24} = .25$, $p > .05$.

The behavioural data above suggested that comparisons between II and CI trials may not actually constitute the expected high versus low control trials for both face targets and face distracters.

Preliminary EEG Results

Grand average waveforms for all participants for induced and evoked, high and low alpha, CI and II, face targets and face distracters (name targets) (total: 16) were calculated. High minus low control (II – CI) condition grand average difference wavelengths were calculated for these trials.

Voltage distribution topographic maps for the II – CI average waveforms were created for -300 to 600 ms at 24 ms intervals. Following theoretical predictions analyses focused on high evoked alpha and are reported below. In order to test the specificity of predictions, and thus the theoretical framework, regarding evoked upper alpha, parallel analyses were conducted using induced upper alpha and induced and evoked lower alpha, but as expected these failed to show similar effects. They are therefore not reported here.

Visual examination of the two main conditions (II – CI face targets and II – CI face distracters) revealed unexpected evoked upper alpha ERD and ERS patterns (Figure 3.5a, b) focused, as in Paper 1 (p. 54), on T6 and P_{PZ}, P4.

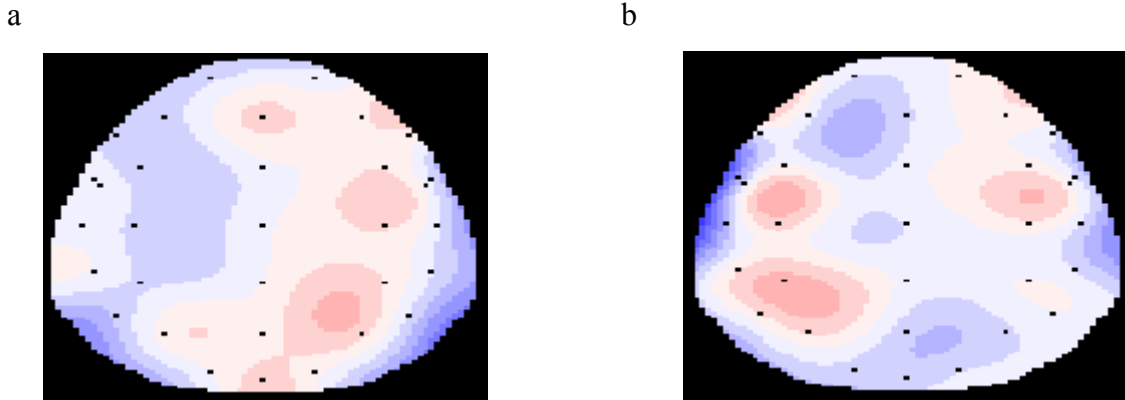


Figure 3.5. Topographic maps of ERS (blue) and ERD (red) pattern of grand average difference waveforms at 168 ms of stimulus onset. Panel a) II minus CI face targets, b) II minus CI face distracters. Colour key Figure 2.1b (p. 43).

Results of the topographic maps for face targets revealed no expected ERD effects at, for example, T6 electrode, in fact ERS was observed. Furthermore, ERS activity was then also observed at T5 electrode on the left side (homologous to T6 location, but now on the opposite side). ERD was observed at P_{PZ, P4}. In effect this is inverse pattern to that obtained in Paper 1 (p. 54). For face distracters, the pattern was highly dissimilar to that obtained in Paper 1, for example, absence of any ERD activity at P_{PZ, P4} electrodes or strong ERS activity at T6. ERD was detected at T5. These results confirmed the behavioural findings that the current paradigm including II, CI, CC and IC sequences within each task was not simply comparable to those observed in the blocked design. Main analyses were performed, as in Paper 1, for face targets and face distracters in II and CI trials.

To better understand the baffling results found for behavioural Stroop and Gratton effects and stimulus topographic maps, and in the context of the limited scope of the current project, further analyses were performed for cues (“face”, “name”). Epochs of -1 000 ms and 2 000 ms were extracted from unfiltered EEG files and processed identically as for stimulus epochs including rejecting unfiltered contaminated epochs based on which epochs were rejected from the filtered EEG files. ERBP was performed, reference interval 0 – 1 300 ms, epochs were trimmed 1 000 ms on the left and 700 ms on the right and ERBP was only performed for high (11 Hz) evoked alpha (Figure 3.6; Appendix A).

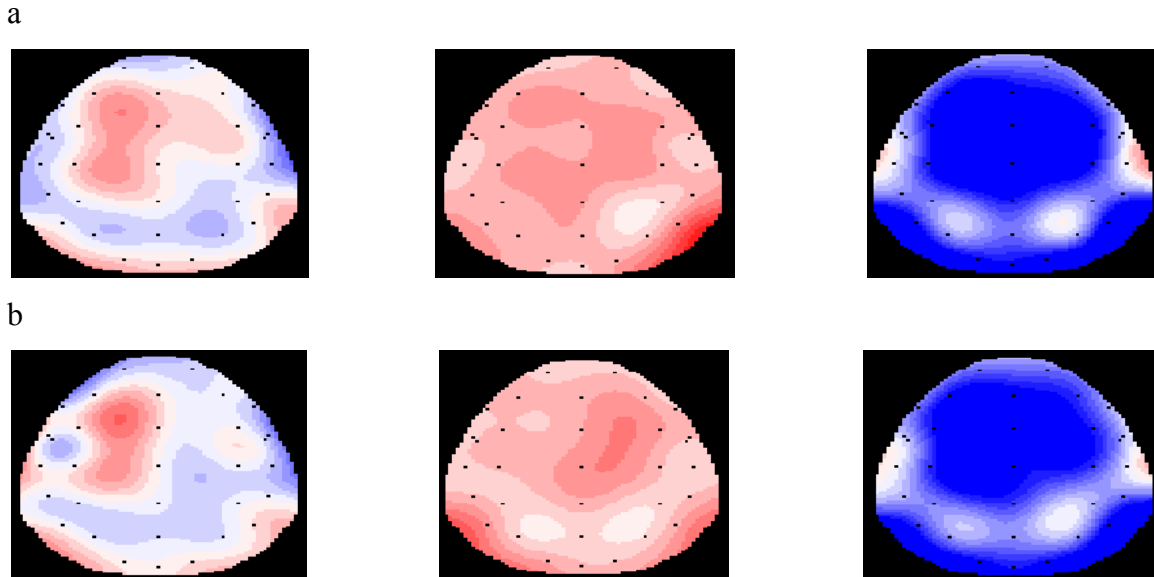


Figure 3.6. Topographic maps of ERS (blue) and ERD (red) pattern of grand average waveforms for cues: left at 0 – 50 ms, middle at 750 – 800 ms, right at 1 200 – 1 250 ms. Panel a) “face” cue, b) “name” cue. Colour key Figure 2.1b (p. 43).

Cue epochs were not analysed any further, but topographic maps were created to explore control effects elicited at the cue processing stage. Topographic maps (Appendix A) of the entire 1 300 ms cue interval indicate that cues were comprised of 3 distinct phases. At 0 – 250 ms interval intense ERD was observed over left dorsolateral prefrontal cortex for both face and name cues; the 500 – 1 000 ms interval exhibited widespread exclusively ERD activity for both face and name cues and the 1 050 – 1 250 ms interval exhibited widespread almost exclusively ERS activity for both face and name cues. Implications of these findings are briefly suggested in the Discussion section.

3.4.3 Main ERD and ERS Results

Area reports were calculated for high evoked alpha for face targets and face distracters (name targets) in CI (high conflict/low control) and II (high conflict/high control) for -500 – 0 ms pre-stimulus and 0 – 250 (encompassing face processing related N170) ms post-stimulus intervals. Occipitally bordering T5, T6 and P_{PZ, P4} electrodes were the focus of the main analyses as occipital electrodes are known to overlie the face processing pathways and regions (Gazzaley et al, 2005), as in Paper 1 (p. 54).

Conflict adaptation effects in target (face target versus face distracter) and control (II versus CI) trials were analysed separately for P_{PZ, P4}, T6 and T5 channels with 2 x 2 repeated measures ANOVAs and planned comparison t-tests. Main effects will not be reported since the primary interest was in the interactions. All ANOVA results are reported with Greenhouse-Geisser adjustment.

Expected conflict adaptation ERD/S effects were not observed in P_{PZ, P4} region at 0 – 250 ms post-stimulus interval (Figure 3.7a). When face served as a target, enhanced inhibition (ERS) was not observed in previously assumed high control II (M = -46.83) compared with low control CI (M = -68.17) trials, $t_{24} = 1.32$, $p > .05$ contrary to results in Paper 1. Furthermore, the relative drop in the mean negative value in II compared with CI trials hinted to the presence of a relative facilitation effect. When face served as a distracter, enhanced facilitation (ERD) was not observed in previously assumed high control II (M = -44.69) compared with low control CI (M = -13.72) trials, $t_{24} = 1.64$, $p > .05$ as unlike in Paper 1, II compared with CI trials did not show a drop in the mean negative value interpreted as relative ERD effect; in fact the opposite occurred. The target x control interaction was marginally significant, $F_{1, 24} = 3.78$, $p = .07$, $\eta^2 = .14$. No significant pattern was found for the -500 – 0 ms pre-stimulus interval.

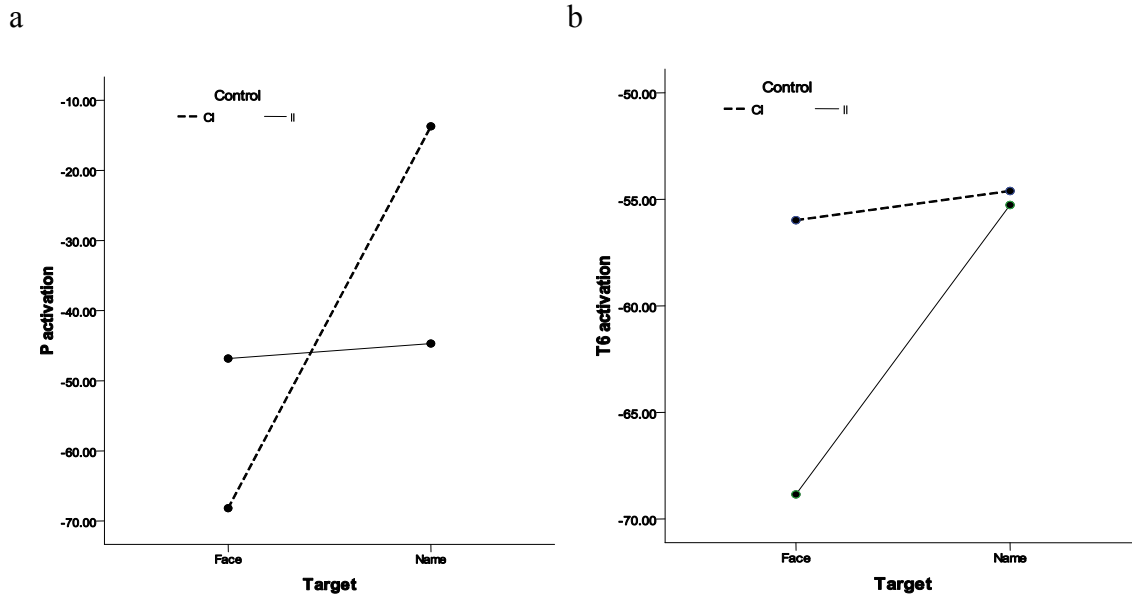


Figure 3.7. Conflict adaptation effects in high II and low CI control trials at 0 – 250 ms post-stimulus interval for face target and face distracter (name target). Panel a) P_{pZ, P4}, b) T6 channel.

Control effects were assessed at T6 channel at 0 – 250 ms post-stimulus interval (Figure 3.7b). When face served as a target, facilitatory (ERD) effects were not observed in previously assumed high control II ($M = -68.85$) compared with low control CI ($M = -55.98$) trials, $t_{24} = 1.47$, $p > .05$ as indicated by higher negative activation values in II compared with CI trials, contrary to findings in Paper 1. When face served as a distracter, somewhat enhanced larger negative (ERS) values were observed in previously assumed high control II ($M = -55.27$) compared with low control CI ($M = -54.61$) trials, but it failed to reach significance level, $t_{24} = .07$, $p > .05$ unlike in Paper 1. The target \times control interaction was not significant, $F_{1, 24} = .86$, $p > .05$, $\eta^2 = .04$. Similarly, no significant pattern was found for the -500 – 0 ms pre-stimulus interval. No facilitatory (ERD) effects at T6 channel were observed in high II compared with low CI control for face targets, contrary to results obtained in Paper 1.

Conflict adaptation ERD/S effects were assessed at T5 channel (homologous position to T6, but now on the left side) at 0 – 250 ms post-stimulus interval (Figure 3.8). When face served as a target, control effects were evident in higher inhibitory (ERS) values in previously assumed high control II ($M = -71.51$) compared with low control CI ($M = -51.01$) trials even though this difference was not significant, $t_{24} = 1.79$, $p > .05$.

The target x control interaction effect was significant, $F_{1, 24} = 8.52$, $p = .008$, $\eta^2 = .26$. When face served as a distracter, there was no significant difference in the level of inhibition between previously assumed high control II ($M = -44.39$) and low control CI ($M = -56.52$) trials, $t_{24} = 1.09$, $p > .05$. Furthermore, II exhibited a relative drop in the mean negative value compared with CI suggesting the possible presence of relative ERD effects.

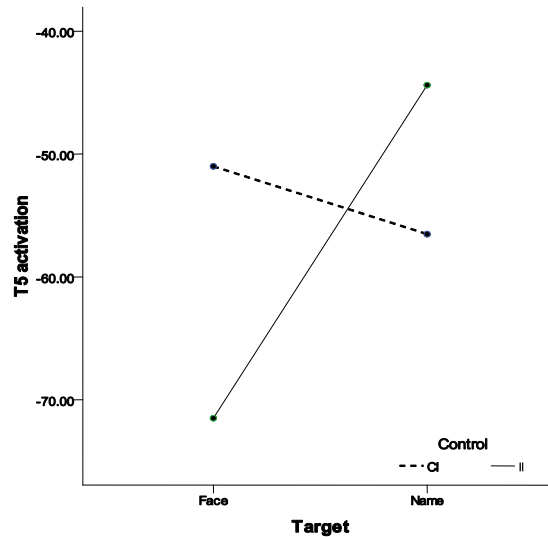


Figure 3.8. Conflict adaptation effects in high II and low CI control trials at 0 – 250 ms post-stimulus interval for face targets and face distracters at channel T5.

No significant inhibitory or facilitatory effects were observed at T5 electrode for face targets or face distracters in II and CI trials at -500 – 0 pre-stimulus interval.

3.4.4 Switch and Stay Trial Sequence Analyses and Results

Conflict adaptation, in the form of the Gratton effect, may have failed to emerge behaviourally in the current experiment because of the additional task switching factor in the experimental design. In the above analyses, CI and II (Gratton effect) trials were averaged across switch (i.e., from responding to face target → to face distracter or vice versa) and stay (i.e., respond to face target → to face target or name target → to name target) trial sequences. Stay trials usually exhibit shorter RT and higher accuracy rates compared with switch trials which, in turn, require task set reconfiguration and hence are both more difficult and require a different form of cognitive control. While conflict

adaptation regulates control by monitoring performance within a task set, task switching (and thus switch trials), requires monitoring and control of the task set itself, *prima facie* implying a higher hierarchical level of the switching control mechanism given that task sets are widely held to be hierarchically organised (Sakai, 2008; Brown et al, 2007). Furthermore, task switching is also known to interact with conflict adaptation (the Gratton effect). Following an incongruent trial the task switching cost may become more pronounced: this is because conflict on the prior incongruent trial reinforces the currently active task set, so when the task changes on the subsequent trial, it results in greater switching difficulty and thus performance deficits (Brown et al, 2007). The control requirements of II trials then are very different depending on whether the consecutive trials require the same task set or switch in task sets. Consequently, the classic conflict adaptation (Gratton type) effect may only emerge in stay trial sequences and may be abolished or even reversed on switch trials (Egner, 2007). This account may explain the puzzling pattern of behavioural results in Paper 2, therefore the possibility was tested by reanalysing that data set.

Hypothesis: Conflict adaptation or specifically the Gratton effect will be evident in stay trial sequences, but not in switch trial sequences for both face targets and face distracter response sets.

All behavioural data, from the second stimulus in each fixed sequence pair (as per previous analyses) were recoded and re-analysed for 25 participants. The previous 8 conditions (face target and face distracter in CC, CI, II and IC trials) were split into sixteen conditions (face target and face distracter in CC, CI, II and IC trials in switch and stay trial sequences). This presented a further problem: once time outs and incorrect responses were taken out, it was discovered that for almost half (10/25) of the participants some conditions (e.g., face distracter II stay trials) had only one correct trial RT which could be used as that participant's "average" RT for this particular condition. Therefore, separate EEG analyses on these recoded trials were ruled out as there would have been insufficient number of epochs in those conditions for reliable estimation of evoked alpha responses.

Task switching effects (switch versus stay trial sequence) for target (face target versus face distracter), control (II versus CI) trials were analysed by means of a 2 x 2 x 2

repeated measures ANOVA. Planned comparisons were conducted for each of the 4 possible II versus CI contrasts at each level of the target and sequence factors.

Results and Implications

Mean reaction times for correct trials are presented in Table 3.3. There was a significant main effect for target with shorter RT for face targets (M = 600 ms) compared with face distracters (M = 723 ms), $F_{1, 24} = 146.97$, $p < .001$, $\eta^2 = .86$. This again suggests that the face is a much more salient attribute (and thus distracter) compared with name in terms of the classic Stroop interference effect.

Table 3.3

Reaction Times (ms) (SD) for Face Target and Face Distracter in CI and II Trials in Stay and Switch Trial Sequences.

	Face Target		Face Distracter	
	Switch	Stay	Switch	Stay
Congruent – Incongruent	624 (88)	563 (70)	725 (56)	723 (78)
Incongruent – incongruent	612 (64)	599 (72)	729 (54)	713 (60)

There was a significant main effect for sequence with switch trials exhibiting longer RT (M = 673 ms) compared with stay (M = 650 ms) trial sequences, $F_{1, 24} = 8.42$, $p = .008$, $\eta^2 = .26$. This illustrates the classic switching cost effect, in the current data on average a 23 ms switching cost.

The main effect for control in low control CI (M = 659 ms) compared with high control II (M = 663 ms) trials was non significant, $F_{1, 24} = .30$, $p = .59$, $\eta^2 = .01$ clearly indicating the *absence* of a simple main effect for conflict adaptation.

The interaction between target (face versus name) and sequence (switch versus stay) was significant $F_{1, 24} = 4.41$, $p = .05$, $\eta^2 = .16$ with switch costs only apparent for face targets as mean the for switch (M = 617 ms) exceeded the upper bound of the 95% confidence interval for stay while the mean for stay (M = 581 ms) lay below the lower bound of the 95% confidence interval for switch (Table 3.4). However, for the name

target (face distracters) both switch (M = 727 ms) and stay (M = 718 ms) mean reaction times lay within each other's 95% confidence intervals (Table 3.4).

Table 3.4

95% Confidence Intervals for Face Target and Face Distracter in Switch and Stay Trials.

	Switch trials		Stay trials	
	Lower bound	Upper bound	Lower bound	Upper bound
Face Target	590	646	558	605
Face Distracter	708	746	696	739

The interactions between target and control, $F_{1, 24} = 1.02$, $p = .32$, $\eta^2 = .04$, and sequence and control, $F_{1, 24} = 1.51$, $p = .23$, $\eta^2 = .06$, were non significant.

The 3 way target x control x sequence interaction was marginally significant, $F_{1, 24} = 3.06$, $p = .093$, $\eta^2 = .12$. For face targets (Figure 3.9a), the Gratton effect was *reversed* for *stay* sequences where high control II trials (M = 599 ms) were *longer* than low control CI trials (M = 563 ms), $t_{24} = 2.13$, $p = .05$. The Gratton effect was not observed for switch trial sequences for face targets $t_{24} = .85$, $p = .41$ and neither in stay $t_{24} = .58$, $p = .57$ nor switch $t_{24} = .34$, $p = .74$ trial sequences for face distracters (Figure 3.9b).

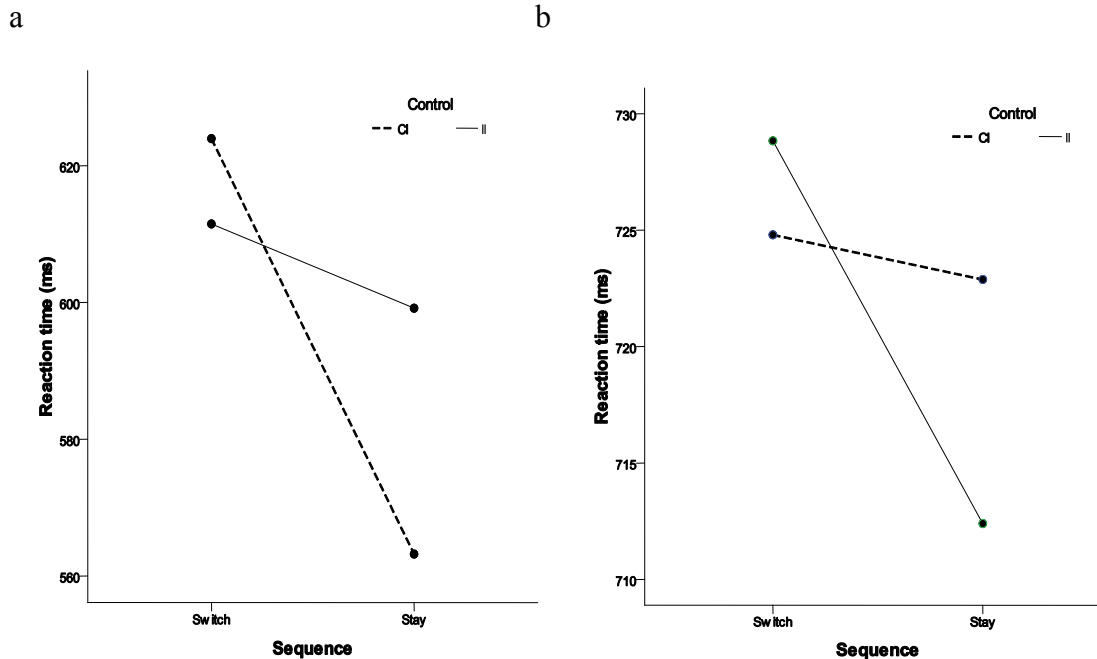


Figure 3.9. Mean group reaction times (ms) for switch and stay trial sequences in high II and low CI control trials. Panel a) face targets and b) face distracters (name targets).

The results indicated the hypothesis that the Gratton effect would be present in stay, but not switch trial sequences was not supported. The above results indicated that faces are more powerful distracters compared with names in terms of Stroop interference effect. This is likely to play a key role in the finding that the classic switching cost effect is found only in the face target task instruction condition and not in the face distracter (name target) instruction condition. The relative salience (to motor responses) of the face attribute also appears to play a role in the 3 way interaction effect where a *reverse* Gratton effect is found for high control compared with low control trials for stay trial sequences for face target, but not for face distracter task instructions. This last point, in turn, can be said to be a conflict adaptation effect in the sense that conflict on the previous trial is eliciting a control response on the present trial, but this is an entirely different type of conflict adaptation effect to the Gratton effect involving a very different type of control mechanism.

The results indicate, contrary to predictions, that when faces served as targets, in switch trials participants were faster in the high control condition compared with the low control condition; in stay trials, however, they *slowed down* (longer RT) more in high

compared with low control trials (see Figure 3.9a) and the former were significantly slower than the latter. When faces served as distracters, this pattern appeared to be reversed as participants were actually slower in high compared with low control trials in switch sequences, but were faster (shorter RT) in high compared with low control trials in stay sequences (see Figure 3.9b) however unlike for the face target instructions these results were non significant.

Control effects elicited here cannot be explained by the additive combination of the operation of classic conflict adaptation and switching cost mechanisms (Egner, 2007) although this may occur in other contexts. Rather the incidental activation (due to the context of a task switching experimental design) of an additional control mechanism (Brown et al, 2007) that results in a more cautious and thus slower response. These results suggest that context is a powerful determinant of control processes elicited. The task set switching context may elicit at least some elements of *between-set switching control* rather than *within-set* conflict adaptation to be operative on stay trials. In addition, the saliency (e.g., face versus name) of relevant versus irrelevant distracter stimulus attributes may also sometimes over ride the effects of control processes.

In summary, current task switching results suggest the existence of multiple control mechanisms operating to regulate control both *within a task set* and *between task sets* (task switching). The operation (and interaction) of specific control mechanisms is highly context dependent and remains to be fully described. However, present results indicate the importance of stimulus salience (to response systems), experimental design (block instructions versus shifting instructions) and the level of conflict on previous and present trials. Difference in the salience of (potentially) conflicting stimulus attributes (faces versus names in the current design) appear to have been a critical (but context sensitive) factor in the current paradigm and require systematic future study in this area. However, the pursuit of these considerations lies beyond the scope of the present research program.

3.4.5 Results Summary

Behavioural data failed to reveal the classic Stroop distracter interference effect for face targets where, contrary to expectations, incongruent trials were faster than congruent. The Stroop interference effect was observed for face distracters (name targets) where

congruent trials were faster than incongruent. The classic Gratton or conflict adaptation effect ($RT_{II} < CI$) was not detected either for face targets or distracters.

Accuracy rates were not significantly different between previously assumed high and low control trials for both face targets and distracters, but congruent trials had significantly higher accuracy rates than incongruent in both low and high control trials as in Paper 1. Overall, face distracters had lower accuracy rates and higher error rates compared to face targets. For both face targets and distracters, time-outs accounted for a significantly higher percentage of total errors compared with actual mistakes in nearly all trial types. Previously assumed high control compared with low control trials did not demonstrate more time-outs for either face targets or face distracters.

In Paper 1, RT for face targets and face distracters (name targets) were in the ranges of 592 – 607 ms and 692 – 748 ms respectively, compared with 600 – 625 ms and 675 – 725 ms respectively, in the current study. For face targets, RT were somewhat shorter in Paper 1, but the RT range was somewhat shorter for face distracters in the current study. Overall accuracy rates were markedly lower in the current experiment with face and name targets in the range of 71 – 78% and 52 – 67% respectively, compared with Paper 1 where accuracy rates were in the ranges of 90 – 94% and 60 – 75% respectively. Accuracy rates were lower for face distracters compared with face targets as in Paper 1.

Unlike in Paper 1, the preliminary EEG topographic map displays failed to reveal the expected facilitatory and inhibitory effects at the $P_{PZ, P4}$, T6 and T5 electrodes for both face targets and distracters. When face served as a target, no enhanced post-stimulus inhibition (ERS) was observed in high compared with low control trials at channel $P_{PZ, P4}$ contrary to expectations and findings in Paper 1. When face served as a distracter, there were higher post-stimulus negative values in previously assumed high control compared with low control trials at channel T6, but, unlike in Paper 1, it did not reach significance level. Furthermore, a higher negative mean value at T6 was observed in assumed high compared with low control trials for face targets, again contrary to findings in Paper 1. Subsequent pre-stimulus interval analyses failed to reveal the expected ERD effect in high compared with low control trials for face targets at T6.

Control effects were assessed at T5 channel for face targets revealing higher inhibitory (ERS) values in previously assumed high compared with low control trials. For face distracters previously assumed high control trials had somewhat (not significantly) lower negative values than low control, suggesting the presence of relative ERD effects.

Preliminary topographic map display analyses of cue epochs revealed that cues in event related design may exhibit three distinct phases, but further analysis of this aspect of the data was beyond the scope of this project.

Switch and stay trial sequence analyses indicated existence of multiple control mechanisms operating to regulate control both *within a task set* and *between task sets* (task set switching). Results indicated the importance of stimulus salience (to response systems), experimental design (block instructions versus shifting instructions) and the level of conflict on previous and present trials. Difference in the salience of (potentially) conflicting stimulus attributes (faces versus names in the current design) appear to have been a critical (but context sensitive) factor in the current paradigm.

3.5 Discussion

The current study was aimed at examining the blocked design study results in Paper 1 which showed inverse evoked upper alpha ERD and ERS patterns at selected cortical regions depending on whether the face was target or distracter. Results of the current event related paradigm did not replicate most of the central findings obtained in the blocked paradigm of Paper 1. The current experiment failed to show the Stroop effect in behavioural data for face targets or the Gratton effect for both face targets and distracters. Topographic map displays and evoked upper alpha ERD and ERS analyses failed to replicate the findings of Paper 1 for corresponding conditions and stimulus types. It was unclear whether effects observed in the current study for previously assumed high control II and low control CI trials represented the same conditions as in Paper 1. For example, congruent trials for face targets had longer RT than for incongruent trials.

In the current study RT in incongruent trials for face targets were shorter than congruent; in effect, congruent trials were behaving as if they were more difficult. The presence of stimulus attributes with values associated with the irrelevant task (even in congruent trials) can cause interference that opposes and even outweighs any benefit of

the same response being activated by both attributes (Monsell et al, 2000). Another possibility is that this effect was related to the relative power of face stimuli to mobilise response systems whether target or distracter, incongruent or congruent. Alternatively, it was possible that in incongruent trials participants were able to filter out distracting (name) information, while in congruent trials distracters failed to generate a facilitatory effect. Another possibility was that the event related design precluded the development of the Stroop interference effect by reducing the influence of distracters through the withdrawal of cognitive resources (e.g., attention) allocated to process background information and instead directed these resources to concentrate on the more important, primary target which was constantly alternating. In blocked design, there are more available resources, since only one task is performed. These resources in turn can be organised more efficiently during the preparation interval and can be shared to process background information. It was unclear, however, why face targets failed to show the Stroop effect considering the argument that processing of faces may be easier as they contain more concrete information compared to names. One possibility is that names, being weaker distracters, had reduced effect both congruent and incongruent.

However, congruent trials demonstrated higher accuracy rates than incongruent trials for both face targets and distracters, consistent with the Paper 1 finding. Face target trials demonstrated higher accuracy rates and lower error rates than face distracter trials. Time-outs, rather than actual mistakes, accounted for a significantly larger percentage of total errors for both face targets and distracters consistent with the Paper 1 finding. RT in the current study did not seem to be markedly longer than those in the blocked paradigm in Paper 1; for face distracters, RT range was even shorter in the current study.

Current results exhibited low accuracy/high error/time out rates, for some conditions accuracy rates were ~50%. If error responses are mostly incorrect responses this represents task performance at chance or effectively a random guessing level. However, there is little reason to interpret participants' performance in this way. Error responses were instead found to correspond largely to high time out rather than incorrect responses, for example see total error analyses results (p. 85). This suggests that the task/s were very difficult and this difficulty resulted in a slowing of responses – more

conservative response criteria – itself an effect of cognitive control rather than random guessing.

It was unclear why there was no observed Gratton effect for either face targets or distracters. One possibility was that the event related design with the inclusion of constantly and unpredictably alternating cues added extra demands for top down control. Preparatory processes, however, would have been compromised by the unpredictably and constantly alternating tasks and cues. The Gratton or conflict adaptation, control effect may not have had the time or resources to develop. The influence of affective factors cannot be overlooked either considering that a consistent, high demand for effort may have resulted in feelings of frustration or besiegement and consequent decrease in effort. Thus, sustained and prolonged conflict, indicating that increased effort was not sufficient to reduce conflict, may have resulted in subjective feelings of frustration and participants may have disengaged from the task. A longer ISI may have helped to improve performance since it is known to have a powerful influence (Eimer, 1999). Response slowing rather than the Gratton effect may have been the most appropriate index of cognitive control in the context of event related/task switching design.

There was also an absence of expected evoked upper alpha ERD and ERS effects as observed in Paper 1 for both face targets and distracters. Constant and unpredictable switching between tasks would have required constant shifting and allocation of resources, abandoning one task set (e.g., face) while establishing a new one (e.g., name), with a similar pattern reflected in the response set (actor versus politician) resulting in near absence of predictability about the upcoming task and, hence an inability to prepare.

Cognitive control during task switch is expected to fluctuate from trial to trial and is mediated by the fluctuating activity of discrete brain regions, hence successful behavioural performance in task switching may depend on whether a specific brain region can be differentially activated to a sufficient degree (Braver et al, 2003). Face and word stimuli are thought to activate distinguishable cortical regions allowing measurement of levels of activity in task selective regions during task switching. For example, in one study (Yeung et al, 2006), areas within the PFC, ACC, pre-SMA, precuneus and parietal cortex showed increased activity during task switching. The right inferior frontal sulcus (IFS) showed selectivity for faces and the left inferior frontal gyrus

(IFG) for words. The PFC is assumed to perform the integrated function of working memory (maintaining task set) and cognitive control (using this information to guide cognitive processing) and, hence, task selective regions should show increased activation during preparation and subsequent performance. The ACC, pre-SMA and posterior cingulate were active during task switching indicating the general regions involved in task switch (Yeung et al, 2006).

Therefore, the absence of the expected evoked upper alpha ERD and ERS patterns may be related to a few possibilities. Firstly, constant switching failed to engage specific brain regions to a sufficient degree. This would explain the absence of the expected ERD and ERS patterns, but this may also have contributed to the puzzling behavioural results. For example, task switching might have prevented sustained cortical processes from developing to support task performance. Secondly, constant and unpredictable task switching required higher levels of top down control and, hence, may now manifest in *dissimilar* evoked upper alpha ERD and ERS patterns. High task demands in the current experiment may have stretched cognitive resources to the limit producing an overall suboptimal performance, but the best possible performance on each trial in its particular context.

The current experiment used identical stimuli to those used in Paper 1, but used an event related paradigm in place of the blocked paradigm of Paper 1. The current behavioural results demonstrated reduced accuracy rates and, unexpectedly, also produced a shorter RT range, for example, for face distracters (name targets). In Paper 1, selective cortical regions demonstrated inverse evoked upper alpha ERD and ERS patterns depending on whether face attribute was the target or distracter. The current results demonstrated more complex ERD and ERS patterns many of which were dissimilar from those observed in Paper 1. Taken together, these factors suggested that fundamentally different control processes to those observed in Paper 1 were at play in the current study. Task switching in event related design likely depends on and exhibits different EEG mechanisms and effects to those observed in blocked designs.

One possibility is that in blocked designs higher and constant predictability elicit more specialised and localised top down control effects such as those convincingly demonstrated by inverse evoked upper alpha ERD and ERS patterns for face targets and

face distracters in Paper 1. In event related design, the constant and high level of unpredictability generated by both alternating tasks and cues produces a constant need for high levels of top down control which may be dependent on a further hierarchical layer of control mechanisms. In addition, predictable tasks may encourage adoption of particular strategies to deal with them and blocking may foster adoption of particular strategy. Task switching, on the other hand, together with a large stimulus set may preclude strategies from developing, hence simultaneously requiring higher levels of top down control and hindering performance enhancing strategies from developing.

Switch and stay trial sequence analyses suggested multiple control mechanisms operating to regulate control both *within a task set* and *between task sets* (task set switching). Results indicated the importance of stimulus salience (to response systems), experimental design (block instructions versus shifting instructions) and the level of conflict on previous and present trials. Difference in the salience of (potentially) conflicting stimulus attributes (faces versus names in the current design) appear to have been a critical (but context sensitive) factor in the current paradigm.

The role of cues in task switching cannot be overlooked since a cue is a precursor of control, and examination of brain activity during the cue may help to localise the neural substrate of task set preparation processes (Monsell & Mizon, 2006). In one study using event related fMRI, separate brain regions were active in response to cues such as the lateral intraparietal sulcus (IPS), superior parietal lobule, posterior cingulate cortex, lateral and medial superior frontal lobes compared with stimulus such as SMA, midcingulate gyrus, ventrolateral prefrontal regions, ventral and dorsal occipital cortex (Hopfinger et al, 2000). Cues signal/instruct the upcoming target and, hence, task related regions are likely to be put in preparatory mode at the cue presentation stage.

During the cues, the DLPFC (subserving role in task set maintenance) may be active while the pre-SMA (with the ACC) may also be involved in monitoring response conflict, implementing rule change. The PFC may select cue related task rules, while the pre-SMA may implement them at the motor control level, hence, activation in motor areas may represent motor preparation of the upcoming response. Correct and incorrect responses can be examined in combination with the neural activity accompanying their cues. For example, activation of the right inferior parietal lobule (IPL) among other

regions may be greater during cues which preceded correct responses (Fassbender et al, 2006).

The current preliminary only analyses of cue epochs exhibited 3 distinct phases with very similar, but not identical patterns for “face” and “name” cues. The first 0 – 250 ms interval demonstrated ERD activity at the left dorsolateral prefrontal cortex for both face and name cues, but the source of that activity did not seem to be in identical locations. There was a high level of widespread, almost exclusively ERD activity at the 500 – 1 000 ms interval for both face and name cues, even though, again, the source of this activation did not seem to be identical. Conversely, there was a high level of central, almost exclusively ERS activity for both face and name cues in the last part of the 1 050 – 1 250 ms cue interval which appeared to suggest that the brain reduced or dampened activity, and thus competition for resources, as a preparation for processing the upcoming stimulus. Considering that control effects may be triggered during the cue presentation time interval, cues warrant further investigations using EEG.

The current experiment convincingly demonstrated that cognitive control is not a homogenous process applied equally to all conflict modulating contexts as evident in the failure of the current event related experiment to replicate the blocked design results of Paper 1. Both facilitatory and inhibitory effects were evident, but their activity was more complex than those engaged by the block design task used in Paper 1. The current event related experiment failed to replicate most of the central Paper 1 blocked design findings partly, without a doubt, because event related and blocked paradigms cannot strictly be assumed to be equivalent in their complexity and processing demands. On the other hand, failure of the current event related design to replicate blocked design evoked upper alpha ERD and ERS patterns demonstrates that cognitive control is not a simple, homogenous mechanism applied equally to all contexts regardless of the processing demands. On the contrary, the current results demonstrate the complexity, heterogeneity and hypothesised, even the hierarchical nature of cognitive control and high sensitivity to task demands. Sensitivity to task demands further raises the question of whether cognitive control is also affected by the nature or the source of the conflict. The following experiment was designed to investigate whether the nature of the conflict also affects ensuing control effects.

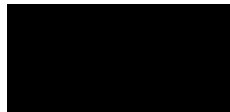
STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Figures	80, 81, 82, 84, 88, 89
	91, 92, 96
Tables	84, 85, 94, 95

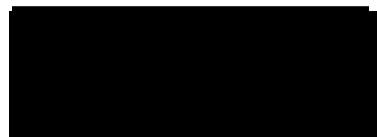
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



Candidate

April 2010



Principal Supervisor

April 2010

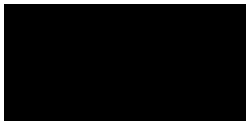
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	% of contribution
Candidate	Daiva Newby	75
Other Authors	Graham Jamieson	25

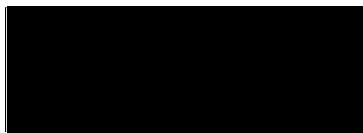
Name of Candidate: Daiva Newby

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April 2010



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April 2010

Paper 3: Stroop Target Unknown: EEG Evidence of Facilitatory and Inhibitory Effects When Targets Precede Cues

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4.1 Abstract

The current experiment investigated whether cognitive control effects differ depending on the source or nature of conflict by measuring evoked upper alpha ERD and ERS and using a new variant of the event related face/name Stroop paradigm. This new event related paradigm presented the stimuli *before* presenting the cues, thus participants first viewed the stimulus not knowing whether the subsequent cue would instruct them to respond to face target or face distracter (name target). This was aimed at separating the initial perceptual stimulus processing conflict from the response conflict and ensuing control effects. The current design, in effect, removed stimulus preparation effects and investigated control effects post-stimulus at post-instructional cue time interval.

A particularly robust behavioural Stroop interference effect was detected for both face targets and face distracters, while a weak Gratton or conflict adaptation effect was detected for face targets, but not for face distracters. Area reports for evoked upper alpha at channels P_{PZ, P4}, T6 and T5 were analysed. For face targets, there was a drop in mean negative values or a relative facilitatory effect at the post-instructional cue time interval in high compared with low control trials at P_{PZ, P4} electrodes. For face distracters, there were higher negative values at the post-instructional cue time interval in high compared with low control trials at channel P_{PZ, P4}. For face targets, there was inhibitory activity at the post-instructional cue time interval in high compared with low control trials at T6. For face distracters, there was inhibitory activity at the post-instructional cue time interval in high control compared with low control trials at channel T6. For face targets, there were higher negative values at the post-instructional cue time interval in high compared with low control trials T5. For face distracters, there was a facilitatory effect at the post-instructional cue time interval in high compared with low control trials at channel T5. Evoked upper alpha ERD and ERS patterns for face target cue and face distracter (name target) cue did not reveal any immediately obvious, systematic patterns. This was further interpreted as supporting the claim that cognitive control is comprised of heterogeneous and perhaps hierarchically organised processes highly sensitive to task demands.

Key words: conflict source, cognitive control, task preparation, Stroop, Gratton effect, facilitation, inhibition, event related design, EEG, evoked upper alpha, ERD, ERS, task set, task switching

4.2 Introduction

Cognitive control is required to resolve conflict between competing representations and responses in order to produce effective behaviour. Conflict can emerge at any stage during information processing anytime between perceptual stimulus processing to actual responding. Evidence is emerging that different types of conflict trigger distinct control systems and mechanisms as shown by fMRI studies (Nelson et al, 2003; van Veen & Carter, 2005). There has been little EEG research in this area. It is unclear, for example, how conflict generated at perceptual, stimulus processing or response selection stages, is modulated depending on the nature of its source and how it manifests in EEG measures.

It is also unclear what kind of, if any, effect preparation has on conflict modulation. In traditional event related paradigms at least a short amount of post-cue and pre-stimulus interval can be spent on preparatory processes. It is unclear what kind of role preparation has in task switching, for example, in engaging task set or presetting perceptual processes. The current study aimed to gather evidence in relation to both the effect of preparation on conflict modulation and the source of conflict and ensuing control effects.

4.2.1 Task Switching and Preparatory Processes

Anticipatory, preparatory behaviour is directed at upcoming events and serves to accommodate faster, more efficient information processing. This is achieved, for example, by pre-setting necessary physiological processes, preparing perceptual processes such as attentional focus towards relevant features of the stimulus and, hence, filtering out irrelevant attributes. Preparation for the upcoming task is, in effect, establishing task set, which in turn, in a task switching context, is time consuming as it requires higher-order neural interactions between regions in prefrontal and posterior association cortices which represent task set. Inefficient preparation may, for example, result in an insufficient degree of recruitment of relevant neural structures (Sakai, 2008) while continuous task set reconfiguration may impair the implementation of early perceptual processing (Jentsch & Leuthold, 2005). Preparation in such a case would then have to be done after stimulus onset, thus postponing it, and generally it would be likely to be less thorough (Monsell & Mizon, 2006).

Task switching requires continuous, effortful and active top down control to change current task sets. Task switch cost, which manifests in slowed or less accurate performance on switch compared with repetition trials, can be reduced but not eliminated by longer preparation intervals. It cannot be eliminated because the task set from the previous trial remains somewhat active and no amount of top down task preparation can provide benefits of complete preparation (Pashler et al, 2001) since task set configuration may not be fully achieved until the appearance of the actual stimulus (i.e. bottom up information) when stimulus response rules are loaded into the working memory (Monsell, 2003). Task set reconfiguration is composed of goals such as task demands and rules on how to meet those demands. Reconfiguration is not just a byproduct of general preparation such as alertness as alertness is not sufficient to complete reconfiguration. Preparation is also not a single process and may be comprised of arousal, prediction of target onset and reconfiguration (Meiran et al, 2000).

Preparation effect is an index of endogenous control of task set reconfiguration before the stimulus and it indexes active preparation rather than just passive dissipation of the previous task set. Active preparation may be precluded by short response stimulus interval and, for example, by articulating irrelevant words during preparation, hence participants may receive a stimulus completely unprepared (Nieuwenhuis & Monsell, 2002) and thus then perhaps rely on mostly bottom up processes.

In conclusion, preparation is aimed at actively preparing the information processing system for the most efficient stimulus processing, for example, by representing goals, rules, targets and response sets. Preparation may manifest as an activation pattern over a task related neuronal population or cortical regions organising perceptual and motor task sets (Sakai & Passingham, 2003), and effective preparation may manifest in performance characterised by short RT or high accuracy rates. During task switching, however, alternative task sets have to be regularly abolished and established, hence, not only producing increased demands, but also presumably less preparation.

Preparatory processes are often appropriately viewed as helping performance, but there is a possibility that preparation in some instances may also have some detrimental effects. For example, efficient preparation for the task may entail sufficient engagement of task related cortical regions and task sets which in turn may be more difficult to get rid

of and hence may produce unwanted lingering effects when task sets change.

4.2.2 Nature of Cognitive Conflict Sources and Ensuing Cognitive Control Effects

According to the PDP model (Cohen et al, 1990), cognitive control is a feedback mechanism primarily guided by the detection of cognitive conflict at various levels of information processing, for example, perceptual, stimulus categorisation or response selection. There is, however, uncertainty as to whether interference or conflict generated at a particular information processing stage such as perceptual, semantic processing or response selection levels, subsequently affects the nature of ensuing cognitive control effects (Nelson et al, 2003; Casey et al, 2001). In one study authors used colour/word Stroop and found that semantic and response conflicts both contributed to the overall Stroop interference effect (van Veen & Carter, 2005). Furthermore, these effects elicited nonoverlapping activation in the ACC, prefrontal and parietal regions; hence the brain may have a distinct, but parallel mechanism for resolving different types of interference. For example, separate regions of PFC such as superior DLPFC for semantic and more inferior for response conflict may resolve semantic and response conflict while separate regions in the ACC, for example, more posterior for semantic and more anterior, consistent with activation by errors, be involved in response conflict. Hence different types of conflict may trigger PFC to overcome particular type of conflict (van Veen & Carter, 2005).

Nelson and colleagues (2003) used fMRI and a verbal working memory task (item recognition) to examine brain activity related to different types of conflict. Results indicated double dissociation with stimulus related conflict resulting in left PFC (inferior frontal gyrus or IFG, BA 45) activation, but not ACC and the reverse pattern for response related conflict. They interpreted this as pointing to differing contributions to cognitive control of specific cortical regions depending on the source of conflict. Since the aim of the experiment was to investigate sources of conflict, the authors did not discuss how that conflict is resolved apart from stating that the ACC signals the lateral frontal cortex to engage cognitive control through excitatory or inhibitory mechanisms.

MacDonald and colleagues (2000) used event related fMRI and a task switching Stroop colour/word task to investigate cognitive control components. In this study,

participants were given a cue indicating whether the response required was to read the word or name the colour. A delay then followed before the stimulus was presented. Hence, the task temporally separated instruction related strategies, for example, representing and maintaining attentional demands of the task, such as colour naming versus word reading, from response related strategies, such as evaluating, monitoring processes. Results indicated that instructions to name the colour, but not to read the word resulted in DLPFC activity, indicating requirements for top down control (e.g., to represent and maintain task demands needed for such control), while no activity in the ACC was observed during the instruction/cue. The authors hypothesised that more activity in the DLPFC should result in the smallest Stroop interference effects. Evidence indeed provided support for this, suggesting that the DLPFC implemented more control, hence reducing conflict, when responding to incongruent colour words. Response results indicated that within the right ACC greater activity was observed in incongruent than in congruent trials for colour naming consistent with conflict monitoring while the DLPFC was similarly active in both congruent and incongruent trials. The authors hypothesised that if the ACC monitors conflict then high conflict should be associated with more ACC activation and evidence provided support for this claim. The left DLPFC may be selectively engaged during the preparatory period by representing and maintaining task demands, while the ACC was selectively engaged during response selection, more so for incongruent than congruent, hence, monitoring for conflict. Conflict and control may be linked in a feedback loop to maintain optimal performance and cognitive control may be a dynamic process implemented by distributed, anatomically dissociable, but nonetheless closely interacting components (MacDonald et al, 2000). Other authors have also found that the ACC was activated during response conflict, while the left PFC was sensitive to non-response conflict (Millham et al, 2001). Thus, cognitive control can be distinctively influenced depending on the nature of conflict.

The current experiment, based on evidence gathered by fMRI studies which found that control is influenced by the nature of the conflict, aimed to gather EEG evidence to inform this issue. More specifically, the aim was to analyse facilitatory and inhibitory control effects in the resolution of specific conflict by manipulating paradigm design and slightly changing the focus of the analysis. The current experiment aimed to expand the

findings from Papers 1 and 2 by disentangling perceptual processing conflict from response conflict and control effects so cue elicited implementation of control could be seen more clearly as distinct from actual signal processing. It has been proposed that inhibition is more important at resolving conflict generated at the response generating rather than the perceptual stimulus processing stage (Nieuwenhuis & Yeung, 2005).

The interest in the current experiment was in *analysing post stimulus instructional cue time interval* when response conflict would be expected to be present and control effects would be expected to be implemented. Cues in Paper 2 were pre-stimulus. Cue contexts between pre-stimulus and post-stimulus would be expected to differ, as both perceptual and response conflict effects would be expected to be pooled at pre-stimulus and only response related conflict at post-stimulus stage. Control effects would also be expected to be better isolated at post-stimulus time interval.

The current study had two fundamental aims. Firstly, it aimed to separate perceptual conflict from response conflict and top down control implementation from actual stimulus processing and in particular perceptual processing of conflicting stimulus dimensions. Secondly, it aimed to completely remove preparation processes such as pre-setting perceptual pathways or establishing task set. The aim of the current experiment was to manipulate the paradigm and observe the manipulation effects on the slightly different aspect of the dependent variables used in Papers 1 and 2 of evoked upper alpha ERD and ERS patterns in topographic maps and area reports in the high (II) compared to low (CI) control in face target cue and face distracter cue.

4.3 Method

4.3.1 Participants

Thirty one naïve participants (16 males and 15 females) aged between 18 and 45 years ($M = 30$, $SD = 9$) recruited at UNE took part in the experiment. The majority of the participants were paid \$10 for their time and effort. Two participants took part for course credit. Participants were right handed, not taking any psychoactive medication and had normal or corrected-to-normal vision. The experiment consisted of a single 1½ - 2 hour session.

4.3.2 Data Acquisition

Data acquisition in the current experiment was identical to that in Paper 1 (Chapter 2) except for the following. The UNE EEG laboratory was updated and NeuroScan 40 channel Quik-Caps with Ag/AgCl coated electrodes were replaced by NeuroScan 40 channel Quik-Caps with Ag/AgCl sintered electrodes designed to minimise DC offset potentials and increase electrode durability. Channel number, positions and application remained unchanged.

4.3.3 Stimuli

Stimuli were created based on the same principles as in Paper 2 (Chapter 3) except in the following. Stimuli consisted of 6 black and white photographs of famous actresses (Nicole Kidman, Cate Blanchett and Angelina Jolie) and politicians (Margaret Thatcher, Hillary Clinton and Julia Gillard). Practice consisted of one photo of a politician (Angela Merkel) and one of an actress (Gwyneth Paltrow). This time names were written in bright blue letters. Again there were 32 stimuli in total with 2 (both incongruent) used in practice and 30 (12 congruent and 18 incongruent) experimental stimuli.

As in Paper 2 (Chapter 3), instructional cue was presented with each picture specifying whether a response was required to name or face in order to classify whether this person was “a politician” or “an actress”. However, in the current study instructional cue *followed* rather than preceded each stimulus (Figure 4.1). Stimuli were presented for 1 000 ms. Participants responded when they were presented with an instructional cue which disappeared when their response was made or when 1 300 ms terminated.

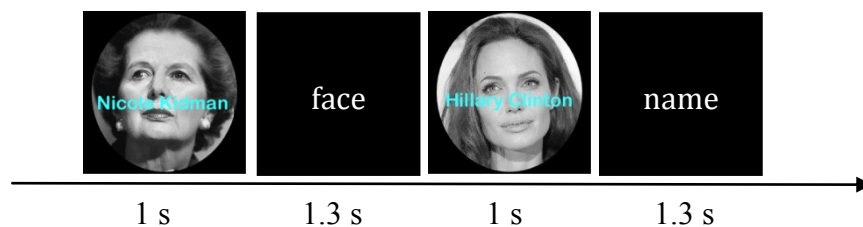


Figure 4.1: Participants had to respond to either face or name, as specified by a cue *following* the picture and classify whether this person was “an actress” or “a politician”.

Again, as in Paper 2 (Chapter 3), there were 64 fixed trial sequences created comprised of 16 trials in each of the four conditions in regard to current and previous trial congruency (CC, IC, CI, II) (Figure 4.2) with an equal number of cue (“face”, “name”) and stimuli (“actress”, “politician”) trial sequences. Again, the predictability of the upcoming stimulus and the required response was reduced by varying the type of the upcoming stimulus and cue as in Paper 2 (Chapter 3).

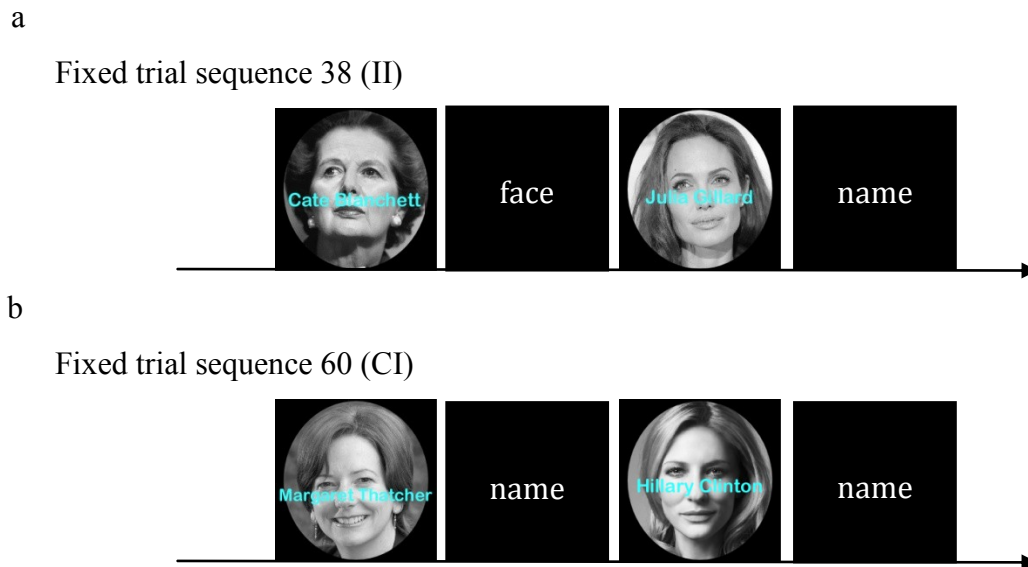


Figure 4.2. Examples of fixed trial sequences. Panel a) Trial sequence 38: II trial; b) Trial sequence 60: CI trial.

Again, as in Paper 2 (Chapter 3), each participant was presented with 192 trials (64 x 3) of 384 (192 x 2) stimuli in total. Fixed trial sequences were presented in pseudo-random order, although only the second stimulus in each fixed sequence was analysed, as in Paper 2 (Chapter 3). Participants again completed an eye-movement-artifact correction task as in Paper 1 (Chapter 2).

4.3.4 Procedure

The procedure in the current experiment was identical to that in Paper 2 (Chapter 3).

4.3.5 EEG Analysis

One corrupt recording (62) was permanently discarded. Processing of EEG files in Paper 3 was identical to that in Paper 1 (Chapter 2). EEG recordings were also ocular-artifact corrected and visually inspected. Epochs of 1 300 ms created for face cue and name cue targets in CI and II trials from unfiltered files were compared to those created from filtered files and rejected accordingly and then ERBP analyses were performed.

4.4 Results

4.4.1 Edinburgh Handedness Inventory Scores

Thirty participants scored >50 and one scored 41 points on EHI, hence all participants were right handed (Figure 4.3).

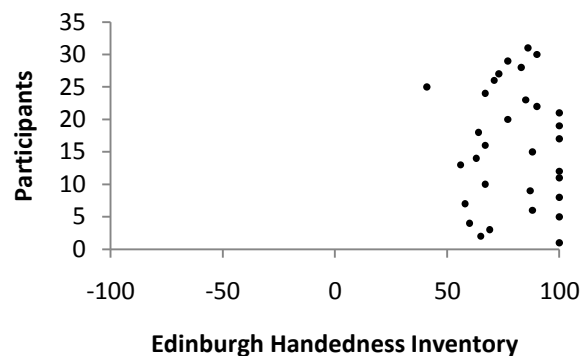


Figure 4.3. Participants' scores on Edinburgh Handedness Inventory.

4.4.2 Behavioural Stroop Effect and Gratton Effect and Preliminary EEG Results

Behavioural Stroop Effect and Gratton Effect Results

Note: There were missing RT data for one participant for II trials for both face target and face distracter. Mean reaction times (ms) and accuracy rates (%) were calculated for all correct trials. There was strong evidence of a classic Stroop interference effect from incongruent distracters for both face targets, incongruent ($M = 674$ ms) compared with congruent ($M = 500$ ms) trials, $t_{28} = 8.88$, $p < .001$, and for face distracters incongruent ($M = 641$ ms) compared with congruent ($M = 493$ ms) trials, $t_{28} = 7.47$, $p < .001$ with congruent means significantly shorter than incongruent means. In fact, the Stroop effect

was markedly robust with the congruent mean RT more than 100 ms shorter than the incongruent and for face targets it was 174 ms shorter. Note also that RT ranges are somewhat similar between face targets and face distracters.

The expected pattern of Gratton or conflict adaptation effect was present for face targets, but the effect was not significant and it was not present for face distracters (Table 4.1; Figure 4.4). For face targets, RT were shorter in expected high control than low control trials ($II < CI$) indicating presence of the Gratton effect, but this difference was not significant, $t_{28} = 1.12$, $p > .05$. There was a significant previous x current trial interaction, $F_{1, 28} = 17.39$, $p < .001$, $\eta^2 = .39$, where the effect of current trial conflict under low control ($CC < CI$), $t_{29} = 9.08$, $p < .001$ was not eliminated under high control ($II > IC$), $t_{28} = 6.77$, $p < .001$.

Contrary to expectations, for face distracters RT were longer in expected high control than low control ($II \geq CI$) even though this difference was not significant, $t_{28} = 1.09$, $p > .05$ failing to show the classic Gratton effect pattern. The interaction between previous x current trials was not significant, $F_{1, 28} = .02$, $p > .05$, $\eta^2 = .001$.

Accuracy rates for face targets indicated no significant differences between expected low and high control trials ($II \leq CI$), $t_{29} = 1.76$, $p > .05$, but there was a significantly higher accuracy rate in low control congruent trials compared with incongruent ($CC > CI$), $t_{29} = 2.24$, $p = .04$ with identical pattern in high control congruent trials compared with incongruent ($IC > II$), $t_{29} = 5.27$, $p < .001$.

Accuracy rates for face distracters were higher in expected low compared with expected high control trials ($II < CI$), $t_{29} = 2.88$, $p = .007$. However, there was a significantly higher accuracy rate in expected low control congruent trials compared with incongruent ($CC > CI$), $t_{29} = 3.74$, $p = .001$ with an identical pattern in high control congruent trials compared with incongruent ($IC > II$), $t_{29} = 4.94$, $p < .001$.

Table 4.1

Reaction Times (ms) and Accuracy (%) for Face Target Cue and Face Distracter Cue in CC, CI, IC and II Trials.

	Face Target Cue		Face Distracter Cue	
	RT (SD)	Accuracy (SD)	RT (SD)	Accuracy (SD)
Congruent – congruent	474 (145)	65% (26)	491 (146)	70% (25)
Congruent – incongruent	685 (73)	58% (27)	639 (80)	57% (24)
Incongruent – congruent	541 (124)	67% (23)	505 (133)	64% (25)
Incongruent – incongruent	670 (64)	54% (25)	649 (87)	51% (25)

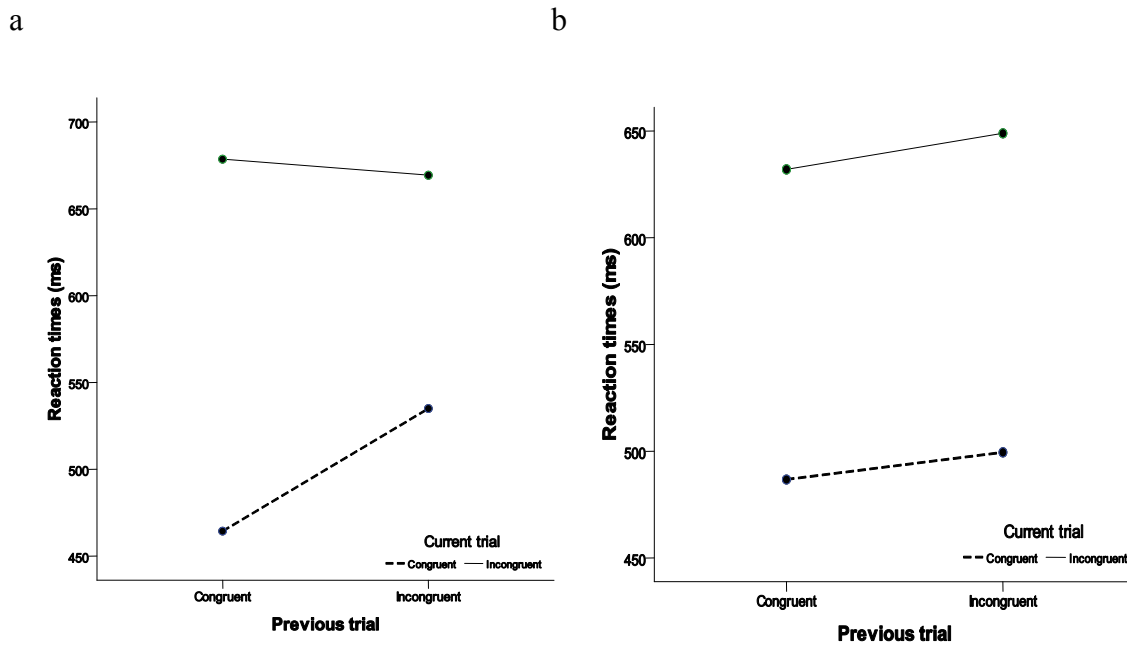


Figure 4.4. Mean group reaction times (ms) in CC, CI, IC and II trials. Panel a) face targets, b) face distracters.

For face targets, expected high control trials did not have fewer overall errors, comprised of actual mistakes and time-outs, compared with expected low control trials (II \geq CI), $t_{29} = 1.71$, $p > .05$ (Table 4.2). For face distracters, expected high control trials had more overall errors compared with low control trials (II $>$ CI), $t_{29} = 2.85$, $p = .008$. Overall errors for face targets were higher in incongruent compared with congruent trials in both low control (CI $>$ CC), $t_{29} = 4.94$, $p < .001$ and high control trials (II $>$ IC), $t_{29} =$

8.06, $p < .001$. Overall errors for face distracters were not significantly different between congruent and incongruent trials in both low control (CI = CC), $t_{29} = .93$, $p > .05$ and high control (II \approx IC), $t_{29} = .95$, $p > .05$ trials.

Table 4.2

Mean (SD) Number of Total Errors (Actual Mistakes and Time-Outs), Percentage (SD) of Actual Mistakes and Time-Outs Accounting for Total Errors in CC, CI, IC and II Trials for Face Target Cue and Face Distracter Cue.

	Face Target Cue			Face Distracter Cue		
	Total	Mistakes %	Time-outs %	Total	Mistakes %	Time-outs %
Congruent - Congruent	8 (6)	21% (29)	73% (34)	9 (7)	15% (25)	85% (25)
Congruent - Incongruent	12 (7)	27% (29)	73% (29)	9 (5)	25% (25)	75% (25)
Incongruent - Congruent	7 (5)	16% (27)	84% (27)	10 (7)	23% (28)	78% (28)
Incongruent - Incongruent	13 (7)	31% (27)	70% (27)	11 (6)	23% (24)	77% (24)

Time-outs accounted for a significantly larger percentage of the overall errors compared with actual mistakes in all trial types for both face targets CC, $t_{29} = 4.96$, $p < .001$, CI, $t_{29} = 4.41$, $p < .001$, IC, $t_{29} = 7.12$, $p < .001$ and II, $t_{29} = 3.98$, $p < .001$ trials and face distracters CC, $t_{29} = 7.81$, $p < .001$, CI, $t_{29} = 5.53$, $p < .001$, IC, $t_{29} = 5.49$, $p < .001$ and II, $t_{29} = 6.31$, $p < .001$ trials.

The mean number of mistakes in expected high compared with low control trials did not differ (II = CI) for face targets, $t_{29} = 1.71$, $p > .05$, but was significantly higher for expected high compared with low control trials (II > CI) for face distracters, $t_{29} = 2.85$, $p = .008$.

Preliminary EEG Results

Grand average waveforms for all participants for ERBP in high evoked alpha, CI and II, *face target cue* and *face distracter (name target) cue* were calculated. Target minus standard (II – CI) grand average difference wavelengths were calculated for these trials.

Voltage distribution topographic maps for the II – CI average waveforms were created for 0 to 1 300 ms at 50 ms interval (Figure 4.5). Following theoretical predictions

analyses focused on high evoked alpha and are reported below. In order to test the specificity of predictions, and thus the theoretical framework, regarding evoked upper alpha, parallel analyses were conducted using induced upper alpha and induced and evoked lower alpha, but as expected these failed to show similar effects. They are therefore not reported here.

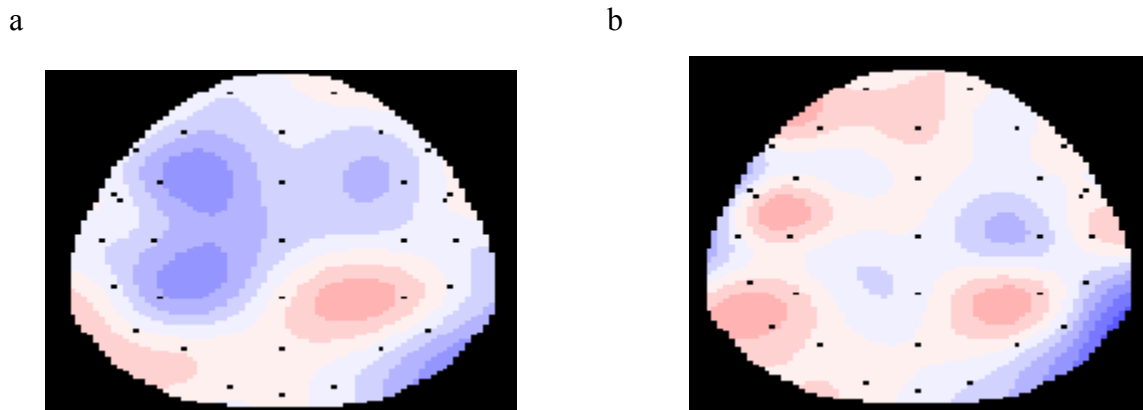


Figure 4.5. Topographic maps of ERS (blue) and ERD (red) pattern of grand average difference waveforms at 200 ms of instructional cue onset. Panel a) II minus CI face target cue, b) II minus CI face distracter cue. Colour key Figure 2.1b (p. 43).

Visual examination of the two main conditions (II – CI face target cue and II – CI face distracter cue) at the onset of the instructional cue was analysed for ERD and ERS patterns at T6, T5 and P_{PZ, P4} electrodes which are known to border face processing pathways and regions (Gazzaley et al, 2005), as in Paper 1 (p. 54). Results of the topographic maps for face target cue revealed ERS at T6 electrode; ERD was observed at P_{PZ, P4}; electrode T5 appeared to be lodged in between ERS and ERD. For the face distracter cue, ERS was observed at T6; P4 lodged between ERD and ERS; ERD at T5 electrode was observed.

4.4.3 Main ERD and ERS Results

Area reports were calculated for high evoked alpha for *face target cue* and *face distracter* (name target) *cue* for CI (high conflict/low control) and II (high conflict/high control) at 0 – 250 ms (encompassing face processing related N170) post-stimulus interval. Electrodes

P (again comprised of summed PZ and P4 channels), T6 and T5 were the focus of the main analyses, as in Paper 1 (p. 54).

The post instructional cue period for target (face target versus face distracter) and control (II versus CI) trials were analysed separately for P_{PZ, P4}, T6 and T5 channels with 2 x 2 repeated measures ANOVAs and planned comparison t-tests. Main effects will not be reported, since the primary interest was in the interactions. All ANOVA results are reported with Greenhouse-Geisser adjustment.

Post instructional cue period ERD/S effects were assessed at P_{PZ, P4} region at 0 – 250 ms (Figure 4.6a). When face served as a target cue, control effects were evident in non significantly reduced inhibitory (ERS) activity, hence relative facilitatory effects in expected high control II (M = -47.49) compared with low control CI (M = -51.34) trials, $t_{29} = .19$, $p > .05$ as indicated by the drop in the mean negative value in II compared with CI trials. When face served as a distracter (name target) cue, control effects were evident in non significant larger negative values (ERS) in expected high control II (M = -58.20) compared with low control CI (M = -55.73) trials, $t_{29} = .13$, $p > .05$. The target x control interaction was not significant, $F_{1, 29} = .05$, $p > .05$, $\eta^2 = .002$.

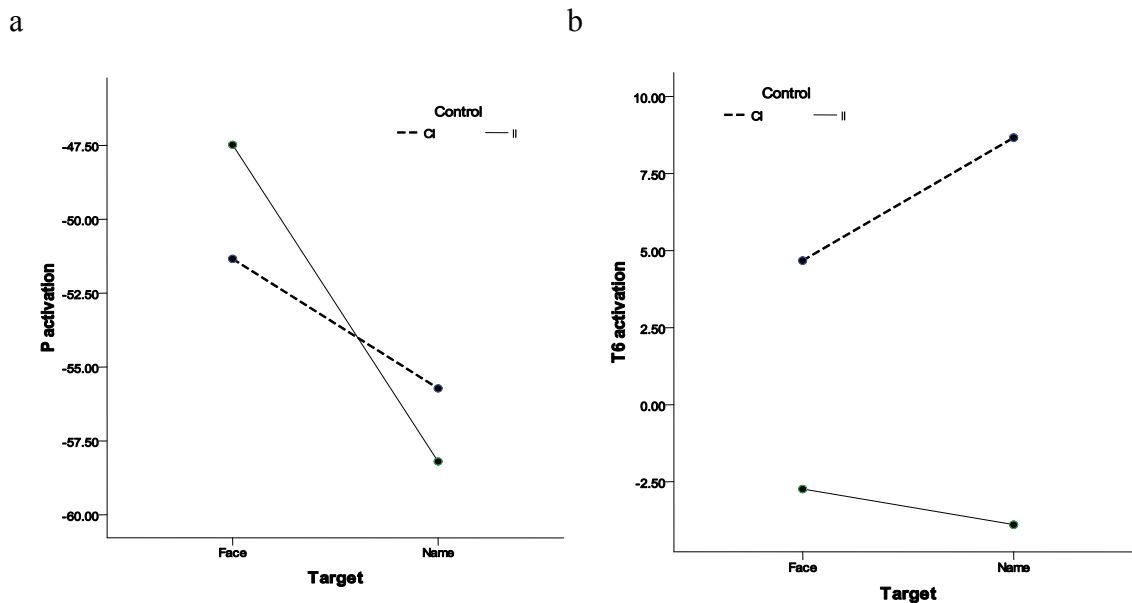


Figure 4.6. Control effects in high II and low CI control trials at 0 – 250 ms post-instructional interval for face target cue and face distracter cue. Panel a) P_{PZ, P4}, b) T6 channel.

Post instructional cue ERD/S control effects were assessed at T6 channel at 0 – 250 ms post-cue interval (Figure 4.6b). When face served as a target cue, control effects were evident in non significant increase in negative value (ERS) in expected high control II ($M = -2.74$) compared with low control CI ($M = 4.68$) trials, $t_{29} = 1.07$, $p > .05$ as indicated by an increase in negative mean value in high compared with low control trials. When face served as a distracter (name target) cue, control effects were evident in negative values (ERS) in expected high control II ($M = -3.89$) compared with low control ($M = 8.67$) trials even though this difference failed to reach significance, $t_{29} = 1.38$, $p > .05$. The target x control interaction was not significant, $F_{1, 29} = .17$, $p > .05$, $\eta^2 = .006$.

Post instructional cue ERD/S control effects were assessed at T5 channel at 0 – 250 ms post-cue interval (Figure 4.7). When face served as a target cue, control effects were evident in non significantly larger negative values (ERS) in expected high control II ($M = -1.96$) compared with low control CI ($M = -.98$) trials, $t_{29} = .12$, $p > .05$. When face served as a distracter (name target) cue, there was evidence of enhanced absolute facilitation (ERD) effects in high control II ($M = 6.22$) compared with low control CI ($M = -14.52$) trials, $t_{29} = 2.18$, $p = .04$. The control x target interaction was marginally significant, $F_{1, 29} = 3.18$, $p = .09$, $\eta^2 = .10$.

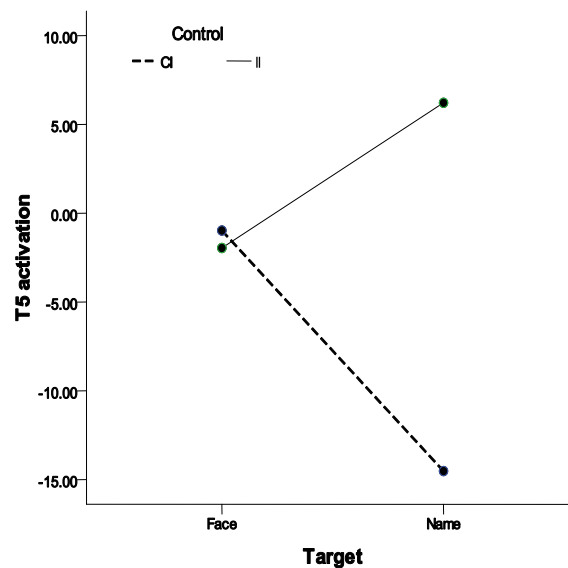


Figure 4.7. Control effects for high II and low CI control trials at 0 – 250 ms post-instructional interval for face target cue and face distracter (name target) cue at channel T5.

4.4.4. Results Summary

Behavioural data revealed a particularly robust classic Stroop interference effect for both face target cue and face distracter (name target) cue. For face target cues, RT in congruent trials were 174 ms shorter than incongruent. The Gratton or conflict adaptation effect was detected for the face target (RT in II < CI) cue, but it failed to reach significance level. There was no Gratton effect detected for the face distracter (RT in II \geq CI) cue.

Accuracy rates were not significantly different between high and low control trials for both face target and face distracter cues, but congruent trials had significantly higher accuracy rates than incongruent trials in both low and high control trials. Face distracter cue high control trials had more overall errors compared with low control trials.

In Papers 1 and 2 and the current Paper, RT for face targets and face distracters (name targets) were in the ranges of 592 – 607 ms and 692 – 748 ms, 600 – 625 ms and 675 – 725 ms, and 474 – 685 ms and 491 – 649 ms respectively. Accuracy rates in Papers 1 and 2 and the current Paper for face and name target cues were in the ranges of 90 – 94% and 60 – 75%, 71 – 78% and 52 – 67%, and 54 – 67% and 51 – 70% respectively. Hence, overall accuracy rates were markedly lower in the current study compared with Paper 1 and more in line with Paper 2. In all three Papers face distracters had lower accuracy rates compared with face targets, suggesting that faces are powerful targets and hence powerful distracters. Error rates in Papers 2 and 3 for face targets and face distracters were in the ranges of 5 – 8 and 9 – 11, and 7 – 13 and 9 – 11 respectively. Hence, at least for face target cues, the current study had higher error rates. Time-outs rather than actual mistakes again accounted for a significantly larger percentage of total errors for both face target cue and face distracter cue in all trial types.

Area reports revealed that when face served as a target cue, relative facilitatory (drop in mean negative value) effects were observed in high compared with low control trials at P_{PZ, P4} region. When face served as a distracter cue, a non significant increase in inhibitory activity was detected at P_{PZ, P4} in high compared with low control trials.

When faces served as a target cue, a non significant increase in inhibitory activity was observed for face targets at T6 in high compared with low control trials. When face

served as a distracter cue, a non significant increase in inhibitory activity was observed in high control compared with low control trials at channel T6.

When face served as a target cue, a non significant increase in inhibitory activity was detected at channel T5 in high compared with low control trials. When face served as a distracter cue there was significant increase in facilitatory activity (ERD) at channel T5 in high compared with low control trials.

4.5 Discussion

The current study aimed to separate perceptual stimulus processing conflict from response conflict by using a paradigm where cues *followed* stimuli. This design also removed all preparatory pre-response effects, since participants viewed the stimuli not knowing whether subsequent instructional cues would designate face as the target or as the distracter (name target). This design was aimed at disentangling initial perceptual processing conflict from response conflict and measuring post perceptual facilitatory and inhibitory control activity. It has been suggested that inhibitory activity is more important in resolving conflict at the response generating rather than the perceptual stimulus processing stage (Nieuwenhuis & Yeung, 2005). Evoked upper alpha ERD and ERS effects at post-instructional cue and post-stimulus time interval were again measured in the same regions as in Papers 1 and 2.

The current experiment demonstrated a particularly robust classic Stroop interference effect for both face targets and face distracters. In fact it may be one of the first experiments to obtain mean congruent RT which was more than 170 ms shorter than incongruent RT for face target cue. In the blocked design of Paper 1, the largest, less than 50 ms, difference between congruent and incongruent RT was detected for face distracter which was in line with the literature where the facilitation effect is assumed to be in the range of 20 – 50 ms (MacLeod, 1991; Cohen et al, 1990) and is thought to reflect the ceiling effect of speeding up already fast response in congruent trials. Furthermore, the robustness of the Stroop effect was a very surprising finding considering that the current experiment was also an event related design as in Paper 2, where the classic Stroop interference effect was not even behaviourally detected for face target RT.

There are a few of possibilities to account for such a robust facilitatory effect. Firstly, all higher order preparatory effects were removed in the current study. Participants viewed the stimulus not knowing whether subsequent responses would be required to face targets or face distracters (name targets), so relevant cortical regions could not be engaged nor stimulus task set could be prepared by top down control. Once the cue was presented, it was assumed that it was mostly, but not solely, bottom up processes responsible for information processing. It is probable that in certain contexts facilitatory effects stem mostly not from top down, but from more basic bottom up effects which are outside participants' control (Jentzsch & Leuthold, 2005) and evidence from the current Stroop data appeared to support this claim. Another possibility was that facilitatory effects stem from the absence of lingering interference generated by top down pre-stimulus preparatory effects such as well established task sets.

Secondly, the current experiment aimed at separating perceptual conflict from response related conflict. Once the cue was presented in the current experiment it was assumed that control elicited was mainly directed at resolving response conflict. Hence it was possible that it was a collective influence of perceptual and response related conflict in more traditional Stroop designs which may generate a ceiling effect for the observed facilitatory effect which is asymmetrical compared with interference (50 versus 100 ms) (MacLeod, 1991). Delaying possible response conflicts appears to have lifted ceiling effects for facilitation on congruent trials particularly for face targets.

A weak, non-significant Gratton effect was obtained for face target cue, but not for face distracter cue. The Gratton effect was only present for face targets in Paper 1 and the current experiment, although it failed to reach significance level in the latter. The Gratton effect was absent for both face targets and face distracters in Paper 2. Again this is puzzling considering that Paper 1 had blocked design while both Paper 2 and the current experiment had event related designs. RT for face targets tended to have lower ranges in all trial types (CC, CI, IC, II) compared with face distracters, with RT faster to faces in both Paper 1 and 2, but RT ranges between face target and distracter cues were very similar in the current experiment.

Current Paper exhibited low accuracy/high error/time out rates, for some conditions accuracy rates were ~50%. If error responses are mostly incorrect responses this

represents task performance at chance or effectively a random guessing level. However, there is little reason to interpret participants' performance in this way. Error responses were instead found to correspond largely to high time out rather than incorrect responses, for example see total error analyses results (p. 119). This suggests that the task was very difficult and this difficulty resulted in a slowing of responses – more conservative response criteria – itself an effect of cognitive control rather than random guessing. Response slowing rather than the Gratton effect may have been the most appropriate index of cognitive control in the context of event related/task switching design.

Accuracy rates were highest for both face targets and distracters in the blocked design experiment of Paper 1 and lower and comparable between the event related design of the current experiment and that of Paper 2. Time-outs rather than actual mistakes were responsible for the largest part of total errors in all Papers. Successful performance in task switching is thought to rely on successful engagement of task related cortical regions (Braver et al, 2003), hence it was possible that in the current experiment conflict modulating regions were not engaged through top down signals to a sufficient degree and, hence, the absence of a Gratton or conflict adaptation effect for face distracters and only a weak, non significant effect for face targets. Another possibility is that the Gratton effect findings in the current experiment may be partly explained by memory factors, as participants had to respond to the stimulus from memory since the actual stimulus was not on the screen when the cue, indicating the required response was presented.

Behavioural findings, except for accuracy rates, in current event related design study generally were more consistent with findings in the blocked task in Paper 1 than the event related task in Paper 2. Similarity between behavioural findings in the current event related experiment and the blocked experiment in Paper 1 may be explained by lower demand for and/or particular loop of top down control, preparatory effects such as goal selection, task set reconfiguration in the post-cue and pre-stimulus interval. In the blocked design experiment in Paper 1, participants knew whether the upcoming target would be face or name; target related task sets did not have to be regularly reconfigured and, hence, there was lower need for top down control effects. In the event related design in Paper 2 participants regularly had to reconfigure target related task sets since targets alternated continuously and unpredictably. This required constant and high involvement

of top down control effects such as selecting goals and evoking preparatory processes – a series of actions presumably triggered by the cue immediately preceding the stimulus. Successful preparatory effects initiated by top down control such as reconfiguration of task sets may subsequently be difficult to eliminate, producing lingering interference. In the current experiment, control effects involved in pre-stimulus preparatory processes were reduced to a minimum since participants viewed the stimulus not knowing whether subsequent responses would be required to face targets or face distracters (name targets). The only preparation participants could do was to maintain general task relevant alertness. Reduced involvement of specific types of top down effects such as not being required to select task goal, reconfiguring, preparing task sets before the actual stimulus in the current event related design may have made it more similar to the blocked design task in Paper 1 than the event related design task in Paper 2.

Deliberate, top down preparation cannot on its own fully prepare for the task. It can improve performance but its effects are not absolute. This is supported by the fact that top down preparation does not eliminate switch cost and thus bottom up processes are just as vital for task performance when the appearance of the actual stimulus triggers perceptual and response selection processes in working memory (Brown et al, 2007). Performance depends on both bottom up and top down processes where top down prepare task set while bottom up actually implement them, and once the stimulus is presented, bottom up processes may be more dominant. Hence, top down processes may prepare more basic mechanisms such as relevant perceptual, sensory bottom up circuits (Ruthruff et al, 2001), but once the actual stimulus appears bottom up processes may be mostly in charge. The ratio between top down and bottom up processes may have been different in the current task with performance mainly depending on bottom up and memory processes with top down effects providing somewhat less significant input.

Noticeably, the current study had quite low accuracy rates, in some cases just about 50% due to time outs rather than actual mistakes. It is likely that such low accuracy rates were related to difficulty in responding from memory since actual stimuli were not on the screen when participants responded. It was also of interest that faces and names had similar accuracy rates suggesting that (in the current design) face stimuli had no particular advantage over names.

Area report analyses revealed slight relative facilitatory effects for face target cue and inhibitory activity for face distracter cue in high compared with low control trials at the composite P_{PZ, P4} channel. Inhibitory activity was observed for both face target cue and face distracter cue in high compared with low control trials at T6. Inhibitory activity was detected for face target cue and significant facilitatory activity for face distracter cue in high compared with low control trials at channel T5. There were no immediately obvious, systematic evoked upper alpha ERD and ERS patterns for face target cue and face distracter cue observed in the current event related task which aimed to separate perceptual from response related conflict and ensuing top down control effects.

Inverse evoked upper alpha ERD and ERS patterns in the blocked design task in Paper 1 indicated that in milliseconds the brain appeared to systematically switch on, engage presumably task related regions and processes and switch off, disengage presumably task unrelated selective regions depending on whether the face attribute was the target or the distracter. This was interpreted as being aimed at effectively processing relevant information while limiting the prescription of cognitive resources to irrelevant information. In the current experiment for face target cue both Stroop and Gratton effects were evident, but no systematic evoked upper alpha ERD and ERS patterns were observed. For face distracters, the Stroop effect was and the Gratton effect was not and again no systematic evoked upper alpha ERD and ERS patterns were present. Poor performance, for example, poor accuracy rates, and absence of systematic evoked upper alpha ERD and ERS patterns depending on whether face was target or distracter in the current event related experiment can be interpreted as an indication that control was less successfully implemented here and in Paper 2, compared with Paper 1 which, in turn, gave the clearest results. This suggests that perhaps blocked designs are more suitable for cognitive control research, for example for investigating *specific* control category - operating to regulate control *within a task set* - rather than *between task sets* as would be required in task switching or event related designs.

The current evoked upper alpha ERD and ERS experiment aimed at separating perceptual from response conflict to investigate post instructional cue interval and the ensuing control effects using a new paradigm where cues followed, rather than preceded, stimuli in an event related paradigm. Since stimulus was not on the screen when

participants made their responses, it was assumed that the current task disentangled perceptual conflict from response conflict and ensuing post-perceptual conflict effects manifesting at the instructional cue time interval. However, current results provided limited insight in this regard because no obvious systematic patterns were present. One possibility is that systematic evoked upper alpha ERD and ERS patterns observed in the Paper 1 blocked task are dependent on blocked design with its relative simplicity and assumed ability to engage a certain control type, which manifested in systematic, inverse patterns depending on whether face attribute was the target or distracter. These control effects can be assumed to be relatively simple considering the simplicity and predictability of the blocked design task. The current event related design, because of its complexity and processing demands, failed to demonstrate systematic, obvious patterns. This again can be interpreted as evidence supporting the claim that cognitive control is heterogeneous, and arguably hierarchically organised considering that task representations themselves are believed to be hierarchical (Sakai, 2008) and highly sensitive to experimental demands; for example, different control categories would be expected to manage interference from distracters versus unexpected changes (Brown et al, 2007).

Despite the absence of obvious systematic patterns in evoked upper alpha ERD and ERS in the current experiment, the role of the nature of conflict and ensuing control effects require further studies using EEG. Using a similar event related design to Paper 2, MacDonald and colleagues (2000) temporally separated instruction processes from those involved in response selection. They found that the left DLPFC may be selectively engaged during the preparatory period by representing and maintaining task demands, while the ACC may be selectively engaged during response selection more so for incongruent than congruent, hence monitoring for processing conflicts (MacDonald et al, 2000). Nelson and colleagues (2003) used fMRI and a verbal working memory task to examine brain activity related to different types of conflict. Results indicated double dissociation with stimulus related conflict resulting in left PFC activation, but not ACC, and a reverse pattern for response related conflict. This was interpreted as pointing to differing contributions to cognitive control of specific cortical regions depending on the

source of conflict. There is no reason to assume that such differences would not be reflected in EEG measures.

Cognitive control cannot be assumed to be a uniform entity as evident in the current experiment's complex results. Simple blocked designs with relatively simple demands and hence distinct conflict sources may be more successful in eliciting and determining certain, for example, more basic, simpler control loops, for example *within a task set* rather than between task sets as would be required in task switching or event related designs. Complex event related tasks with complex processing demands and distinctive conflict characteristics may elicit and manifest in more complex, advanced control effects. Interaction between distinct conflict and ensuing control systems and mechanisms has already been demonstrated by fMRI studies (van Veen & Carter, 2005; Nelson et al, 2003). Further EEG research is needed.

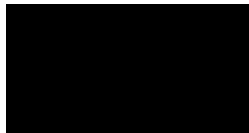
STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Figures	114, 115, 116, 118
	120, 121, 122
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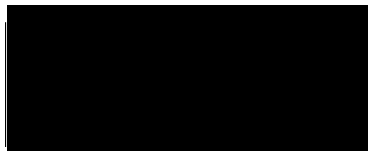
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



Candidate

April 2010



Principal Supervisor

April 2010

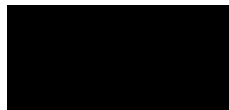
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	Author's Name (please print clearly)	% of contribution
Candidate	Daiva Newby	75
Other Authors	Graham Jamieson	25

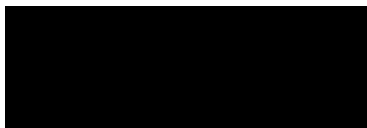
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



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April 2010



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April 2010

Paper 4: Evoked Upper Alpha ERD and ERS as Measures of Facilitation and Inhibition: Evidence from Face/Name Stroop Go/No-Go and Oddball Tasks

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5.1 Abstract

This study was aimed at cross validating evoked upper alpha ERD and ERS as measures of facilitation and inhibition respectively using face/name Stroop go/no-go and oddball tasks by comparing infrequent no-go trials in the go/no-go task requiring inhibition of responses with respond trials in the oddball task which require generation of behavioural responses. Inhibition (ERS) was expected for no-go trials for both face targets and face distracters (name targets). Facilitation (ERD) was expected for oddball respond trials for both face targets and face distracters. Behavioural data for the majority go trials in the go/no-go task in Block 1 did not reveal the Stroop interference effect for face targets. Congruent trials had longer RT than incongruent, but it was detected for faces distracters (name targets), therefore replicating the Paper 2 pattern. A non significant Gratton or conflict adaptation effect was detected for both face targets and face distracters. Evoked upper alpha ERD and ERS patterns representing facilitation and inhibition of activity respectively were compared between respond and no/go trials for face targets and face distracters (name targets). Topographic maps of evoked upper alpha revealed ERS (inhibition) at T6, T5 and PZ channels and ERD (facilitation) at P4 for face targets, and ERS (inhibition) at T6, T5 and PZ for face distracters. Non significant relative ERD (facilitation) at P_{PZ, P4} channel was detected in respond trials compared with no-go trials for both face targets and face distracters. Non significant relative ERD (facilitation) was detected at T6 channel in respond trials compared with no-go trials for both face targets and face distracters. Enhanced absolute ERD (facilitation) at pre-stimulus interval was detected at T5 channel in respond compared with no-go trials for face targets and non significant relative facilitation for face distracters. Non significant enhanced inhibition at channel T5 at post-stimulus interval was detected for face targets and a non significant enhanced facilitation effect for face distracters in respond compared with no-go trials. No-go trials demonstrated higher evoked upper alpha ERS means compared with respond trials as would be expected of a valid measure of inhibition. Respond compared with no-go trials demonstrated mostly decreased evoked upper alpha ERS values interpreted as a relative ERD effect rather than expected positive, absolute ERD. Evoked upper alpha ERD and ERS appear to be valid measures of facilitation and inhibition.

Exploratory sLORETA results indicated that for face targets, the bilateral superior frontal gyrus containing the PMA and SMA was the most probable source of inhibitory effects, while the ACC was the most probable source of facilitatory effects. For face distracters (name targets), the left superior temporal gyrus part of Wernicke's area was the most probable source of inhibitory effects, while the left postcentral gyrus, the region implicated in spoken language, was the most probable source of facilitatory effects.

Key words: conflict, cognitive control, Stroop, Gratton effect, facilitation, inhibition, blocked design, event related design, EEG, evoked upper alpha, ERD, ERS, go/no-go task, oddball task

5.2 Introduction

The central aim of the current project was to examine whether processing conflict (at least in the face/name Stroop task) is resolved through facilitation of correct information pathways, inhibition of irrelevant information pathways or both. To examine this, evoked upper alpha ERD and ERS as EEG measures of facilitation and inhibition respectively were used. Alpha ERD and ERS reflect engaged and disengaged thalamocortical information transfer respectively (Rippon, 2006; Pfurtscheller & Lopes da Silva, 2005; Penny et al, 2002) and manifest as percentage increase or decrease compared with the baseline in the alpha power band. The goal of the current experiment was to cross validate the functional interpretation of evoked upper alpha ERD and ERS measures by contrasting their topography in otherwise identical paradigms of behavioural responding and behavioural inhibition. For this purpose the face/name Stroop task was adapted to the classic go/no-go and oddball paradigms.

5.2.1 Go/No-Go and Oddball Tasks

Go/No-Go Task

In the stop signal paradigm, participants make responses to the majority (e.g., 80%, 90%) of standard stimuli and on irregular, infrequent (e.g., 20%, 10%) trials they are presented with a (usually auditory) signal which indicates that a response must be withheld. Thus, the stimulus which most frequently requires a response is, on infrequent trials, presented with a simultaneous or subsequent additional stimulus/signal that instructs that the usual response should be withheld. The go/no-go task is a variation of the stop signal paradigm. In a go/no-go task participants make responses to a majority of stimuli (standards), but withhold responses to infrequent targets. For example, standard stimuli may consist of squares (go) while circles may comprise withhold (no-go) targets. Thus in the go/no-go task participants are required to make responses on the majority of trials, but to behaviourally inhibit, withhold their highly primed responses when designated infrequent targets appear. The signal not to respond is presented externally (e.g., auditory signal) in the stop signal task, but it is contained within stimuli in the go/no-go task as certain stimuli are designated as no-go targets.

The stop signal task measures the ability to interrupt motor response after it has been initiated and, in go/no-go task, respond and stop signals are presented simultaneously. The same mechanisms are believed to initiate inhibition of responses in stop signal and go/no-go paradigms as in both cases stopping is an internally generated act of control changing the current course of action to meet a new goal and, hence, requires top down control to stop, that is, *to inhibit responding* on infrequent trials. The frontal cortex has been reported as the source of an early response time locked to the stop signal which precedes inhibition at the site of the motor cortex (van Boxtel et al, 2001).

Response inhibition requires suppression of action (including activation of previous goal representation) which is now contrary to updated goals. Experimentally, inhibition may be better observed in the go/no-go paradigm where a standard stimulus is consistently associated with releasing a response and the designated target stimulus with inhibiting it, whereas in the stop signal paradigm this association is inconsistent (Verbruggen & Logan, 2008) as stop signal can be associated with any stimuli.

Stopping is an important form of internally generated control as the organism decides not to act. Stopping is the first step in reorienting to new goals and is, hence, required for cognitive control networks to change the current course of action (e.g., responding) or thought in line with changing goals. Stopping provides a paradigmatic act of control even though successful stopping produces no overt behaviour. Stopping mechanisms can be slow, variable or fail to be triggered, thus diminishing the ability to inhibit responding. Stopping, which can be achieved in ~200 ms, is a prerequisite for control over thoughts and action (Logan, 1994). Stopping is not itself an observable effect, but can be estimated from observed behaviour if certain assumptions are met. Impaired stop task performance and/or inhibition of responding has been linked to such impulse disorders as ADHD, OCD, cocaine, and alcohol use among others (Barch et al, 2009; Verbruggen & Logan, 2008).

The role of response selection and task switch costs also appear to be very closely related as indicated by a recent study using the go/no-go paradigm (Schuch & Koch, 2003). In that study a no-go stimulus occurred unpredictably with stimulus onset so that all trials required task preparation, but only go trials required response preparation. Results indicated that switch costs were absent after no-go trials, as there was no

response selection since it required no application of the relevant task set. This suggested that response selection is critical for switch costs (Schuch & Koch, 2003) and of course length of RT. Thus, interference of cognitive sets on response times (switching costs) may be confined to response selection and may not occur with preparatory processes. In this case the cognitive control system is not limited with respect to early perceptual processing, but rather by the constraints which must be set on action selection to enable coordinated action (Schuch & Koch, 2003).

Oddball Task

In the oddball task, participants only respond to infrequent and irregular (e.g., 5%, 10%) target stimuli (i.e. oddballs) interspersed within a series of standard stimuli (e.g., 95%, 90%) to which participants are required not to respond. When targets appear participants are required to either make a behavioural response such as pressing a key or updating a mental task. Thus, the majority of trials in the oddball task require no response. Non-responding to repeated non-targets can, therefore, become automatic and this is not likely to require PFC. However, a response is required to infrequent targets, hence frequent non-responding must be inhibited and a new, apt response must be selected. Infrequent targets are associated with infrequent responses and require adjustment in behavioural strategy and, hence, top down control *to initiate responding* on infrequent trials. In the oddball task, participants must bias their strategy towards non-responding since it is the most frequently required response, but this frequency based strategy has to be inhibited on target trials in order to produce a correct response (Huettel & McCarthy, 2004). Varying the ratio between standard and target stimuli or target probability is known to produce varying (e.g., higher or lower) levels of interferences at both stimulus and response levels which therefore require varying levels of cognitive control to resolve (Casey et al, 2001).

The oddball or target detection task has been extensively used in animal and human research ranging from memory, attention to stimulus (novelty, habituation) processing in visual, acoustic and somatosensory modalities using a variety of methods from single neuron, intracranial recordings, imaging to neuropsychiatric research on disorders that affect the central nervous system (CNS) function such as schizophrenia, Alzheimer's and

Parkinson's diseases. Many different functional systems have been found to be simultaneously active in the areas of the frontal, temporal and parietal cortices during target detection (Mantini et al, 2009). This may be surprising considering the apparent simplicity of the task itself. However, it is believed to be related to the salience of infrequent targets which must be marked as task relevant by top down processes (Kiehl et al, 2005).

Functionally go/no-go and oddball tasks can be considered as reversed versions of each other since go/no-go tasks require responding to the majority of stimuli and withholding response to a minority of stimuli, while in the oddball task responses are withheld to the majority of stimuli and responses are generated only to a minority of stimuli. Minority stimuli on both tasks would be expected to generate conflict since they require change in response strategy from that used for the majority of stimuli and require conflict resolution. It is expected that facilitation, activation of correct responses is essential for successful cognitive control on minority response trials in the oddball task, while inhibition of incorrect responding is essential for successful cognitive control on minority no-go trials in the go/no-go task.

5.2.2 Cortical Regions and Effects Associated with Go/No-Go and Oddball Tasks

The go responding on the go/no-go task has been found to be associated with activation of the cortico-basal-ganglia-thalamocortical circuit, while stopping has been found to be associated with activation of the fronto-basal-ganglia circuit including the inferior frontal gyrus (IFG; especially right IFG), VLPFC, DLPFC, medial frontal gyrus (MFG), basal ganglia, and pre-SMA which may be involved in inhibition of hand movement (Verbruggen & Logan, 2008; Badre & Wagner, 2006). The ACC, which monitors performance, is also often activated on successful response inhibition trials (Verbruggen & Logan, 2008; Badre & Wagner, 2006). Recruitment of prefrontal regions to guide response inhibition appears to depend on the demands of the task: if manipulation of stimulus-response association in working memory is required the DLPFC may be recruited and if maintenance of stimulus-response association is required, the inferior frontal cortex (IFC) may be recruited (Mostofsky & Simmonds, 2008). The right inferior

frontal gyrus is thought to be critical for stopping while the SMA and pre-SMA are also important for response inhibition (Barch et al, 2009).

Go/no-go and stop signal tasks require speeded, rapid responses to go trials and inhibition on no-go or stop trials. Such response inhibition usually activates the right lateralised inferior frontal gyrus (IFG) and the importance of this region for response inhibition is provided from studies of people with lesions in the IFG. The right IFG may also be coactivated during response inhibition in task switching, interference suppression; hence, the right IFG may play a role in inhibiting response tendencies across a range of tasks (Aron et al, 2003).

The SMA has been implicated in response preparation, selection and execution. Single unit recordings at pre-SMA in the go/no-go task in monkeys have shown that the onset of neural discharge was earlier for the neurons preferentially active on no-go trials than those active on go trials (Sakai, 2008). Thus, findings from go/no-go tasks demonstrated that the pre-SMA contains neurons which respond to no-go, others to go stimulus and yet others to both (Mostofsky & Simmonds, 2008). No-go and dual type neurons became active before go neurons, suggesting that the pre-SMA first inhibited automatic response and then facilitated new, controlled response. Hence, neurons within the pre-SMA may inhibit prepotent response and then select new motor response. Commission errors have also been associated with lesions in the pre-SMA. The right IFC and right inferior parietal cortex may orient attention to the relevant stimulus and work together with the pre-SMA to guide response inhibition (Mostofsky & Simmonds, 2008). Hence, the pre-SMA may first use inhibition to control incorrect automatic responses.

In one study, authors (Rubia et al, 2001) tested (using 15 males only) different versions of go/no-go and stop tasks differing in probability of inhibitory signals and contrast conditions and common activation to all tasks was predominantly on the right ACC, SMA (initiation and suppression of voluntary movements) and inferior prefrontal and parietal cortices. Go/no-go requires response selection between executing or inhibiting motor response, and, hence has high demands on decision making, response selection and response inhibition; therefore, it has a higher load on response selection than a stop task which in turn has a higher load on withholding response. Two go/no-go tasks had predominantly left /bilateral regions including middle BA 9 and inferior frontal

gyri BA 44/45, left and right mesial frontal cortex including the ACC and pre-SMA (BA 8, 32, 6), left inferior parietal lobe (BA 40) among others activated, while for the stop signal task it was predominantly on the right and common regions included BA 6, 32, 40. In go/no-go, focus is on response selection hence mostly left pre-SMA, ACC, BA 40 activity rather than focus on inhibiting motor response as in the stop task (Rubia et al, 2001).

There is debate and uncertainty about the agent, the site and the target of inhibition. The agent refers to locus or source, site refers to process by which it is exerted and can be studied by inquiring the point of no return in a stop signal task aimed at controllability processes, and manifestation refers to location where reduction of response activity can be recorded and may not necessarily be associated with the site of inhibition (Band & van Boxtel, 1999). The SMA may be an agent of inhibition which in turn occurs after the response has been selected, at the response selection stage while the site of inhibition is not known, but it would be expected to be strategic and not necessarily hard wired (Burle et al, 2004). The PFC and basal ganglia are other candidate agents of response inhibition, while possible sites of inhibition may be the thalamus and motor cortex. Neural structures that support activation of response can provide a valuable framework for localising inhibition. Inhibition of response (no-go compared with go) has been associated with heart rate deceleration and, because deceleration of the heartbeat is controlled by midbrain centres, noncortical brain mechanisms may be related to response inhibition. The agent of inhibition may be in the PFC, possibly affecting the motor cortex through the modulation of the SMA (SMA times the onset of response execution) (Band & van Boxtel, 1999).

The majority of EEG studies of oddball task analyse particular ERP components (e.g., P3), but some rare studies have also applied alpha ERD and ERS measures. In one oddball task a warning signal preceded targets. Phasic alertness (6.4 - 8.4 Hz) was indicated by desynchronisation as response to a warning signal and target only. Intermediate band (8.4 - 10.4 Hz) (tonic response) reflecting expectancy ERD about ~1 s before a target or non target appeared since prestimulus period would not differ between targets and non targets. However, upper alpha ERD (10.4 - 12.4 Hz) appeared only after a target reflecting task performance, thus the post stimulus period may be different for

targets and non targets and may reflect target related processing. Thus, lower alpha reflected attentional demands such as alertness and expectancy while upper alpha task related effects (Klimesch et al, 1998). Consequently, upper alpha ERD is believed to be distinctively associated with task performance and task related processing networks.

The aim of the current experiment is to validate the patterns of evoked upper alpha ERD and ERS previously interpreted in the context of high and low control trials in the face/name Stroop paradigm as reflecting the engagement of top down facilitation and inhibition of task relevant and irrelevant processing respectively. This will be done by comparing ERD and ERS to the same face/name Stroop stimuli in both the go/no-go and oddball paradigms. In the former, infrequent trials require inhibiting of responses to these stimuli and, in the latter, initiating responses to these stimuli. Consequently, this allows a direct comparison of ERD and ERS to these stimuli when facilitatory and inhibitory control processes are known to be engaged. It is therefore expected that evoked upper alpha ERD will be evident in respond trials for face targets in face processing pathways and for name targets in name processing pathways in the oddball task. Evoked upper alpha ERS will be evident in no-go trials in the go/no-go task for face targets in face target processing pathways and for name targets in name processing pathways.

5.3 Method

5.3.1 Participants

The same participants who participated in the Paper 3 (Chapter 4) experiment also participated in the current experiment.

5.3.2 Data Acquisition

Data acquisition in the current experiment was identical to that in Paper 3 (Chapter 4).

5.3.3 Stimuli

Stimuli were created based on the same principles as in the previous three Papers except in the following. This time stimuli consisted of 10 black and white photographs of famous actors (Mel Gibson, Robert De Niro and Johnny Depp), musicians (Jimmy Barnes, Robbie Williams and Jon Bon Jovi) and a photo of one politician (Kevin Rudd)

and one sportsman (David Beckham). Practice consisted of a photo of a musician (Paul McCartney) and an actor (Eric Bana).

As in the previous three Papers, each photograph had a name written across it, this time in ivory letters. However, this time there were 56 stimuli in total with 2 (both incongruent) used in practice and 54 experimental stimuli: 12 congruent and 18 incongruent in relation to actors and musicians (total 30); 12 in relation to actors and musicians and a politician and another 12 in relation to actors and musicians and a sportsman (total 24).

Participants again had to respond to either face or name and to classify whether this person was “a musician” or “an actor”. A cue, comprised of a word “face” or “name” lasting 1 300 ms, as in Paper 2, preceded each stimulus (Figure 5.1). Participants responded when they were presented with a photograph which disappeared as soon as the response was made or when 1 000 ms terminated.

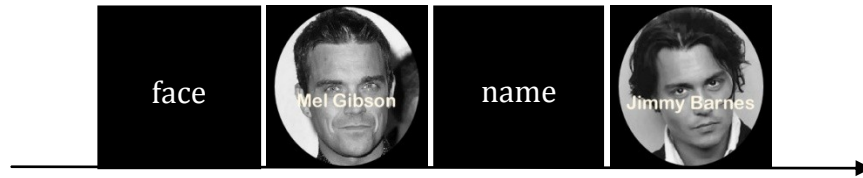


Figure 5.1. Participants had to respond to either face or name, as specified by a preceding cue and classify whether this person was “an actor” or “a musician”.

As in Papers 2 and 3, there were 64 fixed trial sequences created comprised of 16 trials in each of the four conditions in regard to the current trial and previous trial congruency (CC, IC, CI, II) (Figure 5.2). Again, there was an equal number of cue (“face”, “name”) and stimuli (“actor”, “musician”) trial sequences.

a

Fixed trial sequence 38 (II)



b

Fixed trial sequence 60 (CI)

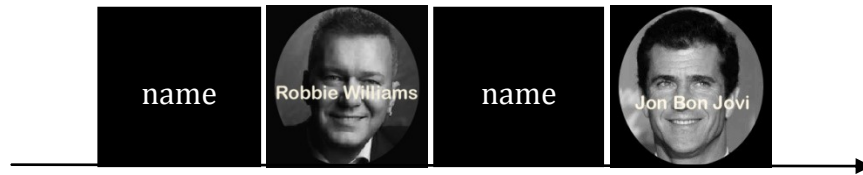


Figure 5.2. Examples of fixed trial sequences. Panel a) Trial sequence 38: II trial; b) Trial sequence 60: CI trial.

As in the previous three Papers, the classification of names and faces formed the basis of the current experiment. However, in the current experiment the paradigm was further divided into two blocks. Block 1 consisted of a go/no-go task and Block 2 of an oddball task. In the go/no-go task (Block 1) participants were required to classify faces/names of actors and musicians (go) on 85% of trials, but were required to withhold (no-go) their responses to face/name of a person who was not an actor or a musician (e.g., a politician or a sportsman) on 15% of trials (Table 5.1). In the oddball task (Block 2) participants were required to withhold their responses to faces/names of actors/musicians on 83% of trials and only make a response to face/name of a person who was not an actor or a musician (again either a politician or a sportsman) on 17% of trials. The identity of the person (i.e. politician or sportsman), presented on the minority of trials in both go/no-go and oddball tasks, was pseudo-randomly allocated across participants (Table 5.1).

Table 5.1

Block 1 (Go/No-Go Task) and Block 2 (Oddball Task).

		Half participants	Half participants
Block 1			
Go	(85%):	Actors and musicians	
No-go	(15%):	David Beckham	Kevin Rudd
Block 2			
Withhold	(83%):	Actors and musicians	
Respond	(17%):	Kevin Rudd	David Beckham

The order of Block 1 (go/no-go) followed by Block 2 (oddball) was fixed for all participants and never randomised. The oddball task required suppression of responses to actors/musicians while in the go/no-go task this classification formed 85% of the required responses. Hence, to have the oddball task preceding the go/no-go task was considered as potentially leading a mental set which may give rise to a global negative priming effect (i.e. current distracter turns into subsequent target) and was likely to produce confusion in an already complicated task.

Again, each participant was presented with 192 trials (64 x 3) of 384 (192 x 2) photographic stimuli in total. The go/no-go task consisted of 96 fixed trial sequences (192 pictures) in total with 68 go trials (136 pictures) and 28 (28/56 pictures) no-go trials which were always the second picture in a fixed sequence trial (Figure 5.3). No-go trials were distributed in pseudo-random order among go trials with a minimum of 1 and a maximum of 15 pictures separating go and no-go pictures.

The oddball task consisted of 96 fixed trial sequences (192 pictures) in total with 64 trials (128 pictures) requiring withholding a response and 32 trials (32/64 pictures) required generation of a response, which again was always for the second picture in a fixed sequence trial (Figure 5.3). Trials requiring generation of response were distributed in pseudo-random order among trials requiring withholding a response with a minimum of 1 and a maximum of 15 pictures separating them.



Figure 5.3. Fixed trial sequence where the second stimulus served as either no-go trial in the go/no-go task or requiring response generation in the oddball task.

Evidently, all pictures containing the face/name of a politician or a sportsman were incongruent (I). The go/no-go task contained 15 no-go trials to faces (11 following congruent and 4 following incongruent trials) and 13 to names (6 following congruent and 7 following incongruent). The oddball task contained 17 trials requiring response generation to names (6 following congruent and 11 following incongruent trials) and 15 to faces (7 following congruent and 8 following incongruent trials).

Fixed trial sequences were presented in pseudo-random order, although only the second stimulus in each fixed sequence was analysed as in Paper 2 (Chapter 3). Again, participants completed eye-correction task as in Paper 1 (Chapter 2).

5.3.4 Procedure

The procedure for the current experiment was identical to that in Paper 3 (Chapter 4) except for the following. Participants responded with left and right hand index finger button presses on the computer keyboard. Half of the participants responded with a right (m) button press for musicians and left (z) for actors and the other half responded with right (m) button press for actors and a left (z) for musicians. Response types (i.e. for actor or musician) were kept to ≤ 4 in a row. Half of the participants responded with left (z) and half responded with right (m) button press to stimuli (politician or sportsman) requiring response generation in the oddball task. The experiment lasted approximately 20 minutes with a fixed 2 minute rest time between Block 1 and 2. During the rest time the experimenter interacted with the participant with the main aim of assessing the participant's wellbeing.

Preparing participants for earlier experiments sometimes took ≥ 1 hour mainly when encountering problems with equipment or high impedances while each experiment lasted ≤ 20 minutes. This was assessed as an uneconomical use of participants and equipment.

Hence, data for Papers 3 and 4 were collected simultaneously. Half (16) of the participants completed the Paper 3 experiment first and the other half (15) completed the Paper 4 experiment first. Response buttons (e.g., left (z) for actors/actresses) were always kept the same between the two experiments for individual participants to maintain consistency and to reduce confusion in already demanding tasks.

There was a 5 - 15 minute (depending on participant's needs) break between Paper 3 and Paper 4 experiments during which time participants were encouraged to have refreshments (water, chocolates) and the experimenter maintained general conversation with participants as a fill-in activity. A more uniform, computer based fill-in activity was deliberately avoided so participants could rest their eyes and hands. Some participants were given the option of going for a short walk within the laboratory floor by temporarily disconnecting electrode cap from the EEG amplifier, but none took the offer.

5.3.5 EEG Analysis

Four corrupt recordings (57, 59, 69 and 77) were permanently discarded. Processing of EEG files in the current experiment was identical to that in Paper 1 (Chapter 2) except in the following. Epochs were created separately for face targets and face distracters (name targets) for no-go trials in the go/no-go task and for response generation trials in the oddball task. As in Paper 1, EEG recordings were ocular-artifact corrected and visually inspected. Epochs created for face and name targets in go/no-go and oddball tasks from unfiltered files were again compared to those created from filtered files and rejected accordingly. ERBP analyses were then performed. Source localisation analyses were performed for no-go and respond trials for face targets and face distracters' (name targets) ERPs at 170 ms post-stimulus as in Paper 1 (Chapter 2).

Note: ERBP analyses, area reports and ERP/sLORETA could not be performed for two participants' (73 and 80) EEG files, thus final EEG results are reported for 25 participants.

5.4 Results

5.4.1 Edinburgh Handedness Inventory Scores

Participants in the current experiment also participated in the Paper 3 (Chapter 4) experiment and their EHI scores can be reviewed on page 116.

5.4.2 Behavioural Stroop Effect and Gratton Effect and Preliminary EEG Results

Behavioural Stroop Effect and Gratton Effect Results

Note: Behavioural data were only analysed and reported for those 25 participants whose final EEG results were available. Additionally, there were missing RT data in some trials. Mean reaction times (ms) and accuracy rates (%) were calculated for all correct trials. For the go/no-go task in Block 1, accuracy rates for no-go trials for both face targets and face distracters (name targets) were >90%, but no-go trials for face targets demonstrated significantly higher accuracy rate compared with face distracters, $t_{24} = 3.09$, $p = .005$ (Table 5.2).

Stroop and Gratton effects were analysed for go trials in the go/no-go task in Block 1. Unexpectedly, the results for classic Stroop interference effect from incongruent distracters were mixed. Similar to the Stroop results from Paper 2, go face targets incongruent ($M = 689$ ms) trials were significantly shorter than congruent ($M = 723$ ms), $t_{17} = 2.21$, $p = .04$. In effect congruent trials for faces behaved as if they were somehow more difficult than incongruent trials. Again repeating the findings of Paper 2 for go face distracters, incongruent ($M = 744$ ms) trials were longer than congruent ($M = 737$ ms) even though this difference failed to reach significance, $t_{18} = .61$, $p > .05$. The Stroop interference effect was evident in RT behaviour only for go face distracters. This pattern replicates the unexpected behavioural findings obtained in Paper 2 (Chapter 3).

A weak Gratton or conflict adaptation effect was obtained for both go face targets and go face distracters in the go/no-go task in Block 1 (Table 5.2; Figure 5.4). For go face targets, RT were shorter to distracters in what are usually expected to be high compared with low control trials ($II < CI$) consistent with the Gratton effect even though this difference, as in Paper 3, was not significant, $t_{21} = .11$, $p > .05$ (Figure 5.4a). There was no significant interaction between previous x current trials, $F_{1, 17} = .95$, $p > .05$. A similar weak Gratton effect pattern was also obtained for go face distracters, as RT were shorter

to distracters in expected high compared with low control trials ($II < CI$) even this difference again failed to reach significance, $t_{18} = .49$, $p > .05$ (Figure 5.4b). Interaction between previous x current trials was not significant, $F_{1, 18} = .09$, $p > .05$, $\eta^2 = .005$.

Accuracy rates for go face targets in the go/no-go task in Block 1 indicated no significant differences between expected low and high control trials ($II \approx CI$), $t_{24} = 1.09$, $p > .05$ and there was no higher accuracy rate in expected low control congruent trials compared with incongruent ($CC \approx CI$), $t_{24} = .79$, $p > .05$ with the same pattern in expected high control congruent trials compared with incongruent ($IC \approx II$), $t_{24} = .07$, $p > .05$.

Accuracy rates for go face distracters in the go/no-go task in Block 1 reflected a similar pattern to that observed for go face targets. No significant differences in accuracy were found between expected low and high control trials ($II \approx CI$), $t_{24} = .78$, $p > .05$ and no higher accuracy rate in expected low control congruent trials compared with incongruent ($CC \approx CI$), $t_{24} = .46$, $p > .05$ with an identical pattern in expected high control congruent trials compared with incongruent ($IC \approx II$), $t_{24} = .79$, $p > .05$.

Overall, accuracy rates for go trials in the go/no-go task in Block 1 were $<50\%$ for both face targets and face distracters, hence a cautious approach was required to related interpretations.

Table 5.2

Reaction Times (ms) and Accuracy (%) for Face Targets and Face Distracters in Blocks 1 and 2.

	Face Target		Face Distracter	
Block 1				
Go	RT (SD)	Accuracy % (SD)	RT (SD)	Accuracy % (SD)
Congruent – congruent	747 (77)	39% (31)	733 (70)	45% (30)
Congruent – incongruent	712 (68)	44% (26)	745 (55)	43% (32)
Incongruent – congruent	721 (59)	47% (30)	743 (56)	42% (24)
Incongruent – incongruent	696 (66)	47% (27)	739 (68)	39% (31)
No-go		97% (4)		91% (9)
Block 2				
Withhold				
Congruent – congruent		100% (.0)		99% (2)
Congruent – incongruent		100% (.0)		99% (2)
Incongruent – congruent		100% (.0)		99% (2)
Incongruent – incongruent		100% (.0)		100% (.0)
Respond	557 (86)	94% (8)	618 (72)	88% (16)

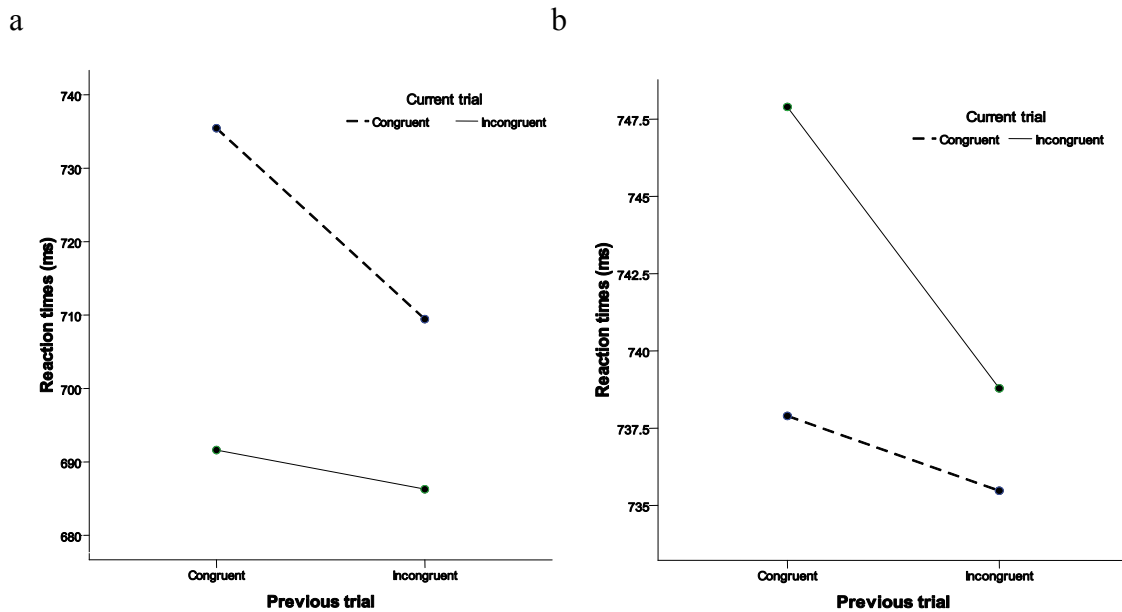


Figure 5.4. Mean group reaction times (ms) in CC, CI, IC and II trials for go trials in the go/no-go task in Block 1. Panel a) face targets, b) face distracters.

Time-outs accounted for a significantly larger percentage of the overall errors compared with actual mistakes in all trial types for both go face targets CC, $t_{24} = 5.03$, $p < .001$, CI, $t_{24} = 6.03$, $p < .001$, IC, $t_{24} = 11.05$, $p < .001$ and II, $t_{24} = 5.16$, $p < .001$ trials and go face distracters CC, $t_{24} = 8.59$, $p < .001$, CI, $t_{24} = 4.79$, $p < .001$, IC, $t_{24} = 10.71$, $p < .001$ and II, $t_{24} = 7.04$, $p < .001$ in go/no-go task in Block 1 (Table 5.3).

Table 5.3

Mean (SD) Number of Total Errors (Actual Mistakes and Time-Outs), Percentage (SD) of Actual Mistakes and Time-Outs Accounting for Total Errors in Go CC, CI, IC and II Trials for Face Targets and Face Distracters in Go/No-Go Task in Block 1.

Go	Face Target			Face Distracter		
	Total	Mistakes %	Time-outs %	Total	Mistakes %	Time-outs %
Congruent - Congruent	3 (2)	18% (30)	79% (34)	6 (4)	13% (22)	87% (22)
Congruent - Incongruent	5 (3)	22% (24)	79% (24)	4 (2)	19% (28)	74% (35)
Incongruent - Congruent	5 (3)	11% (18)	89% (18)	6 (3)	13% (18)	88% (18)
Incongruent - Incongruent	6 (3)	23% (27)	78% (27)	4 (2)	13% (24)	84% (30)

Withhold trials in the oddball task in Block 2 demonstrated near perfect accuracy of $\geq 99\%$ (Table 5.2) and respond trials $\geq 88\%$ providing confidence in the validity of respond trial results. Average RT in respond trials in the oddball task in Block 2 were significantly shorter to face targets compared with face distracters, $t_{24} = 6.88$, $p < .001$ and respond trials for face targets had higher accuracy rates compared with face distracters, $t_{24} = 2.05$, $p = .05$ indicating absence of speed accuracy trade off.

Preliminary EEG results

Grand average waveforms for ERBP in evoked upper alpha, for face targets and face distracters in no-go trials in the go/no-go task and respond trials in the oddball task were calculated. No-go minus respond trial ERBP grand average difference wave were calculated. Voltage distribution topographic maps for -300 to 600 ms at 24 ms interval for no-go – respond trials were created as a first exploratory tool (Figure 5.5).

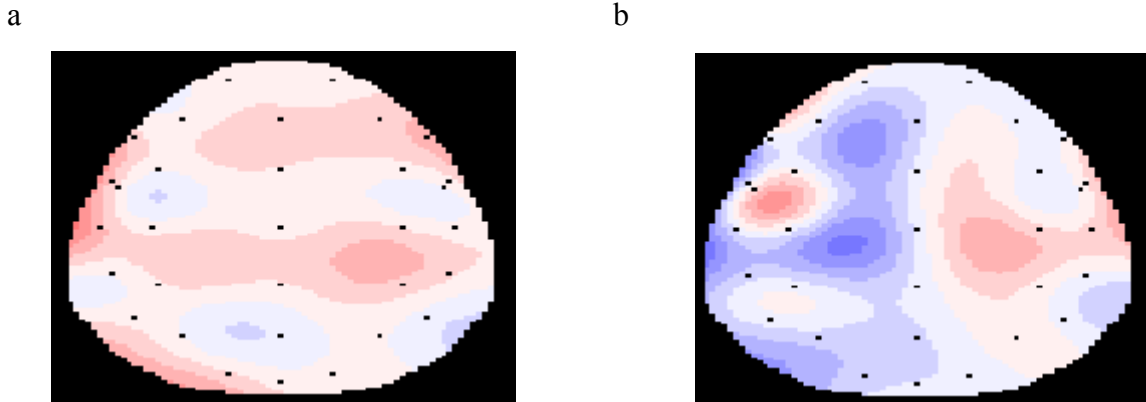


Figure 5.5. Topographic maps of ERS (blue) and ERD (red) pattern of grand average difference waveforms at 168 ms of stimulus onset. Panel a) no-go minus respond face targets, b) no-go minus respond face distracters. Colour key Figure 2.1b (p. 43).

Visual examination of the 2 main conditions (no-go minus oddball response face targets and no-go minus oddball response face distracters) at occipital bordering T5, T6 and P_{PZ, P4} electrodes was made as occipital electrodes are known to overly the face processing pathways and regions (Gazzaley et al, 2005), as in Paper 1 (p. 54). Topographic map displays for face targets revealed ERS near T6 electrode; ERD at T5 electrode. For face distracters, ERS was present near T6, at T5 and PZ electrodes. Electrodes T5, T6, P_{PZ, P4} again were chosen as the focus of the main analyses.

5.4.3 Main ERD and ERS Results

Area reports were calculated for evoked upper alpha for face target and face distracter stimuli in no-go trials in the go/no-go task and for respond trials in the oddball task for 0 – 250 ms (encompassing face processing related N170) post-stimulus interval. ERD/S effects in target (face target versus face distracter) and response (no-go versus respond) trials were analysed separately for P_{PZ, P4}, T6 and T5 channels, as in Paper 1 (p. 54), with 2 x 2 repeated measures ANOVAs and planned comparison t-tests. Main effects will not be reported since the primary interest was in the interactions. All ANOVA results are reported with Greenhouse-Geisser adjustment.

Evoked upper alpha ERD/S effects were assessed at P_{PZ, P4} region at 0 – 250 ms post-stimulus interval (Figure 5.6a). When face served as a target, enhanced, relative

facilitation (ERD) as indicated by lower mean negative value in respond ($M = -15.43$) compared with no-go ($M = -21.89$) trials was present even though this difference failed to reach significance, $t_{24} = .35$, $p > .05$. When face served as a distracter, enhanced, relative facilitation (ERD) as indicated by lower mean negative value in respond ($M = -25.03$) compared with no-go ($M = -30.01$) trials was present even though this difference again failed to reach significance, $t_{24} = .27$, $p > .05$. The target x response interaction was not significant, $F_{1, 24} = .01$, $p > .05$, $\eta^2 = .000$.

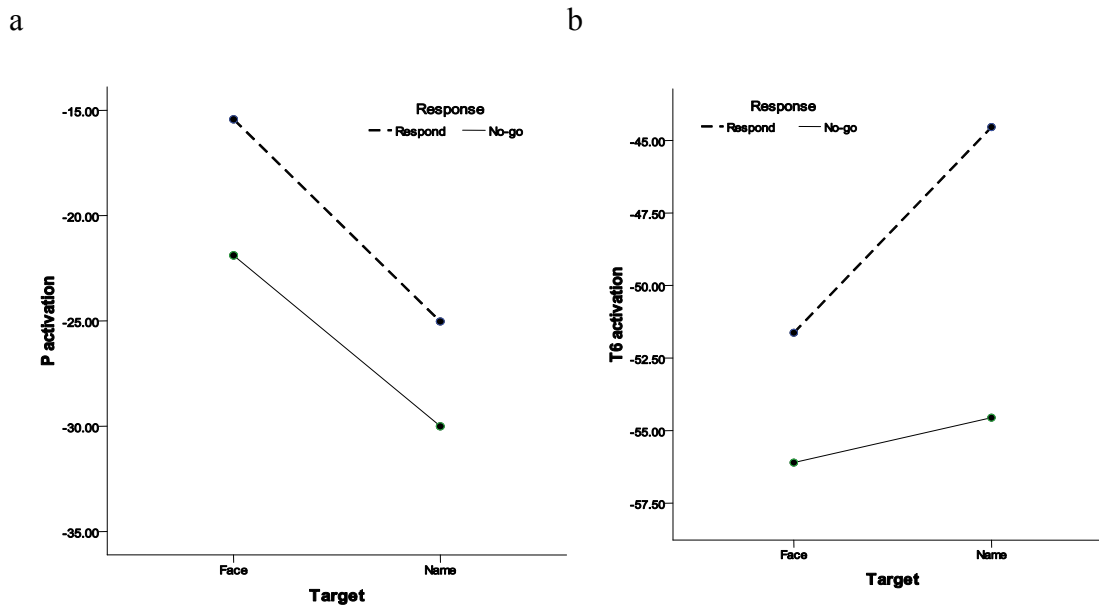


Figure 5.6. Evoked upper alpha in no-go and respond trials at 0 – 250 ms post-stimulus interval for face targets and face distracters. Panel a) at channel P_{PZ, P4}, b) at T6.

Evoked upper alpha ERD/S effects were assessed at channel T6 at 0 – 250 ms post-stimulus interval (Figure 5.6b). When face served as a target, non significant relative facilitation (ERD) effect, as indicated by lower mean negative value in respond ($M = -51.63$) compared with no-go ($M = -56.11$) trials, was present even though this difference again failed to reach significance $t_{24} = .52$, $p > .05$. When face served as a distracter, non significant relative facilitation (ERD), as indicated by lower mean negative value in respond ($M = -44.54$) compared with no-go ($M = -54.56$) trials, was present even though this difference yet again failed to reach significance, $t_{24} = .98$, $p > .05$. The target x response interaction was not significant, $F_{1, 24} = .13$, $p > .05$, $\eta^2 = .005$.

Evoked upper alpha ERD/S effects were assessed at channel T5, firstly at -500 – 0 ms pre-stimulus interval (Figure 5.7a). When face served as a target, enhanced absolute facilitation (ERD) in respond (M = 4.37) compared with no-go (M = -6.98) trials was present, $t_{24} = 2.07$, $p = .05$. When face served as a distracter, there was evidence of relative facilitation (ERD) effects as indicated by lower mean negative value in respond (M = -2.89) compared with no-go (M = -7.91) trials without reaching significance, $t_{24} = .52$, $p > .05$. The target x response interaction was not significant, $F_{1,24} = .32$, $p > .05$, $\eta^2 = .02$.

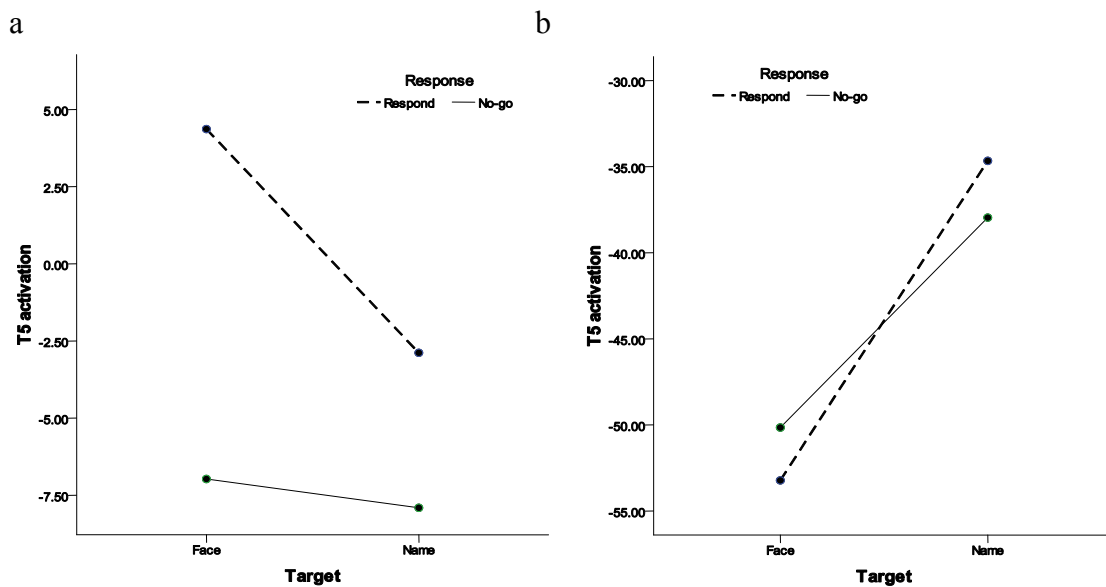


Figure 5.7. Evoked upper alpha in no-go and respond trials at channel T5 for face targets and face distracters (name targets). Panel a) at -500 – 0 ms pre-stimulus interval, b) at 0 – 250 ms post-stimulus interval.

Evoked upper alpha ERD/S effects were assessed at channel T5 at 0 – 250 ms post-stimulus interval (Figure 5.7b). When face served as a target, non significant inhibition (ERS) effect in respond (M = -53.22) compared with no-go (M = -50.16) trials was observed, but did not reach significance, $t_{24} = .31$, $p > .05$. When face served as a distracter, there was non significant enhanced facilitation (ERD) as indicated by lower negative values in respond (M = -34.67) compared with no-go (M = -37.96) trials without

reaching significance, $t_{24} = .26$, $p > .05$. The target x response interaction was not significant, $F_{1, 24} = .14$, $p > .05$, $\eta^2 = .01$.

5.4.4 sLORETA Results

sLORETA was performed on evoked upper alpha ERP at 170 ms post-stimulus, as in Paper 1, for no-go trials in the go/no-go task versus respond trials from the oddball task for face targets and face distracters (name targets) respectively (Figures 5.8). Blue denotes lower voxel values (estimated source activity) of evoked upper alpha in the first condition relative to the second and red an increase in these voxel values in the first condition relative to the second. Following the inhibition timing interpretation of evoked upper alpha (Klimesch et al, 2007a), voxels indicated in blue show a facilitation of activity in these voxels, while those in red show an inhibition of activity in these voxels.

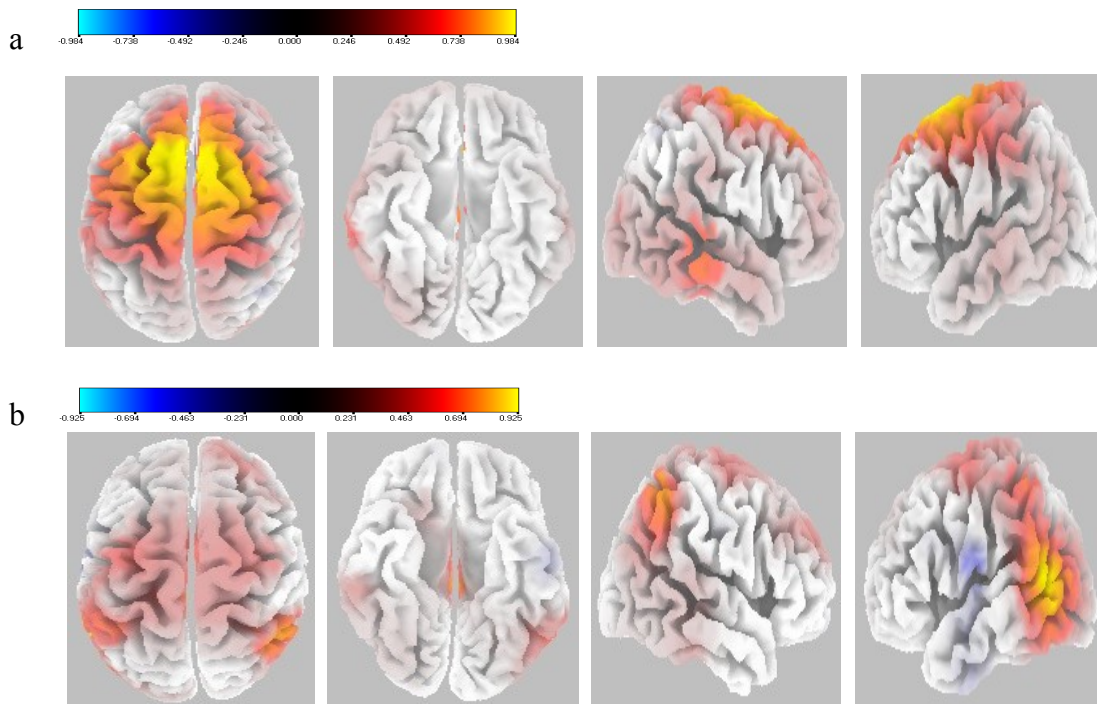


Figure 5.8. From left to right: top and bottom views, right and left hemispheres. Panel a) face targets, b) face distracters.

For face targets, sLORETA maximum solution values between no-go and respond trials were bilaterally in superior frontal gyrus (BA 6) indicating the source of inhibitory

activity and minimum solution value indicating the source of facilitatory activity in the anterior cingulate gyrus (BA 24) (Figure 5.9a).

For face distracters, sLORETA maximum solution value between no-go and respond trials were in the left superior temporal gyrus (BA 22 Wernicke's area) indicating source of the inhibitory activity and minimum solution value indicating source of facilitatory activity in the left postcentral gyrus (BA 43) (Figure 5.9b).

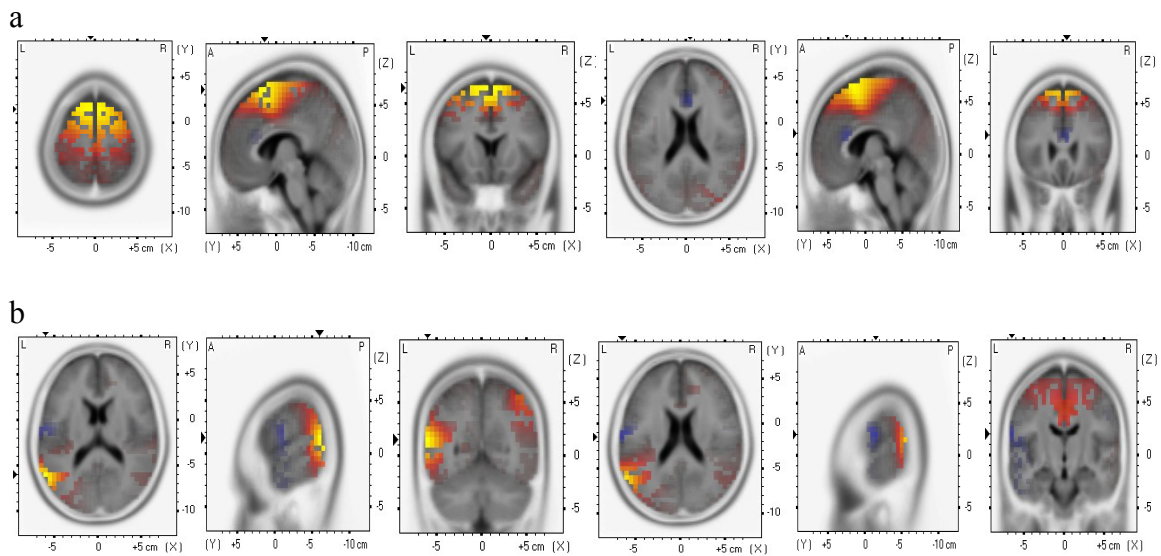


Figure 5.9. Panel a) face target: MNI xyz = -5, 15, 65 ($t = .99$, $p > .05$) maximum and MNI xyz = 5, 25, 20 ($t = -.54$, $p > .05$) minimum solution value. Panel b) face distracter MNI xyz = -60, -60, 15 ($t = .93$, $p > .05$) maximum and MNI xyz = -65, -15, 20 ($t = -.55$, $p > .05$) minimum solution value.

Probability values of voxels in these whole head sLORETA solutions did not reach significance. Considering that whole head analyses for over 6 239 voxels at 5 mm resolution was used, this was not surprising. However, these results have an important heuristic value. They represent an estimate of the most probable sources of the significant effects obtained in scalp EEG recordings. They also serve to define regions of interest (ROI) which may be specifically tested (with much higher power) in future studies.

5.4.5 Results Summary

Behavioural data for the majority of the go trials in go/no-go task in Block 1 revealed that the reverse of the classic Stroop interference effect was present for face targets; that is, congruent trials had longer RT than incongruent trials. However, the classic Stroop interference effect was present for face distracters (name targets). This pattern replicated the unexpected Stroop effect finding for the similar event related design employed in Paper 2. The classic Gratton or conflict adaptation effect pattern was present for both face targets and distracters (RT in II < CI), but it failed to reach statistical significance in either case. This was the first of the four experiments which found the classic Gratton effect RT pattern for both face targets and face distracters (name targets).

Accuracy rates were not significantly different between high and low control trials for either face target or face distracter (name target) and congruent trials did not have significantly higher accuracy rates than incongruent trials in either low or high control trials, unlike in previous experiments. Time-outs rather than actual mistakes again accounted for a significantly higher percentage of total errors for both face and name targets. This was consistent with findings in Papers 2 and 3.

In Papers 1, 2 and 3, RT for face and name targets were in the ranges of 592 – 607 ms and 692 – 748 ms, 600 – 625 ms and 675 – 725 ms, and 474 – 685 ms and 491 – 649 ms respectively. In the current experiment they were in the ranges of 696 – 747 ms and 733 – 745 ms respectively. Accuracy rates in Papers 1, 2 and 3 for face and name targets were in the ranges of 90 – 94% and 60 – 75%, 71 – 78% and 52 – 67%, and 54 – 67% and 51 – 70% respectively. In the current experiment they were in the ranges of 39 – 47% and 39 – 45% respectively. Hence, RT were longer and accuracy rates were markedly lower in the current study compared with all three previous experiments. Note also that in the first two experiments face distracters (name targets) had longer RT and lower accuracy rates compared with face targets. RT and accuracy rates were similar between face and name targets in the current experiment in line with findings in Paper 3.

Infrequent no-go trials in the go/no-go task in Block 1 had high accuracy rates which were higher for face targets than face distracters (name targets). However, this finding was problematic considering that the average accuracy rate for the majority of go

trials remained below 50% raising the question as to whether no-go trials were executed intentionally or instead resulted from a generally poor responding rate.

In the oddball task in Block 2 the majority of withhold trials had a near perfect accuracy. Respond trials also had high accuracy giving confidence to the validity of the respond trial findings. Respond trials for face targets had shorter RT and higher accuracy rates than for face distracters (name targets).

Preliminary topographic maps of evoked upper alpha ERD and ERS patterns at P_{PZ} , P_4 , T6 and T5 electrodes were assessed. ERS was observed at T6 and PZ channels and ERD at P4 and T5 for face targets, and ERS at T6, T5 and PZ channels for face distracters (name targets). Subsequent area reports revealed relative facilitation (ERD) (drop in mean negative values) at P_{PZ} , P_4 channel in respond trials compared with no-go trials for both face targets and face distracters (name targets) without reaching significance level. Enhanced, relative facilitation (ERD) (drop in mean negative values) was detected at T6 channel in respond trials compared with no-go trials for both face targets and distracters (name targets), but yet again not at a significant level.

Enhanced absolute facilitation (ERD) at -500 – 0 ms pre-stimulus interval was detected at T5 channel in respond compared with no-go for face targets and relative ERD (drop in mean negative value) for face distracters with the latter not reaching significance level. Non significant increase in inhibition (ERS) at channel T5 at 0 – 250 ms post-stimulus interval was detected for face targets and non significant relative facilitation (ERD) (drop in mean negative value) effect was detected for face distracters in respond compared with no-go trials.

As expected for a whole head analysis, voxel t values in sLORETA solutions were not significant. Instead analyses indicated the most probable sources of the effects examined. These results remain to be confirmed by replication on an independent data set using ROI derived from the present analysis. Exploratory results indicated that for face targets, the bilateral superior frontal gyrus containing the PMA and SMA (engaged in planning and preparing motor movements) was the most probable source of inhibitory effects, while the ACC was the most probable source of facilitatory effects. For face distracters (name targets), the left superior temporal gyrus part of Wernicke's area was

the probable source of inhibitory effects, while the left postcentral gyrus part of the spoken language network was the most probable source of facilitatory effects.

5.5 Discussion

The current study aimed to cross validate evoked upper alpha ERD and ERS reflecting the engagement, top down facilitation of task relevant processing and inhibition, disengagement of task irrelevant processing respectively, as valid EEG measures of facilitation and inhibition using go/no-go and oddball tasks. This was done by comparing evoked upper alpha ERD and ERS to the same face/name Stroop stimuli in both go/no-go and oddball paradigms. In the former, infrequent trials were assumed to require the inhibition of responses to these stimuli and in the latter the initiation of responses to these stimuli, thereby allowing a direct comparison of evoked upper alpha ERD and ERS to these stimuli when facilitatory and inhibitory control processes are known to be engaged. It was therefore expected that evoked upper alpha ERD would be evident in respond trials for face targets in face processing pathways and for name targets in name processing pathways in the oddball task. Evoked upper alpha ERS was expected to be evident in no-go trial tasks for face targets in face target processing pathways and for face distracter (name target) in face distracter (name target) processing pathways in the go/no-go trials.

Again, as in Paper 2 (Chapter 3) and contrary to expectations, behavioural results for face targets in the majority of go trials in the go/no-go task showed longer RT to congruent than incongruent trials and for face distracters (name targets), as expected, longer RT to incongruent than congruent trials. It was unclear why congruent trials for face targets again behaved as if they were incongruent and more difficult. Performance on neutral stimuli can be as good as and sometimes even better than to congruent stimuli, but incongruent trial RT shorter than congruent trial RT was not an anticipated finding. The presence of stimulus attributes value associated with the irrelevant task in any even congruent way may cause interference that opposes and even outweighs any benefit of the same response being activated by both attributes (Monsell et al, 2000).

One possibility as to why congruent RT were longer than incongruent RT in the context of an event related design (Paper 2 and 4), but not blocked design Paper 1, could be that the event related design necessarily incorporates task switching in which the

output of potentially conflicting processing pathways on the present trial would have been correct output for response selection on a recent, if not the immediately previous trial. In switching from selecting the output of one processing pathway on a previous trial to another on the present trial, it may be that the output of that pathway is actively suppressed (inhibited). Thus, when an inhibited output from a potentially misleading processing pathway matches output from the task selected processing pathway, it takes greater time for that response to reach the required activation threshold. However, this account does not explain why this effect occurs for faces, but not for names.

Alternatively, it may have been the case that increased RT for congruent trials represents the activity of some additional monitoring or checking process to ensure that the correct task has been implemented as part of an additional control loop present in the task switching context. In this higher order control loop, insufficient differentiation in the output of task relevant and potentially distracting processing pathways may signal the likelihood that insufficient control has been applied at the task selection level triggering an additional checking operation on the activation of required task representation. Again it is not clear why face targets would be especially responsive to such mechanisms.

Another possibility is that on incongruent face target trials participants were either able to filter out distracting incongruent (name) information or, on congruent trials, congruent distracters (names) failed to generate a facilitatory effect. Absence of a Stroop interference effect as in Paper 2 (Chapter 3) was replicated for face targets, hence suggesting that faces had weaker distracters (i.e. names). Thus, both the congruent and incongruent effect from names was limited explaining the unexpected shorter RT for incongruent compared with congruent trials. However, if this is the case, it is not clear why it did not occur in the blocked design of Paper 1. The task switching context in the current experiment and that in Paper 2, but not in the Paper 1 blocked design, may have been a decisive factor.

Furthermore, just as surprising was the finding that, unlike in Paper 2 (Chapter 3), the Gratton effect pattern emerged for both face targets and face distracters (name targets). This provides evidence that Stroop and Gratton effects operate independently. The Stroop interference effect results from conflict which emerges when incongruent distracters interfere with processing of the target and takes place on a single trial. The

Gratton effect, on the other hand, is related to conflict adaptation when the information processing system aims to regulate or adapt to this conflict with the aim of producing a correct response and is a relationship between two consecutive (previous and current) trials. Thus, logically, the Gratton effect (conflict adaptation) would be expected to presuppose the Stroop effect (response conflict).

Current Paper exhibited low accuracy/high error/time out rates, for some conditions accuracy rates were <50%. If error responses are mostly incorrect responses this represents task performance at chance or effectively a random guessing level. However, there is little reason to interpret participants' performance in this way. Error responses were instead found to correspond largely to high time out rather than incorrect responses, for example see total error analyses results (p. 150). This suggests that the task/s were very difficult and this difficulty resulted in a slowing of responses – more conservative response criteria – itself an effect of cognitive control rather than random guessing. Response slowing rather than the Gratton effect may have been the most appropriate index of cognitive control in the context of event related/task switching design.

The Stroop and Gratton effects discussed above, which were derived from the majority of go trials in Block 1, were of secondary importance to the current experiment and provided a context or vehicle to generate critical no-go trials in the go/no-go task in Block 1 and response trials in the oddball task in Block 2. The critical, infrequent no-go trials in the go/no-go task demonstrated high accuracy rates. However, under pressure of time, complex go/no-go task demands such as classifying actors and musicians while remembering not to respond to a sportsman/politician resulted in generally poor responding and accuracy rates in the majority of go trials and, hence, the validity of the high accuracy rate in the infrequent no-go trials was highly questionable. The implication of this is that EEG data obtained from critical no-go trials may have lacked fundamental electroencephalographic elements which were not isolated or restricted since the majority of behavioural go trials in a sense had the same non responding characteristic as the ones which were aimed to be selectively produced by the infrequent no-go trials. However, in the former case participants should have been (and probably were) trying to respond, but in the latter they were not: this is an important difference. Nonetheless, interpretative caution is necessary. Successful performance in task switching is thought to rely on

successful engagement of task related cortical regions (Braver et al, 2003) whereas complex and rapidly changing demands in the current task may have failed to engage to a sufficient degree task relevant cortical regions and EEG processes or perhaps ceiling effect may have been reached in performance manifesting in poor responding and accuracy rates.

Behavioural results obtained from the oddball task in Block 2 and consequently EEG results, on the other hand, provide confidence about the validity of information obtained from the infrequent respond trials since both the majority of withhold and infrequent respond trials demonstrate high accuracy. The potency of face stimuli is also evident in the finding that RT were shorter and accuracy rates were higher for face targets compared with name targets. There is also a possibility of perceptual difficulties in extracting name information in extremely limited time.

The go/no-go task in Block 1 was undoubtedly a much more difficult task than the oddball task in Block 2. In the former, participants kept track of four target related aspects (respond to actors and musicians, respond to either face or name, make a correct response using one of two alternatives, selectively not respond to politician/sportsman), while in the latter, tracking of only one target related aspect was required (selectively respond to politician/sportsman with only one possible response). Therefore, there was much more background related processing in the go/no-go compared with the oddball task and, hence, the two tasks in Block 1 and 2 were not matched on difficulty.

The current experiment was aimed at cross validating EEG measures of alpha ERD and ERS as valid measures of facilitatory and inhibitory effects (Klimesch et al, 2007a; Rippon, 2006; Pfurtscheller & Lopes da Silva, 2005; Penny et al, 2002). Evoked upper alpha ERS, as a valid measure of inhibition, was supported by the fact that all area report analyses of mean bandpower activation (increase indicates ERS, decrease indicates ERD) at chosen channels revealed negative mean values in no-go trials compared with respond trials. However, validation of evoked upper alpha ERD as a measure of facilitation was not so straightforward. Even respond trials, which were expected to rely on facilitatory effects, mostly demonstrated negative event related bandpower means and hence only relative ERD or a drop in mean negative value, rather than absolute ERD or a positive mean value. However, only respond trials, and not no-go trials, demonstrated absolute

ERD or a positive mean value at pre-stimulus interval for face targets at T5 even though the pre-stimulus interval generally would not be expected to differ between respond and no-go trials.

It is puzzling why no expected absolute ERD, positive evoked upper alpha mean value was observed for respond trials at post-stimulus interval. Choice of reference is one possible explanation. ERBP is calculated as a percentage change relative to some reference interval. Ideally the reference interval is free of the processes under consideration; however, in neuroscience research it is often difficult to achieve a neutral baseline, and thus ERBP is inherently a relational measure. Even so, it is necessary to consider relative as well as absolute difference in assessing ERBP predictions.

Nevertheless, the pattern (relative direction) of ERBP results between conditions was as expected even though the sign of values obtained was not always as expected. This was most likely due to use of the whole epoch, which included the entire pre- and post-stimulus event period, as the reference interval over which ERBP was calculated. Choice of a “neutral” pre-stimulus baseline, if such is available, may change the signs (negative or positive) of values obtained, but would not change the pattern of findings. The practical difficulty of such a procedure (versus the one adopted here) is that the pre-stimulus period is also one of active control and task related modulation of neural activity in preparation for stimulus processing and response selection. That is, in reality there is no clear period of “neutral” or “baseline” processing from which to provide an “absolute” 0 and “absolute” negative and positive values.

In light of the current experiment, predictions and interpretations must be modified. In appropriately designed functional contexts, relative evoked upper alpha ERD and ERS differences between conditions (rather than the absolute sign of ERBP values) can provide valid indicators of selective facilitation and inhibition of task relevant cortical processing. In this context it is well to remember that the EEG signal itself (measured in microvolts) is a measure of the relationship between two points: a recording electrode and a reference electrode. Changing the reference electrode would change all other recorded values (including potentially changes in the sign of the voltages recorded). However, provided all recording electrodes share the same reference, these changes will preserve the pattern of relationships between the recording electrodes and, thus, the

information in the recording. The pattern and relative direction of ERBP results for respond and no-go trials was in fact as expected, suggesting that evoked upper alpha ERD and ERS can validly index facilitatory and inhibitory cortical processes respectively.

In addition, it was also possible that there was an unequal functional allocation between facilitatory and inhibitory processes to manage complex task performance. Both infrequent respond trials in the oddball task and infrequent no-go trials in the go/no-go task had a common characteristic in that they required inhibition of a prepotent, the most frequent, response strategy whether by not responding in the oddball task or go in the go/no-go task. Participants were required to make a reversal or complete alteration in response strategy (Huettel & McCarthy, 2004; Verbruggen & Logan, 2008). There was an intriguing possibility as to why only evoked upper alpha ERS effects were detected for (as expected) no-go trials and (unexpectedly) for most of the respond trials when, ideally, absolute ERD effects were expected. It may be that inhibition played a primary role in managing this difficult task. One piece of evidence to support this claim comes from the preliminary actual cue analyses in Paper 2 (Chapter 3).

Basic analyses obtained from topographic maps of the actual cues in Paper 2 (Chapter 3) indicated that both “face” and “name” cues demonstrated three highly similar phases (Figure 3.6; Appendix A). Firstly, immediately after the cue presentation there was strong activation of the left dorsolateral prefrontal cortex; secondly, generalised activation (ERD); and, thirdly, immediately before the stimulus presentation, at the very end phase of the cue, there were very high levels of generalised and almost exclusive inhibition (ERS). In the current experiment, area report analyses for 0 – 250 ms post-stimulus interval (immediately following the cue itself) for both no-go and respond trials demonstrated effects similar to the third cue phase described above of high levels of evoked upper alpha ERS as if the brain generally was in a heightened inhibitory state. A heightened overall inhibitory state may enable the brain to reduce competition for resources as a preparation to processing an upcoming stimulus and responding to it.

This points to the possibility that inhibition was given a primary role in managing this complex task where multiple aspects of the alternating targets conflicted with each other both at processing and response levels. Some hypothesised suggestions can be

made as to why inhibition (ERS) rather than facilitation (ERD) may sometimes be used as the primary electrophysiological response to resolve or at least manage cognitive conflict. During complex information processing such as switching on the Stroop task, alternating targets with multiple response alternatives elicit (deliberately) a very high level of conflict by activating not only correct but also distracting information while requiring speedy and accurate responses. The brain may utilise general deactivation or dampening activity of potentially task irrelevant cortical regions to reduce competition as the most efficient way of quickly managing difficult tasks, such as the face/name Stroop task.

Target information (stimulus itself and correct response) may be chosen as a result of inhibiting all alternatives with facilitation selectively focused on targets. This seems to be counter-intuitive as during highly complex information processing more rather than less activation to accommodate higher information processing demands would be expected. However, the dynamic partnership between excitatory and inhibitory neurons allows dramatic changes in excitability in narrow time intervals. Inhibitory neurons assure that excitatory trajectories are effectively routed and competing cell assemblies segregated. Response to the same input can produce different responses depending on inhibitory activity (Buzsáki et al, 2007). Much of the incoming information is behaviourally irrelevant, if the nervous system could not control the flow of information, only a fraction of effort could be devoted to analysing crucial aspects of incoming information. Hence, top down, inhibitory control may allow highly select amplification of information (Treue, 2001). If indeed inhibition (evoked upper alpha ERS) were given the primary role in managing continuous conflict (e.g., inhibiting the prepotent, most frequent, highly primed responding on infrequent trials) in the current experiment, it would explain why absolute facilitatory effects (evoked upper alpha ERD) were infrequent.

All voxels in whole head sLORETA source solutions failed to reach significance. This was no doubt largely accounted for by the fact that >6 000 voxels at 5 mm for the whole head were used. Nonetheless, sLORETA is a robust and reliable neural source localisation technique (Sekihara et al, 2005; Lopes da Silva, 2005) meaning that if source/s can be located, sLORETA will quite accurately locate them. Hence, even though

sLORETA results failed to reach significance, these results are still likely to be highly accurate in suggesting the identity of the neural source/s generating the observed evoked upper alpha ERD and ERS effects. However, although the interpretations suggested the generator of the neural sources, this cannot be absolutely established by the current sLORETA results.

The bilateral superior frontal gyrus (BA 6) which contains the PMA and SMA responsible for movement initiation, was suggested as the generator of inhibitory effects, and the ACC (BA 24) as the source of facilitatory effects in no-go compared with respond to face targets. The left superior temporal gyrus (BA 22), which is part of Wernicke's area was suggested as the source of inhibitory effects, and the left postcentral gyrus of facilitatory effects to face distracters (name targets).

In Paper 1 (Chapter 2) the cingulate gyrus (BA 32) was suggested as one of the sources of inhibitory effects and the precentral gyrus (BA 6) as one of the sources of facilitatory effects in II compared with CI trials to face distracters. Hence, when inhibition was required to face targets in no-go trials in the go/no-go task (Paper 4) and response to face distracters (Paper 1: Chapter 2), the motor cortex (BA 6) generated inhibition effects to face targets and activation effects to face distracters respectively. The cingulate gyrus (BA 24, 32) likely generated facilitatory signals to face targets (Paper 4) and inhibitory signals to face distracters (Paper 1: Chapter 2).

This suggests an intriguing possibility that inhibiting responding to faces, which are assumed to be highly potent stimuli (and, in evolutionary terms, are assumed to be older than names), was managed primarily by the superior frontal gyrus containing the PMA and SMA. It would further suggest that inhibitory control was not directly applied to the FFA when response to faces had to be inhibited (replicating Paper 1 and Egner & Hirsch (2005) findings), as such an inhibitory function might have been temporally managed before face stimuli even reached the FFA; in fact they may not even reach the FFA if inhibition has been successfully applied. The motor cortex was assumed to play a critical role in this inhibitory process. If face processing is completed in stages with response to faces as the final stage of this chain, temporal processing of faces in no-go trials may be rapidly <250 milliseconds terminated (e.g., through ERS) by the motor cortex before the stimulus reaches the FFA and representations are loaded into the motor response system.

For face distracters (name targets), Wernicke's area in combination with the left postcentral gyrus, which takes part in motor and language processing, were suggested as possible sources of inhibitory and facilitatory effects respectively. What is unexpected is the fact that inhibition to face distracters (name targets) seemed to be processed differently to inhibition to face targets. Inhibition to face targets appeared not to involve the FFA, the specialist region for face processing. However, inhibition effects to face distracters (name targets) appeared to be generated by Wernicke's area, the specialist region for language. One possibility is that withholding responses, inhibition to names was triggered at a later processing stage compared to faces, sometime after the stimulus already reached language areas. Another possibility may be that extracting information from names was more perceptually difficult than from faces since they are more abstract and since participants had to read names to decide whether would require a response or no-go response. However, as mentioned above, these interpretations are hypothesised only and require future replication studies to establish it.

The go/no-go task results may have been impacted by known methodological complications of the go/no-go task, which broadly relate to design, elicited neural effects and data analysis. In one neuroimaging study, authors (Durstun et al, 2002) examined the effect of the preceding context by varying the number of go trials (1, 3 or 5) preceding a no-go trial and then compared no-go trials to one another rather than no-go with go, to investigate effects involved in the representation of when not to respond rather than making a choice to respond or not. Results indicated that the ventral PFC (VPFC), cingulate gyrus and superior parietal regions showed an increase in BOLD signal to no-go trials with increasing number of preceding go trials. Hence, they may have maintained task or response demands as interference from go trials increased. The anterior regions in the SMA and premotor cortex showed an increase in BOLD signal on the no-go trials after five preceding go trials, but not after one or three. This may, therefore, reflected preparation for a motor response prior to stimulus onset as after a certain number of responses the system is primed to make a motor response (Durstun et al, 2002). No-go trials are sometimes directly compared with go trials, but others contrast no-go with rest baseline. One study examined both of these contrasts and found robust activation in pre-

SMA for the no-go-versus-baseline but not for no-go versus go (Mostofsky & Simmonds, 2008).

The current study did not control or analyse possible effects generated by the number of go trials preceding no-go trials in the go/no-go task nor in the withholding response trials preceding generate response trials in the oddball task. The ratio between standard and target stimuli is also known to be critical in the oddball task affecting both stimulus and response related conflict and consequent control effects (Casey et al, 2001).

In addition, the current analyses contrasted no-go with generate response trials. Preparatory and movement related activity is also different in respond or go compared with no-go trials. Preparatory activity is supposed to be present in both go and no-go trials, but perhaps with different time courses. Movement related activity (before and after) is present in go, but not no-go trials (Falkenstein et al, 1999). The current study compared infrequent no-go with infrequent respond trials where participants made responses to generate response stimuli, but withheld a response to no-go. Hence, motor activity may have contaminated respond, but not no-go trials. In future studies an alternative response (e.g. pressing spacebar) to no-go stimuli could be included to incorporate motor processes in no-go trials.

The results of the current study suggested that evoked upper alpha ERD and ERS are valid measures of facilitation and inhibition in cognitive control even though evoked upper alpha ERS was easier to validate than evoked upper alpha ERD, either because of the choice of reference of the whole epoch, which included the entire pre- and post-stimulus event period, in ERBP analyses, or because inhibition was given the primary role in managing high levels of conflict and complex demands in the current paradigm. Perhaps inhibition was given the primary role in managing this complex task by dampening or deactivating potentially task irrelevant brain regions as a strategy to reduce high levels of competition present in the current paradigm. Consequently, absolute, rather than relative, evoked upper alpha ERD or facilitation was infrequent and, hence, the difficulty in validating evoked upper alpha ERD. Nonetheless, only respond and not no-go trials exhibited absolute alpha ERD or a positive mean value for face targets at T5 and the overall pattern of ERBP results between respond and no-go trials was as expected (i.e. drop in ERS or relative ERD effects) for both face targets and face distracters. Hence,

current findings suggest that, in an appropriately designed context, evoked upper alpha ERD and ERS can index facilitatory and inhibitory effects in cortical processing even though evidence was more persuasive for evoked upper alpha ERS than ERD.

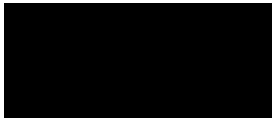
STATEMENT OF ORIGINALITY

We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Figures	142, 143, 145, 149
	151, 152, 153, 154
	155
Tables	144, 149, 150

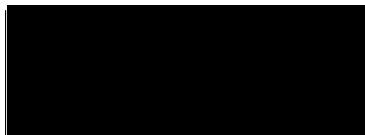
Name of Candidate: Daiva Newby

Name/title of Principal Supervisor: Dr Graham Jamieson



Candidate

April 2010



Principal Supervisor

April 2010

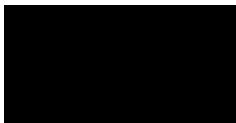
STATEMENT OF AUTHORS' CONTRIBUTION

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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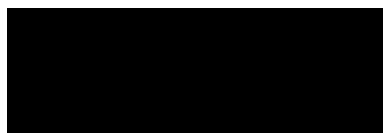
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6 Conclusions

The current cognitive neuroscience research project examined whether cognitive conflict in the face/name Stroop task is resolved by facilitating correct information processing pathways, inhibiting distracting information processing pathways or both. The project used blocked and event related variations of the face/name Stroop task and evoked upper alpha ERD and ERS as EEG measures of facilitation and inhibition respectively in expected high (II) and low (CI) control trials. Three sets of 120 photographic stimuli in total were created from scratch and eight experimental paradigms were produced. Scalp EEG was collected from 84 participants generating 84 EHI forms, 84 eye artifact calibration files and 115 each of experimental EEG and behavioural files.

Paper 1 sought to critically assess the fMRI face/name Stroop blocked design results of Egner and Hirsch (2005) which indicated that cognitive conflict is resolved by amplification of correct information processing pathways, but not inhibition of competing processing pathways. Paper 2 used the same stimuli as in Paper 1, but this time stimuli were arranged in an event related design in an attempt to replicate and extend the main behavioural and evoked upper alpha ERD and ERS results obtained in Paper 1. Paper 3 aimed at separating perceptual from response related conflict and examining the ensuing conflict modulating control effects. Paper 4 aimed to cross validate evoked upper alpha ERD and ERS as EEG measures of facilitation and inhibition respectively in face processing pathways. Evoked upper alpha ERD and ERS results were contrasted for face/name Stroop stimuli in the context of the oddball task (as a classic paradigm of response facilitation) and the go/no-go task (as a classic paradigm of response inhibition).

6.1 Paper Summaries

Paper 1 critically reexamined the findings of Egner and Hirsch's (2005) fMRI study, which used a blocked face/name Stroop task and measured BOLD signal in the FFA which is known to be selectively and sensitively activated by faces. BOLD results demonstrated that activity in the FFA was enhanced in II versus CI (high versus low control) trials in the face target block indicating amplification of relevant information, but remained unchanged in high compared with low control trials in the face distracter block. This was interpreted as the absence of inhibitory control effects on the processing of face

distracters. This fMRI evidence appeared to demonstrate that control of cognitive conflict involving the FFA employed amplification of task relevant information, but not inhibition of task irrelevant distracters (Egner & Hirsch, 2005).

fMRI has excellent spatial resolution, but poor temporal resolution, hence, raising the question of whether brief inhibitory signals would have been picked up by the fMRI. Furthermore, there are doubts as to whether fMRI can pick up more complex inhibitory effects which may arise, for example, from *activation* of certain cortical regions (e.g., projection from the pallidum to the thalamus) which results in inhibitory effects (Aron, 2007). There is also the question of whether, for example, GABA mediated inhibition may also be reflected in fMRI BOLD changes (Buzsáki et al, 2007). Absence of evidence, although suggestive, does not rule out the possibility that inhibitory processes play a part in cognitive control of processing conflicts. An important related question was whether cognitive control is a single central mechanism, as a purely functional approach might lead one to believe, or whether it is implemented through multiple networks and mechanisms depending on content and context. This thesis questioned whether broad and flexible control can be achieved in the cognitive brain by facilitation alone or whether inhibition, which may operate and manifest in more complex forms than just increased BOLD signal in certain cortical regions, was also a fundamental component of cognitive control.

Paper 1 applied scalp EEG derived measures of evoked upper alpha ERD and ERS as measures of facilitation and inhibition of cortical processing (Klimesch et al, 2007a; Rippon, 2006; Pfurtscheller & Lopes da Silva, 2005; Penny et al, 2002) to the blocked face/name Stroop task pioneered by Egner and Hirsch (2005). Topographic maps revealed inverse evoked upper alpha ERD and ERS patterns at T6 and P_{PZ, P4} channels for face targets and face distracters. Consequent analyses revealed enhanced post-stimulus inhibition in high control compared with low control trials at channel P_{PZ, P4} for face targets and this effect disappeared for face distracters (name targets). Enhanced post-stimulus inhibition was observed in high control compared with low control trials at channel T6 for face distracters and this relationship disappeared for face targets. A drop in the mean negative value of evoked upper alpha at T6 in high control compared with low control trials for face targets was consistent with the presence of relative facilitatory

effects. Subsequent analyses revealed a significant enhanced pre-stimulus effect for facilitation (ERD) in high compared with low control trials at T6 for face targets. This effect was eliminated for face distracters.

Paper 1 results indicated that cognitive conflict is modulated in cortical processing pathways by both facilitation and inhibition. Topographic maps of evoked upper alpha ERD and ERS centered on T6 and P_{PZ, P4} showed inverse patterns for high versus low control face target and face distracter conditions respectively. Evoked upper alpha ERS and ERD results indicated that in milliseconds the brain appeared to up or down modulate processing activity in regions related to face target or distracter processing. For example, anticipation of prepotent and predictable face stimuli appeared to be preceded by a facilitatory burst in cortical regions adjacent to the right FFA (detected most clearly at T6), while inhibitory bursts were applied in other regions (detected most clearly at P_{PZ, P4}) after the face stimulus was presented.

Exploratory source localisation (whole head sLORETA) of the cortical grey matter voxels most likely generating these evoked upper alpha ERD and ERS results indicated that cognitive control in the face/name Stroop task is unlikely to be implemented by a unitary mechanism and that many cortical regions are involved in modulating conflict. sLORETA results suggested that the right superior temporal gyrus extending to the right FFA was the likely source of facilitatory effects for face targets, while the inferior parietal lobule and cingulate gyrus were the likely sources of inhibitory effects for face distracters. Hence, the results suggested the right FFA to be the source of facilitatory control activity for face targets, but not the source of inhibitory control activity for face distracters, replicating the findings of Egner and Hirsch (2005). The results also suggested the parietal lobule, next to the FFA, which is involved in motor planning, to be the source of inhibitory control signals for face distracters.

If distracters, such as faces, are highly prepotent, under demanding task conditions it may be ineffective to inhibit specific, biologically primed cortical regions such as the FFA. Instead, control effects may be applied at the stage where perceptual processing is loaded into the motor system to program the production of behavioural responses. This is consistent with the existence of heterogeneous control mechanisms. Cognitive control likely occurs as a multistage process from stimulus processing to response production

engaging evoked upper alpha ERD and ERS (among others cortical oscillations) as it assembles (and disassembles) functional networks amongst widespread cortical regions on a timescale from tens to hundreds of milliseconds.

The results from Paper 1 left open the question of whether observed effects depend on the blocked paradigm which has a very high level of predictability and, hence may promote development of certain strategies, preparation and expectation effects (e.g., guiding processing, responding) to improve performance. The question then was whether the same observed conflict modulation effects would manifest in an event related paradigm, especially since control effects are assumed to be much more complex in event related compared with blocked design (Ullsperger et al, 2005). Sustained or state activity may be enhanced during processing of an easy task (e.g., blocked paradigm) while a difficult task (e.g., event related paradigm with random switching) may draw more on transient effects (Scheibe et al, 2006).

Paper 2 used the same stimuli as in Paper 1, but arranged in event related, task switching design which has increased demand for top down control with the aim of investigating whether the Paper 1 blocked design evoked upper alpha ERD and ERS results would be replicated and possibly even produce sharper effects. However, blocked and event related paradigms were not assumed to be equal because of more complex demands in the event related paradigm. Results of Paper 2 did not replicate the central alpha ERD and ERS findings obtained in Paper 1. Paper 1 demonstrated inverse evoked upper alpha ERD and ERS topographies depending on whether face was the target or distracter. Paper 2 results demonstrated complex evoked upper alpha ERD and ERS patterns many of which were contrary to expectations. For face targets, no enhanced post-stimulus inhibition (ERS) was observed in high compared with low control trials at composite channel $P_{PZ, P4}$ contrary to expectations and findings in Paper 1. For face distracters (name targets), there was a larger negative (inhibitory) post-stimulus value in high control compared with low control trials at channel T6, but it did not reach significance level, unlike in Paper 1. Furthermore, a higher negative mean value at T6 was observed in high compared with low control trials for face targets, again contrary to expectations and findings in Paper 1. Subsequent analyses of the interval between the

instruction cue and stimulus failed to reveal the expected ERD effect in high compared with low control trials for face targets at channel T6.

These results showed that fundamentally different control processes to those observed in Paper 1 were at play in Paper 2, providing further evidence of the heterogeneity of cognitive control. Blocked design with repetitive stimuli and high predictability may elicit more specialised and localised control effects such as these convincingly demonstrated by evoked upper alpha ERD and ERS patterns in Paper 1. In the event related design, frequent task changes and a high level of unpredictability in target attributes seemed to require additional level or loop of top down control over task selection in addition to that required in the blocked design manifest in distinct topographic patterns.

Current task switching results suggest the existence of multiple control mechanisms operating to regulate control both *within a task set* (blocked design) and *between task sets* (task switching). The operation (and interaction) of specific control mechanisms is highly context dependent and remains to be fully described. Present results indicated the importance of stimulus salience (to response systems), experimental design (block instructions versus shifting instructions) and the level of conflict on previous and present trials. Difference in the salience of (potentially) conflicting stimulus attributes (faces versus names in the current design) appear to have been a critical (but context sensitive) factor in the current paradigm and require systematic future study in this area.

Tasks may also encourage the adoption of particular strategies, preparation or expectation effects such as improving processing, and/or responding and blocking may allow the adoption of a particular strategy, while task switching, together with a large stimulus set, may preclude any particular strategies from developing. Anticipatory behaviour is directed at upcoming events and serves for faster and more efficient information processing, for example, by pre-setting necessary physiological processes, and preparing perceptual processes such as focus towards relevant features of the stimulus (Bastiaansen et al, 2002). If relevant stimuli appear in a predictable pattern, as in the blocked task, neuronal oscillations may entrain (phase-lock) to the structure of the attended stimulus stream and, hence, serve as an instrument of sensory selection (Lakatos et al, 2008) while this preparation may not develop in a swiftly paced event related task.

Hence, cognitive control did not appear as a single homogenous process present across all conflict modulating contexts. The Paper 2 event related task failed to replicate most of the central blocked design findings of Paper 1 either with facilitatory and inhibitory evoked upper alpha ERD and ERS effects or with behavioural findings. If task demands change frequently, then conflict between expected and actual demands may be effectively addressed by general slowing to prevent erroneous responses before stimuli are adequately processed, and, hence, there may possibly be more involvement from inhibitory processes. If the task requirements change little, but strong task irrelevant conflicting stimuli appear, then performance may be best served by increasing attention to the relevant stimuli, hence, more involvement from facilitatory effects. If there were a single control mechanism, it would not be optimal across specific task situations since a non-specific response slowing mechanism would not increase attention to relevant and away from irrelevant stimuli. An attention focusing mechanism alone would be ineffective in responding to unexpected changes in task requirements. Hence, there are likely to be multiple conflict control loop mechanisms associated with adjusting specific forms of control (Brown et al, 2007). Paper 2 failed to replicate the central findings of Paper 1, suggesting heterogeneity and probably even a hierarchy in cognitive control mechanisms.

Paper 3 aimed to disentangle perceptual conflict from response related conflict and to investigate post instructional cue interval and associated control effects employing an innovative event related paradigm where task cues *followed* each stimulus; hence, participants viewed each stimulus not knowing whether the required response will be to the face target or the face distracter (name target) attribute. It is known that interference, conflict generated at particular information processing stage such as perceptual processing, semantic processing or response selection may subsequently affect the nature of ensuing cognitive control effects (Nelson et al, 2003; Casey et al, 2001). For example, semantic and response conflicts may both contribute to the overall Stroop interference effect (van Veen & Carter, 2005) and may elicit nonoverlapping activations in the ACC, prefrontal and parietal regions. The brain may, therefore, have distinct, but parallel mechanisms for resolving different types of interference. For example, separate regions of the PFC, such as the superior DLPFC for semantic and more inferior for response

conflict, may hold task representations which act to resolve semantic and response conflict, while separate regions in the ACC, for example, more posterior for semantic conflict and more anterior for activation by errors, may be involved in conflict monitoring. Hence, different types of conflict may trigger different PFC representations to modulate a particular type of processing conflict (van Veen & Carter, 2005).

Paper 3 results revealed relative facilitatory effects in high compared with low control trials at P_{PZ, P4} region for face target cues. For face distracter (name target) cues, higher, but non significant mean negative values were detected at P_{PZ, P4} in high compared with low control trials. For face target cues, higher, but non significant mean negative values were observed at T6 in high compared with low control trials. For face distracter cues, higher, but non significant mean negative values were observed in high control compared with low control trials at channel T6, but it failed to reach significance. For face target cues, there was higher, but non significant mean negative values detected at channel T5 in high compared with low control trials. For face distracter cues, there was significant facilitatory activity (ERD) detected at channel T5 in high compared with low control trials. Consequently, there were no immediately obvious, systematic evoked upper alpha ERD and ERS patterns for face target cues and face distracter cues observed in the current event related task which aimed to separate perceptual from response related conflict and ensuing top down control effects.

One possibility is that the systematic evoked upper alpha ERD and ERS patterns observed in the Paper 1 blocked task are dependent on blocked design with its relatively simple demands and an assumed ability to engage a certain control type which manifested in systematic, inverse patterns depending on whether face attribute was the target or distracter. These control effects can be assumed to be relatively simple, *within a task set* compared, for example control effects required to regulate *between task sets* in task switching or event related designs, considering the simplicity and predictability of the blocked design task. The current event related design, because of its complexity and processing demands, failed to demonstrate systematic, obvious patterns. This again can be interpreted as evidence supporting the claim that cognitive control is heterogeneous and perhaps hierarchically organised considering that task set representations themselves are believed to be hierarchically organised (Sakai, 2008), and highly sensitive to

experimental (blocked versus event related task) demands. In addition, different control categories would be expected to manage interference from distracters (e.g., *within* blocked task) versus unexpected changes (e.g., *between task* sets in event related design) (Brown et al, 2007).

Despite the absence of any obviously systematic evoked upper alpha ERD and ERS patterns in Paper 3, the role of the nature of conflict and the ensuing control effects require further studies using EEG. Complex event related tasks with complex processing demands and distinctive conflict characteristics may elicit and manifest in more complex and hypothesised, possibly even hierarchical control effects. Interaction between the nature, source of conflict and ensuing control systems and mechanisms has already been demonstrated by fMRI studies (van Veen & Carter, 2005; Nelson et al, 2003) and further EEG research is needed.

Paper 4 aimed at cross validating evoked upper alpha ERD and ERS as measures of facilitation and inhibition of cortical processing responses respectively. The face/name Stroop task was adapted for use in the go/no-go task and the oddball task, classic paradigms of response inhibition and response generation respectively. Evoked upper alpha ERD and ERS measures were then contrasted for face targets and face distracters (name targets) across the two paradigms. In the go/no-go task participants make responses (go) to a majority of standard stimuli, but irregularly and infrequently withhold it to targets (no-go). Stopping on no-go trials requires change in the most frequent course of action (go) to meet the new goal (no-go) and, hence, requires top down control *to stop, inhibit responding* on infrequent no-go trials. In the oddball task, participants only respond to infrequent and irregular target stimuli (i.e. oddballs) interspersed within a series of standard stimuli to which participants are required not to respond. Infrequent targets (oddballs) are associated with infrequent responses and require top down control *to initiate responding* on infrequent respond trials.

Paper 4 results indicated relative facilitation (ERD) at the composite P_{PZ, P4} channel in respond trials compared with no-go trials for both face targets and distracters (name targets) without reaching significance level. Relative facilitation (ERD) was detected at T6 channel in respond trials compared with no-go trials for both face targets and distracters, but again was not statistically significant. Enhanced absolute facilitation

(ERD) at -500 – 0 ms pre-stimulus interval was detected at T5 channel in respond compared with no-go for face targets and relative ERD for face distracters, with the latter not reaching significance level. Higher mean negative (ERS) values were detected at channel T5 at 0 – 250 ms post-stimulus interval was detected for face targets and lower mean negative (relative ERD) values for face distracters in respond compared with no-go trials, with neither reaching significance level.

Evoked upper alpha ERS as a valid measure of selective inhibition of cortical processing (at least for face stimuli) was supported by the fact that all area report analyses for face stimuli at channels previously identified as sensitive to face processing (Gazzaley et al, 2005) revealed ERS in no-go trials compared with generate response trials. Thus, evoked upper alpha ERS appears to be able to index functional inhibition of cortical face stimulus processing. However, validation of evoked upper alpha ERD as a measure of facilitation was not so straightforward. Oddball response trials, which were expected to rely on facilitatory effects, generally demonstrated negative values (ERS) rather than positive values (ERD). A relative shift in the direction of greater ERD was observed (a drop in mean negative or ERS value) rather than an increase in absolute ERD (positive values). This may have been influenced by the use of the whole epoch (including the pre- and post-stimulus event period) as the reference interval over which ERBP was calculated. A different pre-stimulus baseline can potentially change the signs (positive or negative) of values obtained, but would not change the pattern of findings. The finding that only respond trials and not no-go trials demonstrated positive mean bandpower (ERD) at pre-stimulus interval at channel T6 for face targets, and the finding that the overall pattern (relative direction) of ERBP results between no-go and respond trials was as expected, even if the sign of values obtained was not always as expected, indicated that evoked upper alpha ERD and ERS are able to index functional facilitation and inhibition of cortical face stimulus processing in an appropriately designed task.

Moreover, both infrequent respond trials in the oddball task and infrequent no-go trials in the go/no-go task had the common characteristic that they required inhibition of a prepotent, most frequent, response strategy whether that was not responding in the oddball task, or go trials in the go/no-go task, they required a reversal of response tendencies (Huettel & McCarthy, 2004; Verbruggen & Logan, 2008). There was an

intriguing possibility as to why only evoked upper alpha ERS effects were detected (as expected) for no-go trials and (unexpectedly) also for most of the respond trials where ideally absolute evoked upper ERD effects were expected. Inhibition, general deactivation, dampening of activity may have played the primary role in managing this difficult task, for example, disengaging of task irrelevant cortical regions to reduce competition, while facilitation may have been required to selectively engage task relevant cortical regions.

A preparatory state of global cortical inhibition may be aimed at reducing competition for resources and distracting processing conflicts once the anticipated target information appears. This makes sense considering that inhibitory neurons assure that excitatory trajectories are effectively routed and competing cell assemblies segregated, and response to the same input can produce different responses depending on inhibitory activity (Buzsáki et al, 2007). Much of the incoming information is behaviourally irrelevant. If the nervous system could not control the flow of information, only a fraction of effort could be devoted to analysing crucial aspects of incoming information. Hence, top down, inhibitory control may allow concentration (excitation) on a small section of information (Treue, 2001). If indeed inhibition, alpha ERS, was given the primary role in managing conflict (e.g., inhibiting prepotent, most frequent responding) on infrequent trials in Paper 4, it would explain why absolute facilitatory effects (alpha ERD) were infrequent.

Exploratory source localisation sLORETA results suggested that for face targets the bilateral superior frontal gyrus containing the PMA and SMA (engaged in planning and preparing motor movements) was the most probable source of inhibitory effects while the ACC was the most probable source of facilitatory effects. For face distracters (name targets), the left superior temporal gyrus part of Wernicke's area was the probable source of inhibitory effects, while the left postcentral gyrus part of the spoken language network was the most probable source of facilitatory effects.

Inhibition responses to face distracters (name targets) seemed to be processed differently to inhibition responses to face targets. Inhibition to face targets appeared not to involve FFA, a specialised region engaged to processing faces; while cortical inhibition signals to face distracters (name targets) appeared to occur in Wernicke's area,

a specialised region strongly related to assigning meaning to perceived words. One possibility was that by withholding responses, inhibition to face distracters (name targets) was triggered at a later processing stage compared to face targets; sometime after stimulus processing had spread to language interpretation areas. One reason may be that extracting information from face distracters (name targets) was more perceptually difficult than from face targets since they are more abstract and since participants had to read names to decide whether it required a response or a no-go response.

Caveats. Considerations relating to the interpretation of the current four Papers encompass both design and analyses issues. Firstly, all experiments in the current project used short ISI (relative to imaging studies) which would have likely contributed to task difficulty relative to corresponding designs employed in an fMRI context. Although this current ISI were typical of both behavioural and EEG Stroop related paradigms and ultimately brain imaging, behavioural and EEG research results will require to be incorporated in any comprehensive account of cognitive control mechanisms. Nonetheless continuously high attentional demands, highly limited time in which to make a response and limited time for “recovery” in between responding, was evident in the relatively high error rates/low accuracy rates especially in Papers 2, 3 and 4. The shorter ISI may itself be an important factor influencing the development of control effects. Systematic manipulation of this variable is warranted in order to bridge the gap between findings from these research modalities however scope for such manipulation is intrinsically limited in fMRI by the time course of the bold response and are more readily pursued (in relation to neural activity) in EEG paradigms. If a short inter trial period interferes so dramatically with the development of top down control (Notebaert et al, 2006; Egner, 2007) then this raises serious questions as to the ecological relevance of the control processes elicited in current fMRI paradigms.

Secondly, the Gratton or conflict adaptation effect was not observed at a statistically significant level for either face targets or face distracters in any of the Papers presented here. One concern is what that may imply for EEG variables employed to index control related facilitation and inhibition. For example, the absence of a behavioural Gratton or conflict adaptation effect may imply the failure to engage the neural mechanisms believed to underlie these control effects. However, it can be argued that

expected neural effects may not necessarily be reflected at a behavioural level while theory tested in previous findings continues to predict that II compared to CI trials will still reflect higher levels of control even when this does not show up in behavioural data. Perhaps a closely related issue was that the last 3 Papers especially exhibited low accuracy/high error/time out rates, for some conditions accuracy rates were ~50%. If error responses are mostly incorrect responses this represents task performance at chance or effectively a random guessing level. However, there is little reason to interpret participants' performance in this way. Error responses were instead found to correspond largely to high time out rather than incorrect responses, for example see total error analyses results for Papers 2 (p. 85), 3 (p. 119) and 4 (p. 150). This suggests that the task/s were very difficult and this difficulty resulted in a slowing of responses – more conservative response criteria – itself an effect of cognitive control rather than random guessing. Response slowing rather than the Gratton effect may have been the most appropriate index of cognitive control in the context of these later experimental designs.

Thirdly, tasks across Papers necessarily varied in their difficulty and potentially in their demands for/type of cognitive control, but this may limit the comparability of results of the same analysis across the different studies. For example consider Papers' 1 and 2 paradigms: in the former participants knew that in face target block they will be required to respond to face and could prepare for the upcoming stimulus. In Paper 2, despite the identical stimuli and the same 1.3s ISI as in Paper 1, participants had to unpredictably switch between responding to face targets to face distracters. Consequently, within set cognitive control processes may not have been able to develop in the event related paradigm used in Paper 2 leading to a reliance on other types of control process compared to those evoked by the blocked instruction design used in Paper 1.

Fourthly, Papers 3 and 4 were not designed to allow a separate analysis of cognitive control effects (for face target and face distracter stimuli) on switching versus stay trial sequences and analyses or statistically control task switching component was not performed. Task switching control could have interacted with conflict adaptation affecting both behavioural and electrophysiological results in unpredictable ways. In future an appropriate factorial design would allow such effects in principle to be disentangled within the results.

Fifthly, it is unclear if the most optimal channels were chosen for analysis in every Paper. Channels were selected firstly by constraining the region of eligible electrodes based on prior EEG studies of face processing paradigms and then based on priori selection and by examining topographic maps in Paper 1 and applying the selected channels to EEG data analysis in each subsequent paper. However, the interpretable and statistically significant results in Paper 1 strongly suggest that at least in that context, the appropriate channels were chosen. It may be beneficial to perform an entirely objective statistical procedure to select channels and time points for data analyses independently in each Paper to assure its independence and to avoid circularity (Kriegeskorte et al, 2009). While theoretically appealing such an approach is itself both highly novel and untested at this point in the history of the field.

Finally, while legitimately identifying the most probable sources of evoked upper alpha conflict adaptation related patterns observed in the EEG data the statistical values of the sLORETA results, reported in Papers 1 and 4. While suggestive (and sharing important features with regions identified in several PET studies engaged in Stop-task rather than Stroop paradigms) these exploratory results can only serve to generate hypotheses for specific ROI to be employed by subsequent sLORETA analyses in further independent studies.

The current thesis investigated whether cognitive conflict is modulated by facilitation of correct information, inhibition of distracters or both using behavioural and scalp EEG data analyses. The core method utilised in the current thesis centred on methodical manipulation of stimuli and paradigms while the same dependent variables were tracked all through the four non-invasive experiments providing a high degree of behavioural and temporal precision supplemented by exploratory sources localisation of significant EEG effects using sLORETA. These results have methodological ramifications for future studies.

6.2 Cognitive Conflict and Control: Current Knowledge and Future Directions

Cognitive control manages behaviour according to goals; it generates and maintains task sets, monitors outcomes and adjusts behaviour in accordance with goals (Miller, 2000). Cognitive control is usually required when conflict is detected between co-active

information processing streams. Conflict between concurrent information processing networks signals breakdown in performance, increased probability of reduced rewards, negative consequences or loss. The ACC plays a key role in monitoring and signalling the occurrence of such processing conflicts (Kerns et al, 2004; Paus, 2001; Botvinick et al, 2004). ACC conflict detection subsequently modulates task representations which engage control effects such as facilitation of processing relevant information and at least in some circumstances, as is argued in this thesis, inhibition of processing potentially distracting information. Task representations themselves also need to be disengaged as changing circumstances render them unnecessary. Hence, they also require to be themselves monitored and regulated (disengaged) to optimise the use of limited cognitive resources (Mansouri et al, 2009).

The current thesis sought to systematically examine the role of facilitation and inhibition in the adaptive modulation of cortical information processing to minimise cognitive conflict. Results from the blocked design adopted in Paper 1 indicated that in less than 250 milliseconds the brain both up regulated and down regulated (“switched on and off”) processing in discrete cortical regions depending on whether the face attribute was the designated target or distracter. The evoked upper alpha ERD and ERS patterns were inverse for face targets and face distracters; hence the pattern was highly consistent. Such a compelling pattern may, in turn, be related to the repetitiveness and predictability inherent in blocked paradigms which are likely to promote adoption of particular strategies, expectation and require consistent control rather than shifting top down control. Expecting that the same response condition will be repeated on the next trial can result in strategic preparation, hence contributing to a congruency sequence effect (Egner, 2007). On the other hand, a blocked design may be better at isolating simpler control effects proving more interpretable results. The last 3 Papers used event related paradigms and produced more complicated patterns of behavioural and EEG results which may have been related to low levels of predictability, task switching and, hence, reduced probability of adoption of particular strategies. Consequently there may have been a continuous need for goal selection and monitoring in addition to response selection and monitoring. Even when nonsignificant, some results were replicated across experiments (e.g., sLORETA results which indicated that FFA was not the source of inhibitory effects for face

distracters in Papers 1 and 4), which is itself informative if replication is indeed the best statistic (Luck, 2005).

Paper 2 task switching results suggest the existence of multiple control mechanisms operating to regulate control both *within a task set* and *between task sets* (task switching). The operation (and interaction) of specific control mechanisms is highly context dependent and remains to be fully described. However, present results indicate the importance of stimulus salience (to response systems), experimental design (block instructions versus shifting instructions) and the level of conflict on previous and present trials. Difference in the salience of (potentially) conflicting stimulus attributes (faces versus names in the current design) appear to have been a critical (but context sensitive) factor in the current paradigm and require systematic future study in this area.

The results strongly suggested that cognitive control is neither structurally nor functionally homogeneous. Rather, it is extremely sensitive to experimental task demands, and observed control effects are dependent on both spatial and temporal resolution of the imaging method used. Heterogeneity of cognitive control is also evident within fMRI studies, for example, in some studies control effects are lateralised on the left (MacDonald et al, 2000) while in others on the right (Egner & Hirsch, 2005). These differences may in turn reflect different control processes engaged by different tasks such as the go/no-go or event related versus blocked Stroop task. Hemispheric specialisation is thought to depend on the nature of the task rather than the nature of the stimulus, and cognitive control is likely to be localised in the same hemisphere as task execution (Stephan et al, 2003).

Current results caution strongly against an oversimplified account of cognitive control. The path to a more comprehensive understanding of the modulation of cognitive conflict may lie, not in generalising across paradigms and imaging techniques, but rather in clearly defining task demands and matching particular imaging techniques to these experimental requirements. The first priority is to experimentally define and then to accurately and appropriately measure the neurophysiological manifestations of hypothesised control processes. For example, the current thesis sought to systematically investigate temporal control effects operating within ~250 milliseconds of stimulus onset (and in some cases pre-stimulus effects), as evident in control effects related to evoked

upper alpha ERD and ERS which would be invisible within the temporal resolution of fMRI.

The information processing stage at which control is implemented also needs to be explicitly defined. Evoked upper alpha ERD and ERS effects may be implemented not just at one stage, for example, stimulus perceptual processing, but, for example, also at the stage when perceptual representations are loaded into a coordinate system able to guide the motor response system as suggested in Papers 1 and 4.

Current results are inconsistent with the notion that cognitive control is implemented either through facilitation alone or inhibition alone. It is, for example, not clear how facilitation alone can manage prepotent, automatic information which is incorrect or how initiated incorrect responding is managed and how inhibition alone can manage information which is correct and relevant (Brown et al, 2007). One recurring question is whether inhibition is really necessary (MacLeod et al, 2003) in conflict modulation. For example, inhibition may be unnecessary in no-go trials and instead facilitation of the correct response just need time to be activated. In one go/no-go study, authors (Picton et al, 2007) examined the performance of healthy participants and people with focal lesions in the frontal lobes. People with lesions to the superior medial parts of the frontal lobes, in particular to the left superior portion of BA 6 which includes the SMA and PMA, had an increased number of false alarms (incorrect responses to the no-go stimulus) indicating that BA 6 is specifically important in the inhibition of response. People with lesions to the right anterior cingulate (BA 24 and 32) were slower and more variable in their RT, and this has been interpreted by Picton and colleagues as related to an inability to sustain stimulus-response contingencies. Lesions to the right VLPFC (BA 44, 45, 47) also increased the variability of response, perhaps by disrupting monitoring performance. The authors (Picton et al, 2007) proposed that withholding a response to the no-go stimuli may theoretically not require an active inhibitory process and instead the connections between the no-go stimuli and the response system could simply not be activated. If this were so, false alarms would probably never occur, but this is not the case when inhibiting a prepotent response. In the go/no-go task, the brain likely prepares to respond to any visual stimulus, but specifically inhibits the ongoing response whenever a

no-go stimulus is recognised. This explains why false alarms occur; because inhibition is too little or too late (Picton et al, 2007).

A variety of control effects (for example, managing distracters versus unexpected changes; *within task set* as in blocked task or *between task sets* as in task switching paradigm) is now evident in both temporal EEG and hemodynamic fMRI measures. Given the complexity of environmental stimuli and the requirement for novel, rapidly shifting responses, a single control mechanism would result in great restrictions and vulnerability in the operation of adaptive information processing systems. This diversity of control systems makes for more efficient and resilient performance.

Some authors suggest that competition, conflict may even be hard wired to occur within the nervous system (Coulthard et al, 2008), for example, to constantly promote the most effective performance. Complex biological systems including the brain require control through distinct mechanisms that operate on different temporal scales, both rapidly acting and more slowly changing which allows simultaneously for stability and flexibility (Dosenbach et al, 2008). There are multiple inhibitory systems and processes in the CNS and they can be expressed in many different ways, for example, inhibiting motor responding, task switching, during a simultaneous target and distracter presentation and it is a matter of investigation whether they represent the same phenomena (Kok, 1999).

Alpha ERD and ERS measures are themselves heterogeneous (upper and lower alpha; evoked and induced oscillations) measures and offer great opportunities for further study of cognitive control effects. ERD and ERS measures related to ongoing EEG activity are different from iconic, stimulus evoked ERP measures since they represent different neuronal responses in the brain within highly specific frequency bands. Depending on the frequency band, the same and different cortical regions can display ERD and ERS simultaneously. With advancing knowledge the importance of ongoing EEG activity is emerging. In fact, certain ERP components may actually be produced by reorganisation of the phase synchronisation (timing) of ongoing oscillations (Yeung et al, 2004). Thalamic structures are thought to activate cortical regions required at a certain time for processing relevant information and at the same time deactivate cortical regions processing irrelevant or distracting information. Alpha ERS is an important, swift

electroencephalographic process known to mediate powerful inhibitory processing effects, for example, blocking memory searches from entering irrelevant networks (Pfurtscheller & Lopes da Silva, 1999), alpha activity of ~10Hz can improve working memory capacity by suppressing distracters (Sauseng et al, 2009) and local enhancement of alpha oscillations is important in inhibitory motor control which has been shown to be impaired in dystonia (Hummel et al, 2002). In fact, efficient cognitive performance may be closely related to the ability to inhibit task irrelevant cortical regions or processes (Doppelmayr et al, 2005).

The current studies have many implications for future cognitive control research including experiments using alpha ERD and ERS. It is apparent from the results that the blocked design provided the most useful and clearly interpretable results for present purposes. Hence, the distinctive usefulness of blocked paradigms as well as the potential complexity introduced by the event related design with a task switching component common in EEG research, have been highlighted. Blocked tasks can be used to isolate particular effects of interest. However, blocked tasks have high levels of repetition and predictability likely to manifest in the adoption of particular strategies, high level of preparation and expectation effects and specific, possibly simpler top down effects. Event related designs, on the other hand, require constant, shifting, high levels of cognitive control which would be expected to be more hierarchically demanding and complex compared with blocked design control loops: control mechanisms operating in blocked task would be required to regulate control *within a task set* while those operating in task switching would require to regulate control *between task sets*. Furthermore, complex event related design tasks with high levels of conflict and high demand for top down control may also lead to higher arousal and noradrenalin release throughout the brain (Verguts & Notebaert, 2009) compared with blocked design tasks.

Paper 3 aimed at separating perceptual processing from response related conflict by using event related design where stimuli were followed rather than preceded by cues. It would be informative to extend such an experiment by arranging stimuli into face and name target blocks while requiring responses to be made at fixation point after the stimulus has been removed from the screen. The issue of interest is whether removal of task switching while responding to the post stimulus cue (fixation cross) would result in

more interpretable alpha ERD and ERS patterns. However, removal of the task switching component would undoubtedly remove the constant need for higher level control effects.

Control processes elicited by instructional cue presentation also require separate examination, since control related representations will be activated and thus causal origins of control effects (as distinct from the sites where control is expressed) may be more clearly identified. Exploratory analyses in this study suggested that instructional cues (Paper 2) may initiate a sequence of preparatory phases preceding stimulus presentation which may pre-set the cortex to enhance anticipated stimulus processing. TMS can temporarily disrupt neural activity to examine causal, not just correlational relationships between the cortical region and behaviour. TMS can also be used with EEG, for example, applying TMS pulses during the cue-stimulus interval can subsequently reduce or enhance ERP components or, for example, occipital α activity (Driver et al, 2009). It would be informative to apply TMS, for example, at fixation point and cues, to regions manifesting alpha ERS, for example, those identified in Paper 1, and clarify how alpha ERS disruption affects consequent performance.

Looking particularly at the regions of control related alpha ERD and ERS, it remains to be determined which are the origins and which are the targets of inhibitory control responses. In future studies it may be informative to apply the Dynamic Causal Modelling (DCM) approach of Friston and colleagues (2003) in order to test the direction of causal relationships (in ERD and ERS changes) between regions hypothesised to be the origins versus targets of inhibitory control effects in the face/name Stroop task. The application of Dynamic Causal Modelling (or related approaches) in suitable designs will allow analysis to shift from static “snapshots” of control effects to the temporal dynamics of inhibitory control in the interplay between specific anterior and posterior regions.

The sites where inhibitory control may or may not be expressed are of prime interest. The manifestation of inhibition appears to be response specific as it depends on involvement of response structures most likely at the response programming stage (Burle et al, 2004). In this connection lateralised readiness potential (LRP) observed in the EEG during unimanual (right or left) response preparation may serve as an important research tool. The LRP is derived from negative scalp readiness potential (RP) and is thought to reflect unimanual response preparation in the motor cortex and can be isolated by

subtracting the ipsilateral from contralateral potential (Brunia & Van Boxtel, 2000). The latency and magnitude of the negative and positive components of the LRP could be compared between high control (II) and low control (CI) trials to test for facilitatory and inhibitory effects.

A potentially valuable method to specify the causal relationships among cortical regions with alpha ERD and ERS changes sensitive to inhibitory control effects is to map these findings to existing knowledge of fronto-thalamic circuitry where the frontal cortex inputs to the reticular nucleus which in turn sends GABAergic projections to the thalamus inhibiting it and potentially gating incoming information (Aron, 2007) and then examine the resulting models using TMS. It would then be possible to map the temporal dynamics of task related activity in these inhibitory control networks.

This study examined alpha ERD and ERS effects evident < 250 milliseconds and it is unclear what, if any, alpha ERD and ERS effects are evident over longer time frames. The role of ipsilateral versus contralateral control of hemispheric specification of alpha ERD and ERS control effects also awaits further investigation.

Exploratory (whole head) source localisation sLORETA analyses identified conceptually plausible regions of interest which may now serve as specific (constrained) targets of analysis in further studies. Voxel statistical values in the present analyses failed to reach significance due to testing across >6 000 voxels at 5 mm for the whole head. Additional statistical tools are also emerging such as multivariate pattern classifiers which look at patterns of activation across many individual voxels without averaging and shift the focus from trying to identify specific regions that are activated during a particular task to how the relevant information is processed in the brain (Miller, 2008). It would be informative to apply multivariate pattern classifiers to investigate conflict modulation *within a task set in blocked paradigm* and *between task sets in task switching* using face/name Stroop task.

Another area requiring clarification is the relationship between the Stroop effect, the Gratton effect and evoked upper alpha ERD and ERS. It was clear from the current results that, for example, a Gratton type effect can emerge without the classic Stroop effect which is puzzling considering that the Stroop effect manifests differences in response conflict, while the Gratton effect is based upon adaptation to such conflict.

Whether the relationships between the Stroop effect, the Gratton effect and evoked upper alpha ERD and ERS is causal, merely correlative or completely independent, requires further investigation which will need to systematically take into account the switch costs which are present in standard event related Stroop paradigms.

Revealing insights have been gained about cognitive conflict and control effects using a variety of paradigms and imaging techniques. Parallel to the theoretical insights has been an expanding understanding of the relationship between cognitive control and clinical syndromes, for example, ADHD, schizophrenia, OCD and ranging from impairments in inhibitory functions to performance monitoring (Mansouri et al, 2009). There is an urgent need for some of these theoretical discoveries to be translated into clinical benefits and practical interventions. Research is urgently needed to translate possibilities for training in goal maintenance, performance monitoring, inhibition, switching between tasks in systems identified by basic cognitive neuroscience research into improvements in behavioural flexibility and effectiveness in clinical syndromes.

References

- ACD Systems (2004). CANVAS 9.0.4 [Computer software]. Miami, Florida, USA.
- Aron, A. R. (2007). The Neural Basis of Inhibition in Cognitive Control. *The Neuroscientist*, 13, 1-15.
- Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J. & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature neuroscience*, 6, 115-116.
- Aron, A. R., Robbins, T. W. & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, 8, 170-177.
- Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends in Cognitive Sciences*, 12, 193-200.
- Badre, D. & Wagner, A. D. (2006). Computational and neurobiological mechanisms underlying cognitive flexibility. *Proceedings of the National Academy of Sciences USA*, 103, 7186-7191.
- Baker, C. I. (2008). Face to face with cortex. *Nature neuroscience*, 11, 862-864.
- Band, G. P. H. & van Boxtel, G. J. M. (1999). Inhibitory motor control in stop paradigms: review and reinterpretation of neural mechanisms. *Acta psychologica*, 101, 179-211.
- Bandettini, P. A. (2006). Functional Magnetic Resonance Imaging. In C. Senior, T. Russell & M. S. Gazzaniga (Eds.), *Methods in Mind* (pp. 193-235). CA, MA: The MIT Press.
- Barch, D. M., Braver, T. S., Carter, C. S., Poldrack, R. A. & Robbins, T. W. (2009). CNTRICS Final Task Selection: Executive Control. *Schizophrenia Bulletin*, 35, 115-135.
- Barch, D. M., Braver, T. S., Sabb, F. W. & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from fMRI study of overt verb generation. *Journal of Cognitive Neuroscience*, 12, 298-309.
- Bastiaansen, M. C. M., Böcker, K. B. E. & Brunia, C. H. M. (2002). ERD as an index of anticipatory attention? Effects of stimulus degradation. *Psychophysiology*, 39, 16-28.
- Beer, J. S., Shimamura, A. P. & Knight, R. T. (2004). Frontal Lobe Contributions to Executive Control of Cognitive and Social Behavior. In M. S. Gazzaniga (Ed.-in-Chief), *The Cognitive Neurosciences* (3rd ed.) (pp. 1091-1104). CA, MA: The MIT Press.

- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S. & Cohen, J. D. (2001). Conflict Monitoring and Cognitive Control. *Psychological Review*, 108, 624-652.
- Botvinick, M., Braver, T. S., Yeung, N., Ullsperger, M., Carter, C. S. & Cohen, J. D. (2004). Conflict Monitoring: Computational and Empirical Studies. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 91-102). NY: The Guilford Press.
- Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S. & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, 402, 179-181.
- Brass, M. & von Cramon, D. Y. (2004). Selection for Cognitive Control: A Functional Magnetic Resonance Imaging Study on the Selection of Task-Relevant Information. *The Journal of Neuroscience*, 24, 8847-8852.
- Braver, T. S. & Barch, D. M. (2006). Extracting core components of cognitive control. *Trends in Cognitive Sciences*, 10, 529-532.
- Braver, T. S., Reynolds, J. R. & Donaldson, D. I. (2003). Neural Mechanisms of Transient and Sustained Cognitive Control during Task Switching. *Neuron*, 39, 713-726.
- Bressler, S. L. (1995). Large-scale cortical networks and cognition. *Brain Research Reviews*, 20, 288-304.
- Brown, J. W., Reynolds, J. R. & Braver, T. S. (2007). A computational model of fractionated conflict-control mechanisms in task-switching. *Cognitive Psychology*, 55, 37-85.
- Brunia, C. H. M. & Van Boxtel, G. J. M. (2000). Motor preparation. In J. T. Cacioppo, L. G. Tassinary & G. G. Bernston (Eds.), *Handbook of Psychophysiology* (2nd ed.) (pp. 507-532). CA, UK: Cambridge University Press.
- Bullmore, E. T. & Suckling, J. (2001). Functional magnetic resonance imaging. *International Review of Psychiatry*, 13, 24-33.
- Burle, B., Allain, S., Vidal, F. & Hasbroucq, T. (2005). Sequential Compatibility Effects and Cognitive Control: Does Conflict Really Matter? *Journal of Experimental Psychology: Human Perception and Performance*, 31, 831-837.
- Burle, B., Roger, C., Allain, S., Vidal, F. & Hasbroucq, T. (2008). Error Negativity Does Not Reflect Conflict: A Reappraisal of Conflict Monitoring and Anterior Cingulate Cortex Activity. *Journal of Cognitive Neuroscience*, 20, 1637-1655.
- Burle, B., Vidal, F., Tandonnet, C. & Hasbroucq, T. (2004). Physiological evidence for response inhibition in choice reaction time tasks. *Brain and Cognition*, 56, 153-164.

- Buschman, T. J. & Miller, E. K. (2007). Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science*, 315, 1860-1862.
- Bush, G. (2004). Multimodal Studies of Cingulate Cortex. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 207-218). NY: The Guilford Press.
- Buzsáki, G. (2006). *Rhythms of the Brain*. NY: Oxford University Press.
- Buzsáki, G. & Draguhn, A. (2004). Neuronal Oscillations in Cortical Networks. *Science*, 304, 1926-1929.
- Buzsáki, G., Kaila, K. & Raichle, M. (2007). Inhibition and Brain Work. *Neuron*, 56, 771-783.
- Carr, T. H. (2007). Is It Time to Inhibit Inhibition? Lessons from a Decade of Research on the Place of Inhibitory Processes in Cognition. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 307-316). Washington DC: American Psychological Association.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D. & Cohen, J. D. (1998). Anterior Cingulate Cortex, Error Detection, and the Online Monitoring of Performance. *Science*, 280, 747-749.
- Casey, B. J., Forman, S. D., Franzen, P., Berkowitz, A., Braver, T. S., Nystrom, L. E., Thomas, K. M. & Noll, D. C. (2001). Sensitivity of Prefrontal Cortex to Changes in Target Probability: A Functional MRI Study. *Human Brain Mapping*, 13, 26-33.
- Clark, D. L., Boutros, N. N. & Mendez, M. F. (2005). *The Brain and Behavior: An Introduction to Behavioral Neuroanatomy* (2nd ed.). NY: Cambridge University Press.
- Cohen, J. D., Aston-Jones, G. & Gilzenrat, M. S. (2004). A System Level Perspective on Attention and Cognitive Control. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 71-90). NY: The Guilford Press.
- Cohen, J. D., Braver, T. S. & O'Reilly, R. C. (1998). A computational approach to prefrontal cortex, cognitive control, and schizophrenia: recent developments and current challenges. In A. C. Roberts, T. W. Robbins & L. Weiskrantz (Eds.), *The Prefrontal Cortex: Executive and Cognitive Functions* (pp. 195-220). Oxford: Oxford University Press.
- Cohen, J. D., Dunbar, K. & McClelland, J. L. (1990). On the Control of Automatic Processes: A Parallel Distributed Processing Account of the Stroop Effect. *Psychological Review*, 97, 332-361.
- Cohen, J. D., Servan-Schreiber, D. & McClelland, J. L. (1992). A parallel distributed

- processing approach to automaticity. *American Journal of Psychology*, 105, 239-269.
- Compumedics NeuroScan (2003). ACQUIRE 4.3.1 [Computer software]. Texas, USA.
- Compumedics NeuroScan (2003). EDIT 4.3.1 [Computer software]. Texas, USA.
- Compumedics NeuroScan (2003). NuAmps 7181 [Digital Amplifier]. Texas, USA.
- Compumedics NeuroScan (2003). Quik-Cap [Electrode cap]. El Paso, Texas, USA.
- Compumedics NeuroScan (2003). STIM² [Computer software]. El Paso, Texas, USA.
- Constantinidis, C., Williams, G. V. & Goldman-Rakic, P. S. (2002). A role for inhibition in shaping the temporal flow of information in prefrontal cortex. *Nature neuroscience*, 5, 175-180.
- Coulthard, E. J., Nachev, P. & Husain, M. (2008). Control over Conflict during Movement Preparation: Role of Posterior Parietal Cortex. *Neuron*, 58, 144-157.
- Craik, F. I. M. & Bialystok, E. (2006). Cognition through the lifespan: mechanisms of change. *Trends in Cognitive Sciences*, 10, 131-138.
- Croft, R. J. & Barry, R. J. (2000). Removal of ocular artifact from the EEG: a review. *Clinical Neurophysiology*, 30, 5-19.
- Croft, R. J., Chandler, J. S., Barry, R. J., Cooper, N. R. & Clarke, A. R. (2005). EOG correction: A comparison of four methods. *Psychophysiology*, 42, 16-24.
- Dagenbach, D., Carr, T. H., Menzer, D., Duquette, P. J., Chalk, H. M., Rupard, M. & Hurley, R. S. E. (2007). Adventures in Inhibition: Plausibly, But Not Certifiably, Inhibitory Processes. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 45-61). Washington DC: American Psychological Association.
- Davidson, R. J., Jackson, D. C. & Larson, C. L. (2000). Human Electroencephalography. In J. T. Cacioppo, L. G. Tassinary & G. G. Bernston (Eds.), *Handbook of Psychophysiology* (2nd ed.) (pp. 27-52). CA, UK: Cambridge University Press.
- De Jong, R., Berendsen, E. & Cools, R. (1999). Goal neglect and inhibitory limitations: dissociable causes of interference effects in conflict situations. *Acta psychologica*, 101, 379-394.
- Doppelmayr, M., Klimesch, W., Hödlmoser, K., Sauseng & Gruber, W. (2005). Intelligence related upper alpha desynchronization in a semantic memory task. *Brain Research Bulletin*, 66, 171-177.

- Dosenbach, N. U. F., Fair, D. A., Cohen, A. L., Schlaggar, B. L. & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends in Cognitive Sciences*, 12, 99-105.
- Driver, J. (1998). Control freaks, or ghost-(in-the-machine)-busters? *Trends in Cognitive Sciences*, 2, 471-473.
- Driver, J., Blankenburg, F., Bestmann, S., Vanduffel, W. & Ruff, C. C. (2009). Concurrent brain-stimulation and neuroimaging for studies of cognition. *Trends in Cognitive Sciences*, 13, 319-327.
- Durston, S., Thomas, K. M., Worden, M. S., Yang, Y. & Casey, B. J. (2002). The Effect of Preceding Context on Inhibition: An Event-Related fMRI Study. *NeuroImage*, 16, 449-453.
- Egner, T. (2007). Congruency sequence effects and cognitive control. *Cognitive, Affective, & Behavioral Neuroscience*, 7, 380-390.
- Egner, T. & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature neuroscience*, 8, 1784-1790.
- Eimer, M. (1999). Facilitatory and inhibitory effects of masked prime stimuli on motor activation and behavioural performance. *Acta Psychologica*, 101, 293-313.
- Eimer, M. & Schlaghecken, F. (1998). Effects of Masked Stimuli on Motor Activation: Behavioral and Electrophysiological Evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1737-1747.
- Falkenstein, M., Hoormann, J. & Hohnsbein, J. (1999). ERP components in Go/Nogo tasks and their relation to inhibition. *Acta psychologica*, 101, 267-291.
- Fassbender, C., Foxe, J. J. & Garavan, H. (2006). Mapping the Functional Anatomy of Task Preparation: Priming Task-Appropriate Brain Networks. *Human Brain Mapping*, 27, 819-827.
- Faust, M. E. & Balota, D. A. (2007). Inhibition, Facilitation, and Attentional Control in Dementia of the Alzheimer's Type: The Role of Unifying Principles in Cognitive Theory Development. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 213-238). Washington DC: American Psychological Association.
- Fellows, L. K. & Farah, M. J. (2005). Is anterior cingulate cortex necessary for cognitive control? *Brain*, 128, 788-796.
- Fitzgerald, K. D., Welsh, R. C., Gehring, W. J., Abelson, J. L., Himle, J. A., Liberzon, I. & Taylor, S. F. (2005). Error-Related Hyperactivity of the Anterior Cingulate

- Cortex in Obsessive-Compulsive Disorder. *Biological Psychiatry*, 57, 287-294.
- Freunberger, R., Höller, Y., Griesmayr, B., Gruber, W., Sauseng, P. & Klimesch, W. (2008). Functional similarities between the P1 component and alpha oscillations. *European Journal of Neuroscience*, 27, 2330-2340.
- Friedman, N. P. & Miyake, A. (2004). The Relations Among Inhibition and Interference Control Functions; A Latent-Variable Analysis. *Journal of Experimental Psychology: General*, 133, 101-135.
- Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9, 474-480.
- Friston, K. J., Harrison, L. & Penny, W. (2003). Dynamic causal modeling. *NeuroImage*, 19, 1273-1302.
- Frith, C. D., Friston, K. J., Liddle, P. F. & Frackowiak, R. S. J. (1991). A PET study of word-finding. *Neuropsychologia*, 29, 1137-1148.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T. & D'Eposito, M. (2005). Top-down Enhancement and Suppression of the Magnitude and Speed of Neural Activity. *Journal of Cognitive Neuroscience*, 17, 507-517.
- Gilbert, S. J. & Shallice, T. (2002). Task Switching: A PDP Model. *Cognitive Psychology*, 44, 297-337.
- Gratton, G., Coles, M. G. H. & Donchin, E. (1992). Optimizing the Use of Information: Strategic Control of Activation of Responses. *Journal of Experimental Psychology: General*, 121, 480-506.
- Grill-Spector, K., Sayres, R. & Ress, D. (2006). High-resolution imaging reveals highly selective nonface clusters in the fusiform face area. *Nature neuroscience*, 9, 1177-1185.
- Heeger, D. J. & Ress, D. (2002). What does fMRI tell us about neuronal activity? *Nature reviews neuroscience*, 3, 142-151.
- Hester, R., Foxe, J. J., Molholm, S., Shpaner, M. & Garavan, H. (2005). Neural mechanisms involved in error processing: A comparison of errors made with and without awareness. *NeuroImage*, 27, 602-608.
- Herrmann, C. S., Grigutsch, M., & Busch, N. A. (2005). EEG Oscillations and Wavelet Analysis. In T. C. Handy (Ed.), *Event-Related Potentials: A Methods Handbook* (pp. 229-259). CA, MA: The MIT Press.
- Hershey, T., Revilla, F. J., Wernle, A. R., McGee-Minnich, L., Antenor, J. V., Videen, T.

- O., Dowling, J. L., Mink, J. W. & Perlmuter, J. S. (2003). Cortical and subcortical blood flow effects of subthalamic nucleus stimulation in PD. *Neurology*, 61, 816-821.
- Hervé, P.-Y., Mazoyer, B., Crivello, F., Perchey, G. & Tzourio-Mazoyer, N. (2005). Finger tapping, handedness and grey matter amount in the Rolando's genu area. *NeuroImage*, 25, 1133-1145.
- Holroyd, C. B., Nieuwenhuis, S., Mars, R. B. & Coles, M. G. H. (2004). Anterior Cingulate Cortex, Selection for Action, and Error Processing. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 219-231). NY: The Guilford Press.
- Hopfinger, J. B., Buonocore, M. H. & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, 3, 284-291.
- Hopfinger, J. B., Khoe, W. & Song, A. (2005). Combining Electrophysiology with Structural and Functional Neuroimaging: ERPs, PET, MRI, and fMRI. In T. C. Handy (Ed.), *Event-Related Potentials: A Methods Handbook* (pp. 345-379). CA, MA: The MIT Press.
- Huettel, S. A. & McCarthy, G. (2004). What is odd in the oddball task? Prefrontal cortex is activated by dynamic changes in response strategy. *Neuropsychologia*, 42, 379-386.
- Hummel, F. Andres, F., Altenmüller, E., Dichgans, J. & Gerloff, C. (2002). Inhibitory control of acquired motor programmes in the human brain. *Brain*, 125, 404-420.
- Hutchison, W. D., Davis, K. D., Lozano, A. M., Tasker, R. R. & Dostrovsky, J. O. (1999). Pain-related neurons in the human cingulate cortex. *Nature neuroscience*, 2, 403-405.
- Jentzsch, I. & Leuthold, H. (2005). Response Conflict Determines Sequential Effects in Serial Response Time Tasks With Short Response-Stimulus Intervals. *Journal of Experimental Psychology: Human Perception and Performance*, 31, 731-748.
- Kanne, S. M., Balota, D. A., Spieler, D. H. & Faust, M. E. (1998). Explorations of Cohen, Dunbar, and McClelland's (1990) Connectionist Model of Stroop Performance. *Psychological Review*, 105, 174-187.
- Kennerley, S. W., Walton, M. E., Behrens, T. E. J., Buckley, M. J. & Rushworth, M. F. S. (2006). Optimal decision making and the anterior cingulate cortex. *Nature neuroscience*, 9, 940-947.
- Kerns, J. G., Cohen, J. D., MacDonald III, A. W., Cho, R. Y., Stenger, V. A. & Carter, C. S. (2004). Anterior Cingulate Conflict Monitoring and Adjustments in Control. *Science*, 303, 1023-1026.

- Kiehl, K. A., Stevens, M. C., Laurens, K. R., Pearlson, G., Calhoun, V. D. & Liddle, P. F. (2005). An adaptive reflexive processing model of neurocognitive function: supporting evidence from a large scale (n = 100) fMRI study of an auditory oddball task. *NeuroImage*, 25, 899-915.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, 29, 169-195.
- Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T. & Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters*, 244, 73-76.
- Klimesch, W., Sauseng, P. & Hanslmayr, S. (2007a). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, 53, 63-88.
- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W. & Freunberger, R. (2007b). Event-related phase reorganization may explain evoked neural dynamics. *Neuroscience and Biobehavioral Reviews*, 31, 1003-1016.
- Knight, R. T., Staines, W. R., Swick, D. & Chao, L. L. (1999). Prefrontal cortex regulates inhibition and excitation in distributed neural networks. *Acta Psychologica*, 101, 159-178.
- Knösche, T. R. & Bastiaansen, M. C. M. (2002). On the time resolution of event-related desynchronization: a simulation study. *Clinical Neurophysiology*, 113, 754-763.
- Knudsen, E. I. (2007). Fundamental Components of Attention. *Annual Review of Neuroscience*, 30, 57-78.
- Kok, A. (1999). Varieties of inhibition: manifestations in cognition, event-related potentials and aging. *Acta psychologica*, 101, 129-158.
- Kouneiher, F., Charron S. & Koechlin E. (2009). Motivation and cognitive control in the human prefrontal cortex. *Nature neuroscience*, 12, 939-947.
- Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F. & Baker, C. I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. *Nature neuroscience*, 12, 535-540.
- LaBerge, D. (1995). *Attentional Processing: The Brain's Art of Mindfulness*. CA, MA: Harvard University Press.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I. & Schroeder, C. E. (2008). Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection. *Science*, 320, 110-113.

- Levine, D. S. & Brown, V. R. (2007). Uses (and Abuses?) of Inhibition in Network Models. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 281-303). Washington DC: American Psychological Association.
- Lieberman, M. D. & Eisenberger, N. I. (2009). Pains and Pleasures of Social Life. *Science*, 323, 890-891.
- Lindsay, D. S. & Jacoby, L. L. (1994). Stroop Process Dissociations: The Relationship Between Facilitation and Interference. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 219-234.
- Logan, G. D. (1994). On the Ability to Inhibit Thought and action: A User's Guide to the Stop Signal Paradigm. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory Processes in Attention, Memory, and Language* (pp. 189-239). San Diego CA: Academic Press.
- Lopes da Silva, F. (2005). EEG Analysis: Theory and Practice. In E. Niedermeyer & F. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.) (pp. 1199-1231). PA: Lippincott Williams & Wilkins.
- Luck, S. J. (2005). *An Introduction to the Event-Related Potential Technique*. CA, MA: The MIT Press.
- MacDonald III, A. W., Cohen, J. D., Stenger, V. A. & Carter, C. S. (2000). Dissociating the Role of the Dorsolateral Prefrontal and Anterior Cingulate Cortex in Cognitive Control. *Science*, 288, 1835-1838.
- MacLeod, C. M. (1991). Half a Century of Research on the Stroop Effect: An Integrative Review. *Psychological Bulletin*, 109, 163-203.
- MacLeod, C. M. (2007). The Concept of Inhibition in Cognition. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 3-23). Washington DC: American Psychological Association.
- MacLeod, C. M., Dodd, M. D., Sheard, E. D., Wilson, D. E. & Bibi, U. (2003). In opposition to inhibition. In B. H. Ross (Ed.), *The Psychology of Learning and Motivation* (vol. 43) (pp. 163-214). San Diego CA: Academic Press.
- MacLeod, C. M. & MacDonald, P. A. (2000). Interdimensional interference in the Stroop effect: uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, 4, 383-391.
- Makeig, S., Westerfield, M., Jung, T. -P., Enghoff, S., Townsend, J., Courchesne, E. & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked potentials. *Science*, 295, 690-694.

- Mansouri, F. A., Buckley, M. J. & Tanaka, K. (2007). Mnemonic Function of the Dorsolateral Prefrontal Cortex in Conflict-Induced Behavioral Adjustment. *Science*, 318, 987-990.
- Mansouri, F. A., Tanaka, K. & Buckley, M. J. (2009). Conflict-induced behavioural adjustment: a clue to the executive functions of the prefrontal cortex. *Nature reviews neuroscience*, 10, 141-152.
- Mantini, D., Corbetta, M., Perrucci, M. G., Romani, G. L. & Del Gratta, C. (2009). Large-scale brain networks account for sustained and transient activity during target detection. *NeuroImage*, 44, 265-274.
- Mayr, U. (2007). Inhibition of Task Sets. In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in Cognition* (pp. 27-44). Washington DC: American Psychological Association.
- Mayr, U., Awh, E. & Laurey, P. (2003). Conflict adaptation effects in the absence of executive control. *Nature neuroscience*, 6, 450-452.
- Mayr, U., Diedrichsen, J., Ivry, R. & Keele, S. W. (2006). Dissociating Task-set Selection from Task-set Inhibition in the Prefrontal Cortex. *Journal of Cognitive Neuroscience*, 18, 14-21.
- Meiran, N., Chorev, Z. & Sapir, A. (2000). Component Processes in Task-Switching. *Cognitive Psychology*, 41, 211-253.
- Milham, M.P., Banich, M.T., Webb, A., Barad, V., Cohen, N.J., Wszalek, T. & Kramer, A.F. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research*, 12, 467-473.
- Miller, E. K. (1999). Straight from the top. *Nature*, 401, 650-651.
- Miller, E. K. (2000). The Prefrontal Cortex and Cognitive Control. *Nature reviews neuroscience*, 1, 59-65.
- Miller, E. K. & Cohen, J. D. (2001). An Integrative Theory of Prefrontal Cortex Function. *Annual Review of Neuroscience*, 24, 167-202.
- Miller, E. K. & Wallis, J. D. (2009). Executive Function and Higher-Order Cognition: Definition and Neural Substrates. In L. R. Squire (Ed.), *Encyclopedia of Neuroscience* (vol. 4) (pp. 99-104). Oxford: Academic Press.
- Miller, E. K. & Wilson, M. A. (2008). All My Circuits: Using Multiple Electrodes to Understand Functioning Neural Networks. *Neuron*, 60, 483-488.

- Miller, G. (2008). Growing Pains for fMRI. *Science*, 320, 1412-1414.
- Monsell, S., Yeung, N. & Azuma, R. (2000). Reconfiguration of task-set: Is it easier to switch to the weaker task? *Psychological Research*, 63, 250-264.
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, 7, 134-140.
- Monsell, S. & Mizon, G. A. (2006). Can the Task-Cuing Paradigm Measure an Endogenous Task-Set Reconfiguration Process? *Journal of Experimental Psychology: Human Perception and Performance*, 32, 493-516.
- Monsell, S., Sumner, P. & Waters, H. (2003). Task-set reconfiguration with predictable and unpredictable task switches. *Memory & Cognition*, 31, 327-342.
- Mostofsky, S. H. & Simmonds, D. J. (2008). Response Inhibition and Response Selection: Two Sides of the Same Coin. *Journal of Cognitive Neuroscience*, 20, 751-761.
- Nelson, J. K., Reuter-Lorenz, P. A., Sylvester, C.-Y. C., Jonides, J. & Smith, E. E. (2003). Dissociable neural mechanisms underlying response-based and familiarity-based conflict in working memory. *Proceedings of the National Academy of Sciences USA*, 100, 11171-11175.
- Neuper, C. & Pfurtscheller, G. (2001). Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *International Journal of Psychophysiology*, 43, 41-58.
- Niedermeyer, E. (1999). Alpha rhythms as physiological and abnormal phenomena. *International Journal of Psychophysiology*, 26, 31-49.
- Niedermeyer, E. (2005). The Normal EEG of the Waking Adult. In E. Niedermeyer & F. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.) (pp. 167-192). PA: Lippincott Williams & Wilkins.
- Nieuwenhuis, S. & Monsell, S. (2002). Residual costs in task switching: Testing the failure-to-engage hypothesis. *Psychonomic Bulletin & Review*, 9, 86-92.
- Nieuwenhuis, S. & Yeung, N. (2005). Neural mechanisms of attention and control: losing our inhibitions? *Nature neuroscience*, 8, 1631-1633.
- Notebaert, W., Gevers, W., Verbruggen, F. & Liefvooghe, B. (2006). Top-down and bottom-up sequential modulations of congruency effects. *Psychonomic Bulletin & Review*, 13, 112-117.
- Notebaert, W. & Verguts, T. (2007). Dissociating Conflict Adaptation From Feature

Integration: A Multiple Regression Approach. *Journal of Experimental Psychology: Human Perception and Performance*, 33, 1256-1260.

- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97-113.
- Pashler, H., Johnston, J. C. & Ruthruff, E. (2001). Attention and Performance. *Annual Review of Psychology*, 52, 629-651.
- Pasqual-Marqui, R. D., Michel, C. M. & Lehmann, D. (1994). Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. *International Journal of Psychophysiology*, 18, 49-65.
- Paus, T. (2001). Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Nature reviews neuroscience*, 2, 417-424.
- Penny, W. D., Kiebel, S. J., Kilner, J. M. & Rugg, M. D. (2002). Event-related brain dynamics. *Trends in Neurosciences*, 25, 387-389.
- Pessoa, L. & Ungerleider, L. G. (2004). Top-Down Mechanisms for Working Memory and Attentional Processes. In M. S. Gazzaniga (Ed.-in-Chief), *The Cognitive Neurosciences* (3rd ed.) (pp. 919-930). CA, MA: The MIT Press.
- Pfurtscheller, G. (2003). Induced Oscillations in the Alpha Band: Functional Meaning. *Epilepsia*, 44 (Suppl. 12), 2-8.
- Pfurtscheller, G. & Lopes da Silva, F. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology*, 110, 1842-1857.
- Pfurtscheller, G. & Lopes da Silva, F. (2005). EEG Event-Related Desynchronization (ERD) and Event-Related Synchronization (ERS). In E. Niedermeyer & F. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.) (pp. 1003-1016). PA: Lippincott Williams & Wilkins.
- Picton, T. W., Stuss, D. T., Alexander, M. P., Shallice, T., Binns, M. A. & Gillingham, S. (2007). Effects of Focal Frontal Lesions on Response Inhibition. *Cerebral Cortex*, 17, 826-838.
- Posner, M. I. & Rothbart, M. K. (2007). *Educating the Human Brain*. Washington, DC: American Psychological Association.
- Reiman, E. M., Lane, R. D., Van Petten, C. & Bandettini, P. A. (2000). Positron emission tomography and functional magnetic resonance imaging. In J. T. Cacioppo, L. G. Tassinary & G. G. Bernston (Eds.), *Handbook of Psychophysiology* (2nd ed.) (pp. 85-118). CA, UK: Cambridge University Press.

- Ridderinkhof, K. R., de Vlugt, Y., Bramlage, A., Spaan, M., Elton, M., Snel, J. & Band, G. P. H. (2002). Alcohol Consumption Impairs Detection of Performance Errors in Medial Prefrontal Cortex. *Science*, 298, 2209-2211.
- Rippon, G. (2006). Electroencephalography. In C. Senior, T. Russell & M. S. Gazzaniga (Eds.), *Methods in Mind* (pp. 237-262). CA, MA: The MIT Press.
- Roelofs, A. (2003). Goal-Referenced Selection of Verbal Action: Modeling Attentional Control in the Stroop task. *Psychological Review*, 110, 88-125.
- Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., Simmons, A., Williams, S. C. R., Giampietro, V., Andrew, C. M. & Taylor, E. (2001). Mapping Motor Inhibition: Conjunctive Brain Activations across Different Versions of Go/No-Go and Stop Tasks. *NeuroImage*, 13, 250-261.
- Ruthruff, E., Remington, R. W. & Johnston, J. C. (2001). Switching Between Simple Cognitive Tasks: The Interaction of Top-Down and Bottom-Up Factors. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 1404-1419.
- Sakai, K. (2008). Task Set and Prefrontal Cortex. *Annual Review of Neuroscience*, 31, 219-245.
- Sakai, K. & Passingham, R. E. (2003). Prefrontal interactions reflect future task operations. *Nature neuroscience*, 6, 75-81
- Sauseng, P. & Klimesch, W. (2008). What does phase information of oscillatory brain activity tell us about cognitive processes? *Neuroscience and Behavioral Reviews*, 32, 1001-1013.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., Glennon, M., Gerloff, C., Birbaumer, N. & Hummel, F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, 19, 1846-1852.
- Schall, J. D., Stuphorn, V. & Brown, J. W. (2002). Monitoring and Control of Action by the Frontal Lobes. *Neuron*, 36, 309-322.
- Scheffers, M. K., Coles, M. G., Bernstein, P., Gehring, W. J. & Donchin, E. (1996). Event-related potentials and error-related processing: An analysis of incorrect responses to go and no-go stimuli. *Psychophysiology*, 33, 42-53.
- Scheibe, C., Wartenburger, I., Wüstenberg, T., Kathmann, N., Villringer, A. & Heekeren, H. R. (2006). Neural correlates of the Interaction Between Transient and Sustained Processes: A Mixed Blocked/Event-Related fMRI Study. *Human Brain Mapping*, 27, 545-551.
- Schuch, S. & Koch, I. (2003). The Role of Response Selection for Inhibition of Task Sets

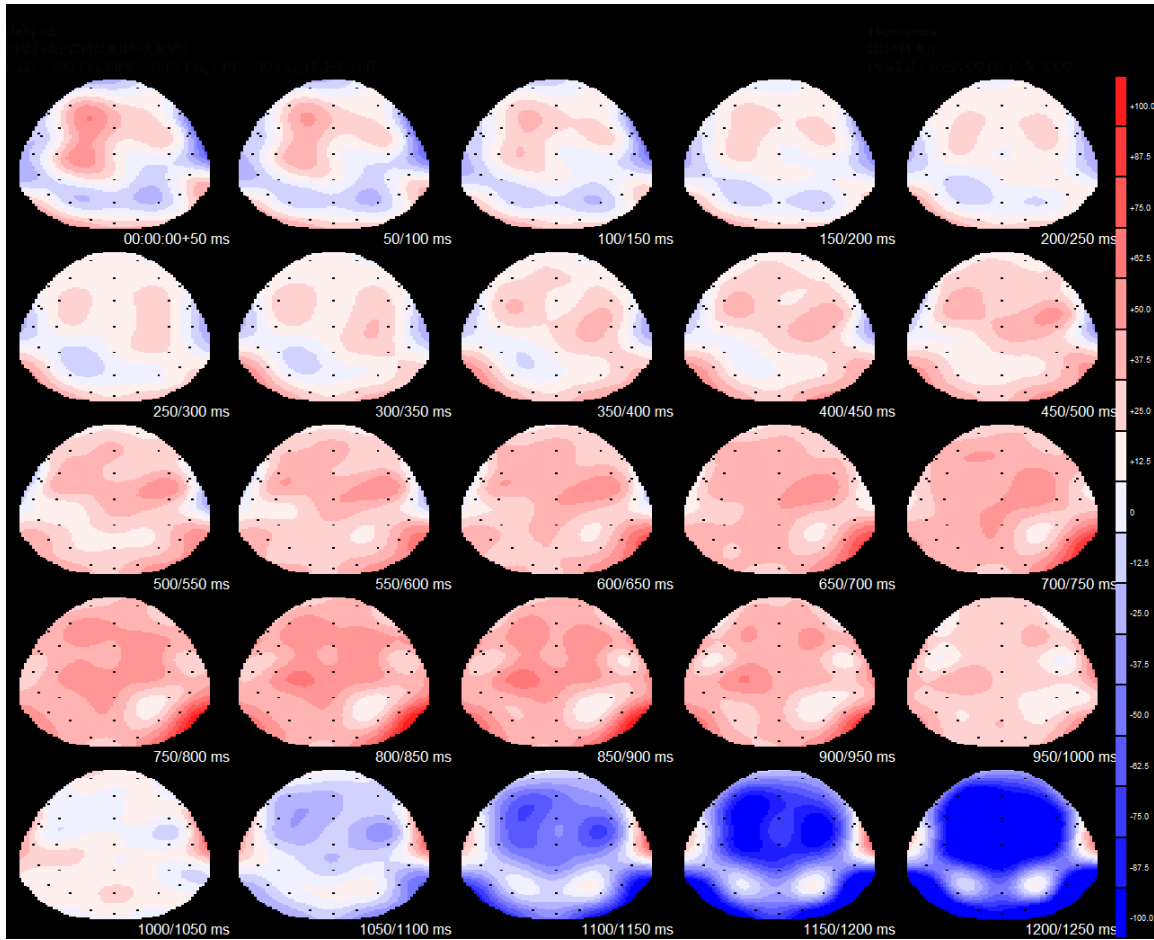
in Task Shifting. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 92-105.

- Sekihara, K., Sahani, M. & Nagarajan, S. S. (2005). Localization bias and spatial resolution of adaptive and non-adaptive spatial filters for MEG source reconstruction. *NeuroImage*, 25, 1056-1067.
- Skrandies, W. (1990). Global Field Power and Topographic Similarity. *Brain Topography*, 3, 137-141.
- Stephan, K. E., Marshall, J. C., Friston, K. J., Rowe, J. B., Ritzl, A., Zilles, K. & Fink, G. R. (2003). Lateralized Cognitive Processes and Lateralized Task Control in the Human Brain. *Science*, 301, 384-386.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643-661.
- Swick, D. & Turken, A. U. (2002). Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. *Proceedings of the National Academy of Sciences USA*, 99, 16354-16359.
- Thut, G. & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS-EEG studies. *Trends in Cognitive Sciences*, 13, 182-189.
- Tipper, S. P. (2004). Attention and Action. In M. S. Gazzaniga (Ed.-in-Chief), *The Cognitive Neurosciences* (3rd ed.) (pp. 619-629). CA, MA: The MIT Press.
- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neurosciences*, 24, 295-300.
- Uhlhaas, P. J. & Singer, W. (2006). Neural Synchrony in Brain Disorders: Relevance for Cognitive Dysfunctions and Pathophysiology. *Neuron*, 52, 155-168.
- Ullsperger, M., Bylsma, L. M. & Botvinick, M. M. (2005). The conflict adaptation effect: It's not just priming. *Cognitive, Affective and Behavioral Neuroscience*, 5(4), 467-472.
- van Boxtel, G. J. M., van der Molen, M. W., Jennings, J. R. & Brunia, C. H. M. (2001). A psychophysiological analysis of inhibitory motor control in the stop-signal paradigm. *Biological Psychology*, 58, 229-262.
- van der Stelt, O. (2008). Development of human EEG posterior alpha rhythms. *Clinical Neurophysiology*, 119, 1701-1702.
- van Veen, V. & Carter, C. S. (2005). Separating semantic conflict and response conflict in the Stroop task: A functional MRI study. *NeuroImage*, 27, 497-504.

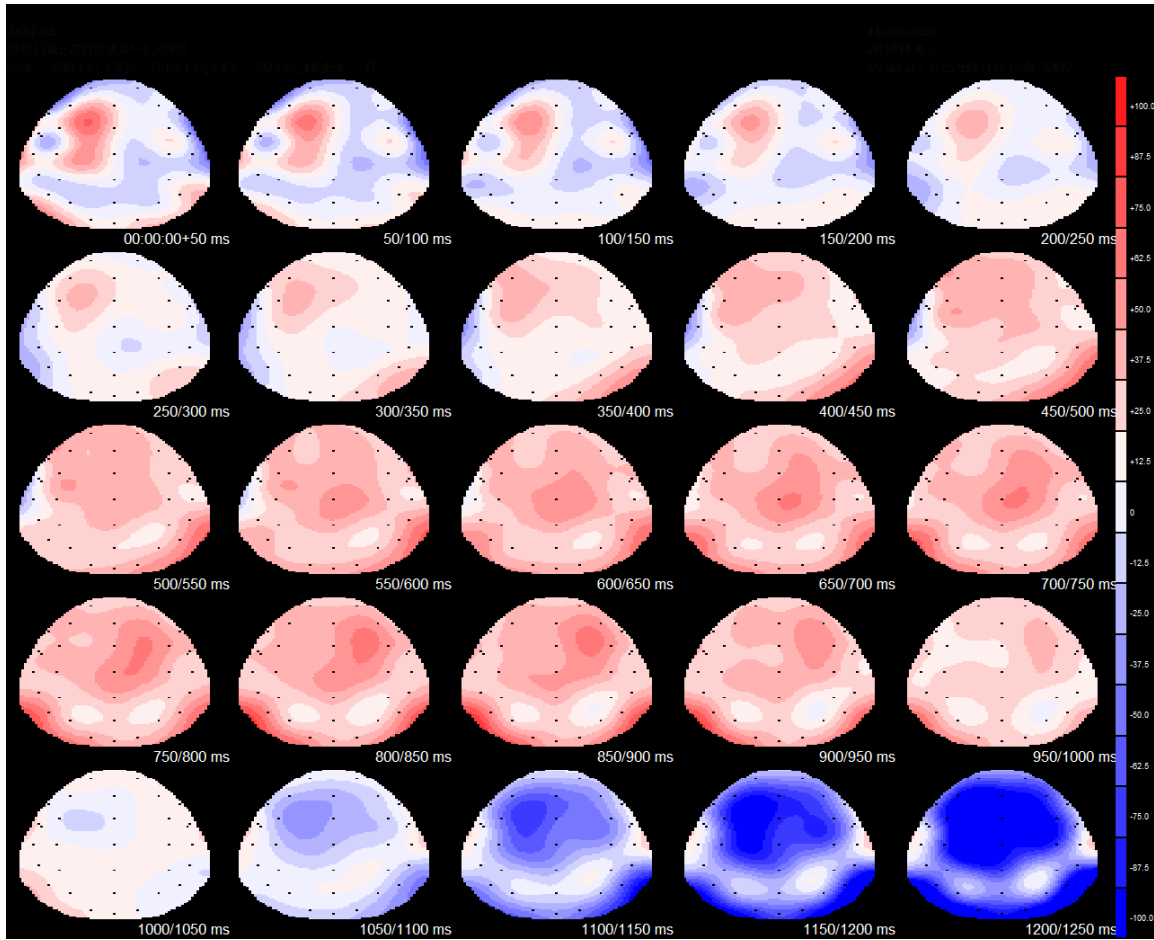
- Varela, F., Lachaux, J.-P., Rodriguez, E. & Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nature reviews neuroscience*, 2, 229-239.
- Verbruggen, F., Liefoghe, B., Vandierendonck, A. & Demanet, J. (2007). Short Cue Presentations Encourage Advance Task Preparation: A Recipe to Diminish the Residual Switch Cost. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 33, 342-356.
- Verbruggen, F. & Logan, G. D. (2008). Response inhibition in the stop-signal paradigm. *Trends in Cognitive Sciences*, 12, 418-424.
- Verguts, T. & Notebaert, W. (2009). Adaptation by binding: a learning account of cognitive control. *Trends in Cognitive Sciences*, 13, 252-257.
- Wagner, A. D. (2001). Synchronicity: when you're gone I'm lost without a trace? *Nature neuroscience*, 4, 1159-1160.
- Wagner, A. D., Bunge, S. A. & Badre, D. (2004). Cognitive Control, Semantic Memory, and Priming: Contributions from Prefrontal Cortex. In M. S. Gazzaniga (Ed.-in-Chief), *The Cognitive Neurosciences* (3rd ed.) (pp. 709-725). CA, MA: The MIT Press.
- Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, 7, 553-559.
- Waldvogel, D., van Gelderen, P., Muellbacher, W., Ziemann, U., Immisch, I. & Hallett, M. (2000). The relative metabolic demand of inhibition and excitation. *Nature*, 406, 995-998.
- Womelsdorf, T., Schoffelen, J.-M., Oostenveld, R., Singer, W., Desimone, R., Engel, A. K. & Fries, P. (2007). Modulation of Neuronal Interactions Through Neuronal Synchronization. *Science*, 316, 1609-1612.
- Yeung, N., Bogacz, R., Holroyd, C. B. & Cohen, J. D. (2004a). Detection of synchronized oscillations in the electroencephalogram: An evaluation of methods. *Psychophysiology*, 41, 822-832.
- Yeung, N., Botvinick, M. M. & Cohen, J. D. (2004b). The Neural Basis of Error Detection: Conflict Monitoring and the Error-Related Negativity. *Psychological Review*, 111, 931-959.
- Yeung, N. & Monsell, S. (2003). Switching Between Tasks of Unequal Familiarity: The Role of Stimulus-Attribute and Response-Set Selection. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 455-469.

Yeung, N., Nystrom, L. E., Aronson, J. A. & Cohen, J. D. (2006). Between-Task Competition and Cognitive Control in Task Switching. *The Journal of Neuroscience*, 26, 1429-1438.

APPENDIX A - Topographic Maps Paper 2 “Face” Cue



APPENDIX A - Topographic Maps Paper 2 “Name” Cue



APPENDIX B - Topographic Map Colour Key

