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Top-Down Modulation of Category Specific Extrastriate Cortex in a Task-Switching Paradigm

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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Abstract

During selective attention, visual stimuli compete for processing capacity. Increased activation is found in extrastriate regions that represent the attended stimulus. However, little research has been done looking at activation in extrastriate regions when attention is shifted between stimulus features. To address this, participants completed a switching task during fMRI scanning. They attended to the colour or motion of bivalent stimuli on different trials. It was hypothesized that attentional modulation would be seen in colour area V4 and motion area V5 and that this modulation would help explain switch costs, a term used to describe why we are slower and more error prone on switch trials. Attentional modulation was found in V4, with greater activity when colour was attended. No modulation was observed in V5. The level of competition between these regions did not differ across switch and repeat trials, suggesting that such competition does not explain switch costs.

Keywords: functional magnetic resonance imaging, top-down modulation, area V4, area V5, task switching.

Dedication

To my husband,

for his endless support and encouragement

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List of Abbreviations

ACC	Anterior cingulate cortex
AIC	Anterior insular cortex
ANOVA	Analysis of variance
BOLD	Blood oxygen level dependent
DLPFC	Dorsolateral prefrontal cortex
dPMC	Dorsal premotor cortex
EEG	Electroencephalography
FDR	False-discovery rate
FFA	Fusiform face area
fMRI	Functional magnetic resonance imaging
GLM	General linear model
HRF	Hemodynamic response function
IFJ	Inferior frontal junction
ITG	Inferior temporal gyrus
ITI	Inter-trial interval
MEG	Magnetoencephalography
PET	Positron emission tomography
PFC	Prefrontal cortex
PPA	Parahippocampal place area
PPC	Posterior parietal cortex
PPI	Psychophysiological interaction analysis
pSMA	Pre-supplementary motor area
ROI	Region of interest

TMS	Transcranial magnetic stimulation
WCST	Wisconsin card sorting task

Chapter 1 - Introduction

> "The brain is the last and grandest biological frontier, the most complex thing we have yet discovered in our universe. It contains hundreds of billions of cells interlinked through trillions of connections. The brain boggles the mind."
>
> James D. Watson, 1992

1.1 Cognitive Control

One of the fundamental questions at the heart of neuroscience is how we, as human beings, are able to perform purposeful, planned behaviours. How is it that the result of the interaction of billions of neurons in the brain can lead to higher-order cognitive functions such as attention, planning and memory? The performance of such tasks requires cognitive control – the ability to guide thought and action based on internal goals (Miller & Cohen, 2001). Such control plays a vital component in our everyday lives. It becomes necessary when a habitual response must be overridden, when distracting stimuli must be ignored, or when we need to shift our attention depending on task requirements. Such behavioural flexibility is crucial as we have limited cognitive resources and we are constantly encountering changing environments. Our actions need to be adapted based on the context, and we must allocate our limited resources to the currently prioritized task. For example, when driving with a passenger on a sunny afternoon, you are capable of both attending to

the road and conversing with your passenger. However, should a snow squall suddenly hit, you would need to stop the conversation and reallocate your full attention to the road to ensure safe arrival at your destination. The change in environmental demands required you to ignore the distracting conversation, inhibit your desire to respond to the passenger, and instead shift your attention to the road in order to successfully perform the task at hand. We are able to perform these selective attention, switching, and inhibition tasks with ease, but a full understanding of how the brain carries out these complex tasks remains to be elucidated.

1.2 Task Switching

While numerous paradigms have been created to assess cognitive control, one that is commonly used is the task switching paradigm. Task switching is the ability to flexibly shift ones attention as the demands of a task change. This ability was first measured in a laboratory setting by Jersild (1927). In a typical task switching experiment, participants are asked to perform a particular task on a discrete set of trials depending on a cue preceding stimulus presentation. The exact task to be performed switches throughout the experiment, so participants must attend to the cue on each trial in order to perform the correct task. Participants typically show switch costs on such tasks, with slower and more error prone responses on switch compared to repeat trials (Kiesel et al., 2010; Monsell, 2003, Vandierendonck, Liefooghe, & Verbruggen, 2010).

There are two main views that attempt to explain the underlying processes behind switch costs. The first is the reconfiguration view (Rogers & Monsell, 1995). This theory emphasizes the need to actively prepare task sets. It suggests that switch costs exist because when a switch of task occurs, task-set reconfiguration must take

place, and this process requires time to readjust what it is that you are attending to. The other prominent hypothesis attempting to explain switch costs is the task-set inertia hypothesis which emphasizes the role of interference rather than reconfiguration (Allport, Styles, & Hsieh, 1994). This theory suggests that switch costs reflect interference from competing stimulus-response mappings with the same stimuli that persist from instructions that were relevant on previous trials.

While both of these theories have been influential in encouraging a surge of research on this topic, neither one has come out as a clear leader. It has been suggested that both of these views are still somewhat incomplete and results do not support one view over the other (Meiran, 1996; Vandierendonck et al., 2010). In fact, one study in particular has demonstrated results which support some aspects of both theories (Cepeda, Kramer, & Gonzalez de Sather, 2001). When participants were given increased time to prepare for the task after a task cue was provided, switch costs were reduced. This result supports the reconfiguration view as when time was provided to readjust ones task-set, the magnitude of the switch cost was reduced. Support was also found for the task-set inertia hypothesis. When the time interval between trials was increased, switch costs were also reduced. In this case, participants weren't aware of which task needed to be performed next during these intervals, so the decreases in switch costs likely reflect decay in interference from the previously performed task. It is evident that both of these theories explain some aspect of the results from task switching studies, but more research in this domain is required to elucidate the underlying processes involved in task switching. These theories are not mutually exclusive, so perhaps a new theory merging the two ideas is required. Alternatively, further exploration of the processing underlying task switching may lead to the emergence of new models to explain switch costs.

1.3 Selective Attention & Top-down Modulation

More theoretical exploration would be useful in the task switching field, and the importance of selective attention in task switching should be considered. Selective attention is the ability to attend selectively to particular information in the environment while ignoring any distracters (Schroeder, 1995). It seems clear that this ability would play an important role in task switching which involves switching one's attention between two stimulus attributes based on which attribute is relevant on a particular trial. Despite the fact that it seems clear that selective attention would be one important component of task switching, surprisingly, these two constructs have been studied independently with little exchange occurring between these two fields of study. Only recently has it been suggested that the underlying processes of task switching and selective attention may be similar (Hanania & Smith, 2010; Meiran, 2000; Meiran, Dimov, & Ganel, 2012). Empirical models of selective attention should be considered in the quest to understand the underlying processes behind switch costs.

Given that we are capable of processing only a limited amount of visual information at a time, exactly how the brain decides what information should be processed is a question of paramount interest to both selective attention and task switching researchers. In an attempt to explore this question, the biased competition model of selective attention was proposed which suggests that objects in our visual field compete for processing capacity (Desimone & Duncan, 1995). Such competition is biased by both bottom-up mechanisms, such as the particular features of the stimulus, and also by top-down mechanisms which bias attention to relevant information. Brain regions in the visual cortex that are selective for the different stimuli in the visual field compete with each other via mutual inhibition. Excitatory top-down signals from the prefrontal cortex (PFC) bias this competition by increasing

the activity of neurons representing the stimulus relevant to the current task, and the consequence of this for irrelevant information is inhibition (Miller & Cohen, 2001). The neurons with higher levels of activity 'win' the competition and the stimulus features that they represent gain further access to memory systems and motor systems where the 'winning' information guides action and behaviour (Kastner & Ungerleider, 2000).

There is some disagreement about whether the biasing of extrastriate regions by top-down control is achieved by the amplification of task-relevant features, the suppression of task-irrelevant features, or both. Theoretical models suggest that this competition is represented in visual regions as an enhancement of task-relevant information (Desimone & Duncan, 1995; Miller & Cohen, 2001), and some empirical support has been provided for this assertion (Egner & Hirsch, 2005). In contrast, other research points to the importance of suppression in the biasing of extrastriate regions (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005). The different results found in these studies may be due to methodological differences in defining baseline activity to measure enhancement and suppression against. The current study hopes to provide some insight into the mechanisms at play during these competitive interactions in extrastriate brain regions. While this theory of biased competition was originally proposed as a model of selective attention, this competition may also take place in the context of task switching (Morton & Munakata, 2002). Looking more closely at competition in visual regions during switching compared to when a task is repeated may help to shed some light on the existence of switch costs.

1.4 Evidence of Top-Down Modulation

Preliminary evidence for the biased competition model of selective attention has emerged from a number of studies over the years. One of the earliest studies to find support for the idea that activity in perceptual visual regions is modulated by attention was a single cell recording study in monkeys (Moran & Desimone, 1985). This study demonstrated for the first time that visual area V4 could be modulated by attention. The response of V4 cells was determined not by the physical properties of all the visual stimuli in the array, but instead by the properties of the attended stimulus. This same attentional effect has also been found in area MT in monkeys (Treue & Maunsell, 1996).

More recent studies in humans using a variety of neuroimaging techniques have also provided support for the biased competition model of attention. Early studies used selective attention paradigms alongside positron emission tomography (PET; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991), functional magnetic resonance imaging (fMRI; Buchel et al., 1998; Chawla, Rees, & Friston, 1999; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Shibata et al., 2008), magnetoencephalography (MEG; Schoenfeld et al., 2007; Shibata et al., 2008), and electroencephalography (EEG; Schoenfeld et al., 2007) to show that activity in extrastriate regions V4 and V5 could be modulated based on attentional goals. Area V4 and V5 are both category specific regions in extrastriate cortex that have been shown to respond selectively to colour and motion, respectively (Zeki et al., 1991). In one study examining this modulatory effect in selective attention, participants were shown the same bivalent moving coloured dot array on all trials, attending to motion on some blocks, and colour on other blocks. Higher activation was seen in area V4 when colour stimuli were attended, while higher activation was seen in area V5 when

stimulus motion was attended (Shibata et al., 2008). These identical visual stimuli produced different activation patterns in these extrastriate visual regions based on attentional goals. These regions are likely receiving top-down signals which are biasing attention towards stimuli that are relevant to the current task. This attention modulation effect has also been observed in other extrastriate brain regions such as the fusiform face area (FFA) when subjects are asked to selectively attend to faces, and the parahippocampal place area (PPA) when subjects are instructed to attend to houses (O'Craven, Downing, & Kanwisher, 1999). These studies provide support for the idea that the top-down modulation of extrastriate regions is reflected in an enhancement of brain regions that represent information that is task relevant.

More recent research has begun to look at the role of suppression in task irrelevant regions to further explore the competitive interactions of extrastriate visual regions during attention. Such research is particularly interesting because in addition to looking at the role of suppression in competition, these studies have focused on identifying the role of extrastriate regions during working memory, a more challenging cognitive control task. Using both univalent and bivalent stimuli in the context of working memory paradigms, several studies have found evidence for top-down modulation in extrastriate regions (Gazzaley, Cooney, McEvoy et al., 2005; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Rutman, Clapp, Chadick, & Gazzaley, 2010; Zanto & Gazzaley, 2009; Zanto, Rubens, Bollinger, & Gazzaley, 2010; for review see Gazzaley, 2010 and Gazzaley, 2011).

In the context of working memory, competition in extrastriate regions takes place due to both the enhancement of task-relevant information and the suppression of task-irrelevant information. This finding was elucidated in a study which had participants perform a working memory task during fMRI scanning (Gazzaley,

Cooney, McEvoy et al., 2005). On each trial, four stimuli were sequentially presented, 2 images of faces, and 2 images of scenes. Following this was a delay period and then a probe enquiring about a feature of the relevant stimulus dimension on that particular trial. On some trials participants were instructed to attend to the face, on other trials they were to attend to the scenes, and on others they were to just passively view the stimuli. Participants showed evidence of top-down modulation of the FFA when faces were to be recalled, and the PPA when scenes were the stimuli to be recalled. Both enhancement and suppression of these brain regions was found relative to the passive viewing baseline depending on the task instruction given such that, the PPA, a scene selective brain area, showed higher activity when scenes were attended compared to the passive view baseline, and also reduced activity compared to baseline when scenes were to be ignored. This study provides evidence for the hypothesis that competition in extrastriate visual regions is represented by both an enhancement of task-relevant information and a suppression of task-irrelevant information. In a similar working memory task, but substituting the face and scene stimuli for motion and colour stimuli, similar attentional modulation has been found in V4 when colour was to be remembered and V5 when direction of motion was to be recalled (Zanto et al., 2010).

The top-down modulation of these extrastriate regions is also related to subsequent working memory performance. Using EEG, it has been shown that the N1 component is modulated by attention to colour while the P1 component is modulated by attention to motion (Zanto & Gazzaley, 2009). This modulation is also related to task performance. High working memory performance on the colour task was associated with attentional modulation of the N1 component, while a lack of such modulation was associated with low working memory performance. Similarly, low

working memory performance on the motion task was associated with a lack of modulation of the P1 component (Zanto & Gazzaley, 2009).

While these working memory experiments suggest that competition in extrastriate regions takes place due to both the enhancement of task-relevant regions and the suppression of task-irrelevant regions, other research suggests that this may not be the case. It has been suggested that instead, such competition is reflected by an enhancement of task-relevant information, but not a suppression of task-irrelevant information (Egner & Hirsch, 2005). This study examined modulation in the FFA while participants performed a variant of the Stroop task which involved discriminating between actors and political figures. Faces with names superimposed on them were presented to participants, and on some trials participants categorized the face as actor or politician, and on other trials they categorized the name written over the face as actor or politician. When faces were the target stimuli, activity in the FFA was enhanced; however when faces served as the distracting stimuli, cognitive control had no effect on FFA responses, thus no suppression was found.

It is evident that modulation of extrastriate regions is present even on challenging cognitive control tasks such as working memory and inhibition, and such modulation is tightly related to performance on such tasks. This presents the possibility that the same modulation may be seen during the performance of switching tasks. Such competition between regions may play an important role in explaining switch costs if the degree of competition differs between switch and repeat trials. Whether this competition plays out in terms of an enhancement of task-relevant information alone, or the enhancement of relevant information and the suppression of task-irrelevant information remains to be determined.

1.5 fMRI Studies of Task Switching

Before delving into studies which have begun to explore whether similar top-down modulation exists in extrastriate regions during task switching, it is important to note the other brain regions that are associated with performance on switching tasks. Functional neuroimaging studies have identified a distributed fronto-parietal network that is consistently activated during the performance of task switching in a variety of studies using different paradigms and stimuli (Badre & Wagner, 2006; Braver, Reynolds, & Donaldson, 2003; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Gold, Powell, Xuan, Jicha, & Smith, 2010; Liston, Matalon, Hare, Davidson, & Casey, 2006; Liu, Slotnick, Serences, & Yantis, 2003; Morton, Bosma, & Ansari, 2009; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; Yeung, Nystrom, Aronson, & Cohen, 2006). The key cortical regions involved in this network include the anterior cingulate cortex (ACC)/ pre-supplementary motor area (pSMA), the dorsolateral prefrontal cortex (DLPFC), the inferior frontal junction (IFJ), the anterior insular cortex (AIC), the dorsal pre-motor cortex (dPMC), and the posterior parietal cortex (PPC). These regions are consistently activated in studies of task switching, and they have also been found to form a functionally connected network (Cole & Schneider, 2007). These regions work together to implement cognitive control during switching tasks.

Studies that have moved away from looking specifically at these cognitive control regions, and have instead explored activation in pathways processing the different stimuli used in the task have led to some interesting findings. It has been suggested that switch costs may be in part due to the activation of areas that are associated with processing the irrelevant task, suggesting that competition between extrastriate brain regions may be playing a role in creating switch costs. The

competition hypothesis was proposed which suggests that stimuli are processed according to all of the stimulus-response rules that have been learned in the past (Wylie, Javitt, & Foxe, 2003a, 2004a, 2004b). So, when bivalent stimuli are used, and a task is performed on each dimension of that stimulus, the processing pathways for the two dimensions will be activated on each trial regardless of which task is currently relevant. Some sort of competition will then occur and only the pathway that processes the currently relevant task representation will win that competition. This hypothesis suggests that in the context of a cognitively demanding task such as switching, competition between brain regions may be important for successful performance. This theory is similar to the task set inertia hypothesis (Allport et al., 1994), but extends these ideas by suggesting how they may play out at a neural level.

A number of studies have provided support for this competition theory. In order to examine competition between stimulus processing pathways, one such study had participants complete a switching task during fMRI scanning (Wylie et al., 2004a). The stimuli used during this task consisted of bivalent face/colour stimuli and motion/thickness stimuli. The experiment consisted of three stages. During the initial stage, participants were presented with the two different types of stimuli mentioned above, and they attended and responded to the face when a face/colour stimulus was presented and to the thickness of the stimuli when motion/thickness stimuli were presented. They switched between performing these two tasks depending on which stimulus was presented. In the second stage, participants had to perform an entirely different task with the same stimuli. They had to attend and respond to the colour of the face/colour stimuli, and to the motion of the motion/thickness stimuli. Again, participants switched between these two tasks throughout the stage. Finally, during the third stage, participants went back to performing the same task that had been

performed in stage one. They had to respond to the faces and the thickness of the stimuli depending on which was presented. The stimuli presented in this third were exactly the same stimuli that were used in stage one. Activation during the third stage was contrasted with activation during the first stage to examine whether performing a different task on the same stimuli in stage 2 had any impact on performance. This experimental design allowed for the examination of the impact that adding a different stimulus-response mapping would have on behavioural performance and/or brain activation. Brain areas that were associated with motion and colour, which were irrelevant on both stage one and stage three, were more active on the third block than on the first block. Participants also showed larger switch costs on the third block compared with the first block even though the task they performed was identical. These results suggest that the tasks that were learned in stage two interfered with performance during stage three both at a behavioural and neural level. It appears that performance on switching tasks is impacted by interference from stimulus-response mappings that were once relevant, but are now irrelevant, consistent with the competition hypothesis.

Of particular interest though, is not whether some sort of interference is occurring, but what the effect of that interference is in specific regions of extrastriate cortex. Evidence for such competition within the extrastriate cortex during task switching has been found in the FFA and the PPA using fMRI (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004). Participants performed a switching task which involved shifting attention between superimposed faces and houses. Prior to scanning, subjects memorized two houses, and two faces. One of these indicated that the participant should hold their attention on the current dimension, while the other signalled a switch, indicating that participants should switch their attention to

the other dimension. Participants followed the instructions of these targets, and pressed a button to indicate that a target had been detected. Activity in the FFA was higher when participants were supposed to be attending to faces rather than houses. Similarly, the PPA was more active when participants were attending to houses rather than the faces. This modulation of FFA during task switching has been replicated, and attentional modulation in the inferior temporal gyrus (ITG) has also been observed when participants were performing a task that involved switching between attending to faces and attending to words (Yeung et al., 2006). The results of this study suggest that modulation can be observed in FFA, PPA, and ITG based on attentional goals.

To date, only three studies have been conducted to examine modulation in colour area V4 and motion area V5 in humans in the context of task switching, but these studies have left some unanswered questions. The first study used fMRI to explore the neural mechanisms of feature based attentional control (Liu et al., 2003). In this study, participants viewed bivalent stimuli consisting of moving, coloured dots. Both the colour and the direction of motion of the dots changed once per second. Participants were instructed of two target colours and two target directions of motion prior to beginning the task. One target of each dimension instructed participants to shift their attention from the currently attended dimension, while the other targets indicated that participants should maintain their attention on the currently attended feature. Participants pressed a button when a target was viewed. In order to assess whether attentional modulation had taken place, brain activity on attend to motion trials was contrasted with activity on attend to colour trials. Modulation was found in the left inferior temporal gyrus when participants held their attention on motion, and modulation in the right fusiform gyrus was found when participants held their attention on colour. This study did not use an independent localizer to determine

individual colour and motion areas. While the fusiform gyrus showed attentional modulation when participants attended to the colour of the stimuli, this activation did not fall in area V4, an area that has been implicated in colour processing. While this study seems to suggest that modulation based on attention does occur in task switching studies of motion and colour, the question still remains as to whether this modulation occurs in category specific areas V4 and V5.

Another study which was conducted to examine competition in motion and colour processing areas was interested in examining the conflict monitoring hypothesis of attention. This hypothesis suggests that the ACC monitors for any conflict in information processing while the DLPFC then acts to resolve that conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001). In order to test this hypothesis, an experimental paradigm designed to instigate conflict was used so that the mechanisms involved in resolving this conflict could be explored using fMRI (Liston et al., 2006). On each trial, participants were presented with a pair of square-wave gratings located on either side of the screen. These gratings were either red or blue and were moving up or down. On some trials, a cue instructed participants to press the button corresponding to the side the red stimulus was on, and on other trials the cue switched and instructed participants to choose the side with upward motion. In order to assess the role that the prefrontal cortex plays in conflict processing, a conflict index was calculated. Based on the contrast of colour shift trials and motion shift trials, three brain regions were identified as colour sensitive, and three regions were identified as motion sensitive. A conflict index was then calculated as a product of activity in the three motion sensitive areas and the three colour sensitive regions. Conflict was significantly higher on switch trials than repeat trials, suggesting that competition is greater on switch trials. Like Wylie et al. (2004a), this study does support the idea that

competition takes place in regions responsible for processing the relevant stimulus dimensions. However, it still does not offer any indication of whether modulation takes place in area V4 or V5. Again, a functional localizer was not used to identify motion area V5 and colour area V4. A localizer task should be administered in order to address the question of whether competition is taking place in category specific extrastriate regions V4 and V5. Only with the use of such a methodology can modulation within these category specific regions be examined.

The need for a localizer scan to independently identify these extrastriate regions before examining modulation within them is clearly an important next step to determining whether top-down modulation and competition between early visual regions occurs in the context of task switching. Only one study to date has independently localized area V4 and V5 before examining modulation within these regions using fMRI. However, the focus of this study was not on whether modulation occurs in these regions during stimulus presentation, but whether competition can be seen in these early visual areas prior to stimulus presentation during the preparation phase of a task switching study (Wylie, Javitt, & Foxe, 2006). The stimuli used in this study were coloured rotating rectangles. Depending on a cue preceding stimulus presentation, participants had to indicate whether the rectangle was red or blue, or whether it was moving slowly or quickly. The cue switched throughout the course of a run. In addition, univalent trials were included which were used to independently identify motion and colour areas of the brain. The analyses focussed solely on activation during cue presentation. Modulation in the regions identified by the localizer was seen during the cue period of the colour task, with participants showing higher activation in area V4 when preparing to attend to colour. This modulation which is in an index of preparation proved to be very useful for performance on the

switching task as no switch costs were found during the colour task. In contrast, modulation was not found during the cue period in V5, suggesting that participants were less able to prepare for this task, and this was reflected in the behaviour of participants as they displayed large switch costs during the motion task. While these results are interesting, the researchers did not examine modulation in these same regions during the actual stimulus presentation. Studies have shown that baseline increases in activation in area V5 related to the expectation of motion do not predict the modulation of neural responses that occur when the actual stimulus is presented (McMains, Fehd, Emmanouil, & Kastner, 2007). Thus a key question of interest that remains unaddressed is whether modulation is seen in area V4 and area V5 when bivalent colour-motion stimuli are presented and different aspects of the stimuli are relevant on different trials. This study hopes to shed some light on this issue.

1.6 The Role of Prefrontal and Parietal Regions in Top-Down Modulation

An important question emerges from a consideration of these previous findings which suggest that you do see modulation in extrastriate regions based on attentional goals. The question of which brain regions are actually responsible for providing these biasing signals remains to be addressed. Miller and Cohen's (2001) model of PFC function suggests that modulation takes place due to top-down influences from PFC structures. The PFC is thought to provide biasing signals which guide neural activity in visual regions to process task relevant information. The PFC is well-suited anatomically for implementing such biasing signals. It sends and receives projections from almost all cortical sensory and motor systems as well as many subcortical structures (Miller & Cohen, 2001; Tanji & Hoshi, 2008). These

extensive anatomical connections would suggest that the PFC would be able to perform such a modulatory role.

In additional support of this idea, axonal tract-tracing studies in monkeys have shown that long range reciprocal cortico-cortical connections exist between the PFC and the visual association cortex, suggesting that it is certainly possible that the PFC may bias extrastriate regions (Cusick, Seltzer, Cola, & Griggs, 1995; Petrides & Pandya, 2002; Rempel-Clower & Barbas, 2000; Ungerleider, Gaffan, & Pelak, 1989). Reciprocal connections have been identified between the PFC and colour area V4 (Rempel-Clower & Barbas, 2000) as well as motion area V5 (Cusick et al., 1995). Other evidence in support of the assertion that the PFC biases extrastriate regions during selective attention comes from lesion studies in humans. It has been shown that people with DLPFC lesions have difficulty detecting visual targets, and importantly, this behavioural deficit is accompanied by diminished extrastriate responses (Barcelo, Suwazono, & Knight, 2000). This result suggests an important relationship between the PFC and extrastriate visual regions during visual attention tasks.

More controlled, but indirect evidence of a functional relationship between the PFC and extrastriate brain regions has begun to emerge with the introduction of functional connectivity analyses used with fMRI data. In an fMRI study of working memory processing, attentional modulation was found in area V4 and area V5 (Zanto et al., 2010). Motion and colour stimuli were presented to participants on each trial, and when they were to attend to and remember the coloured stimuli, activity was higher in area V4 than when they were to ignore the coloured stimuli. Similarly, activity in area V5 was higher when participants had to attend to and remember the direction of motion of the stimuli, rather than ignore the direction of motion. In order to determine which brain regions were responsible for modulating activity in these

extrastriate regions, a functional connectivity analysis was conducted. The IFJ was found to be involved in modulating both area V4 and V5. The time course of activity in the IFJ showed a higher correlation with activity in area V4 during the attend colour condition compared to the ignore colour condition, and also showed a higher correlation with activity in area V5 during the attend motion condition compared with the ignore motion condition. Causal evidence has also been found for the role of the IFJ in top-down modulation. When transcranial magnetic stimulation (TMS) was applied to the right IFJ, creating a virtual lesion in this area, modulation of extrastriate regions was reduced (Zanto, Rubens, Thangavel, & Gazzaley, 2011). This reduced modulation was also accompanied by poorer working memory accuracy on the working memory colour task. These results suggest that the IFJ plays a vital role in modulating both area V4 and V5, and that this modulation is important for task performance.

It has been suggested that in conjunction with the PFC, parietal regions also provide top-down signals to extrastriate cortex in order to bias processing towards information that is currently relevant (Corbetta & Shulman, 2002). Just like the PFC, the parietal cortex shares a functional relationship with visual regions. TMS applied to the angular gyrus leads to a modulation in the excitability of visual cortex (Silvanto, Muggleton, Lavie, & Walsh, 2009). Similarly, TMS to the inferior parietal sulcus has an effect on the blood oxygen level dependent (BOLD) signal in a variety of visual regions including area V4 and V5 (Ruff et al., 2008). These results suggest an important relationship between parietal regions and area V4 and V5. A number of neuroimaging studies have also found that a variety of regions in the parietal cortex appear to modulate extrastriate areas during selective attention and working memory tasks (Giesbrecht, Woldorff, Song, & Mangun, 2003; Hopfinger, Buonocore, &

Mangun, 2000; Herrington & Assad, 2010). Specifically, one study has shown that the supramarginal gyrus/angular gyrus plays an important role in modulating colour area V4 when participants are to attend to colour and ignore another stimulus dimension (Zanto et al., 2011). It seems that a network of fronto-parietal regions may be responsible for providing top-down modulatory signals to extrastriate regions in order to bias processing in these regions towards information that is behaviourally relevant.

1.7 Area V4 and V5

Motion and colour were used as the stimulus features of interest in this study because distinct extrastriate regions respond selectively to each of these categories with area V4 responding to colour and area V5 to motion (Zeki et al., 1991). Area V4 and V5 are particularly useful extrastriate regions for examining competitive interactions for a number of reasons. Colour information flows into the ventral visual pathway, and it is along this pathway that area V4 is located (Goodale & Milner, 1992; Ungerleider, Courtney, & Haxby, 1998). Studies using both PET and fMRI have consistently shown that when participants passively view coloured stimuli compared with achromatic versions of the same stimuli, an area of the ventral occipitotemporal cortex is activated (McKeefry & Zeki, 1997; Zeki et al., 1991). Colour stimulation is consistently associated with activation in this area, which is referred to as area V4. The actual location of area V4 can differ somewhat across individuals, but it is always located on the lateral aspect of the collateral sulcus of the fusiform gyrus (McKeefry & Zeki, 1997). This colour sensitive region is activated both when participants attend to and make decisions based on colour and when they merely passively view coloured stimuli (Chawla et al., 1999; Grill-Spector & Malach, 2004; McKeefry & Zeki, 1997).

Unlike colour, motion is processed by the dorsal visual pathway (Goodale & Milner, 1992; Ungerleider et al., 1998). One particularly important region for motion processing within this pathway is area V5 which is located in the temporo-parieto-occipital junction (Grill-Spector & Malach, 2004; Zeki et al., 1991). Using both PET and fMRI, it has been shown that this brain region displays greater activation when participants are passively viewing moving dots, moving square patterns or moving checkerboards than it does to these same stimuli when they are stationary (Dumoulin et al., 2000; Watson et al., 1993; Zeki et al., 1991). The importance of area V5 for motion processing was highlighted in a study which demonstrated that TMS to this area is effective in abolishing the perception of motion (Beckers & Zeki, 1995). While the location of area V5 does differ somewhat across subjects it usually falls just posterior to the meeting point of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus (Dumoulin et al., 2000; Watson et al., 1993). Area V5 is activated both while passively viewing moving objects and also when purposefully attending to the movement of objects (Chawla et al., 1999). This highlights the important role that this region plays in the visual perception of motion.

It is clear that area V4 and area V5 are separate regions, both anatomically, and functionally. In addition to this spatial and functional separation, area V4 and V5 also fall into different visual processing streams. Despite all of these factors demonstrating the differences between area V4 and V5 they also share a relationship to one another, and this makes the investigation of these two regions particularly interesting. Evidence for a competitive relationship between these two brain areas has been presented, suggesting that an inhibitory relationship exists between area V4 and V5. In an experiment designed to examine the functional role of V5, TMS was applied to area V5 and participants were then asked to perform a series of visual

search tasks with both moving and coloured stimuli (Walsh, Ellison, Battelli, & Cowey, 1998). TMS applied to V5 had a detrimental effect on tasks which involved motion as the relevant stimulus dimension, with participants showing increased reaction times on these tasks. In contrast, the TMS actually facilitated performance on tasks in which colour was relevant, with reaction times decreasing on these trials. TMS to V5 may have been beneficial to performance on the colour task due to disinhibition of the colour area when the normal role of V5 was eliminated. These results suggest that area V4 and area V5 do compete for processing resources, and hold the type of competitive relationship proposed by Desimone and Duncan (1995). As such, motion and colour seemed to be ideal stimuli to use in order to examine whether competition between category specific regions takes place during task switching.

1.8 Purpose and Hypotheses

Having the ability to rapidly switch our attention between tasks is a vital part of our daily functioning. This study aimed to shed some light on the neural mechanisms that underlie this ability by exploring whether the top-down attentional modulation of extrastriate visual regions seen in selective attention paradigms is also present during task switching. Another aim of this study is to determine whether such modulation may help to explain the existence of switch costs.

In order to explore the neural regions involved in switching and to elucidate the role of top-down modulation in such tasks, this study utilized a switching paradigm during event-related fMRI scanning. The task involved participants viewing bivalent moving coloured dot stimuli on each trial. On some trials participants were instructed to attend to the motion of the dots, while on other trials they were instructed

to attend to the colour of the dots. The relevant feature switched throughout the experiment. An independent functional localizer was administered to independently identify area V4 and V5 in each individual subject so that modulation in these specific regions could be explored. Other brain regions recruited during the switching task were also examined. Using this paradigm, the question of whether top-down modulation can be observed in colour area V4 and motion area V5 based on attentional goals was examined in the context of task switching. Another question of interest was whether this competition between extrastriate visual regions was greater on switch trials compared to when the task was repeated. If this was the case, this greater competition between visual regions processing both relevant and irrelevant features may explain why switch costs are found using such paradigms. While some studies have begun to examine these questions in the context of task switching, they have failed to use an independent localizer to identify category specific regions (Liu et al., 2003; Liston et al., 2006) or have not looked at modulation within these regions during stimulus presentation when one would expect competition to be strongest (Wylie et al., 2006). This study hopes to fill these gaps and shed more light on these important questions.

The first hypothesis predicted that activation would be seen in the network of brain regions that has been described as the cognitive control network when participants switch between tasks. This would include activation in ACC/pSMA, DLPFC, dPMC, AIC, IFJ, and PPC (Cole & Schneider, 2007). Activation in these regions was expected because switching attention requires cognitive control. The implementation of this control will likely recruit these regions in order to successfully perform the required task.

Secondly, it was hypothesized that modulation would be expected in both area V4 and area V5 based on the goals at the time of encoding the stimulus. It was expected that top-down modulation would enhance activity in the region specialized for processing the relevant stimulus dimension (Miller & Cohen, 2001). Modulation in these regions has been found in the context of simple selective attention tasks (Buchel et al., 1998; Chawla et al., 1999; O'Craven et al., 1997; Schoenfeld et al., 2007; Shibata et al., 2008), and also in more cognitively demanding working memory tasks (Zanto et al., 2010; Zanto et al., 2011). The explanation for why modulation was found in these working memory tasks was that it was due to the vital role that selective attention plays in the completion of such tasks. It was expected that in the context of task switching, modulation in these regions will also be seen since selective attention also plays a key role in performance during switching.

The third hypothesis explores how such modulation and competition will differ across switch and repeat trials. There are three potential hypotheses regarding exactly how the differences in competition may play out across the different trial types. First, it was possible that we would see this competition indexed by an enhancement of task-relevant regions, but with no differences in activation in the task-irrelevant region akin to the findings of Egner and Hirsch (2005) (Figure1a). Second, it was possible that we would see a suppression of task-irrelevant regions, with no differences in activation in task-relevant brain areas (Figure 1b). The final possibility was that competition would take place in these extrastriate brain regions through both the enhancement of task-relevant regions and the suppression of task-irrelevant regions as suggested by Miller and Cohen (2001) and Gazzaley, Cooney, McEvoy et al. (2005) (Figure1c). Regardless of which of these suppositions is true, it was expected that the level of competition would be strongest on the switch trial, and

would subsequently decrease with each repeat trial. This would fit nicely with the findings of Liston et al. (2006) which demonstrated greater competition between motion and colour relevant regions on switch trials relative to repeat trials. It also falls in line with the ideas presented by Wylie et al. (2004a, 2004b) who suggested that competition between stimulus-response mappings would take place on all trials when more than one response was associated with a given stimulus, but such competition will be more pronounced on switch trials. It is expected that competition will be smallest on the late repeat trials when participants would have been performing the same task for a large number of trials.

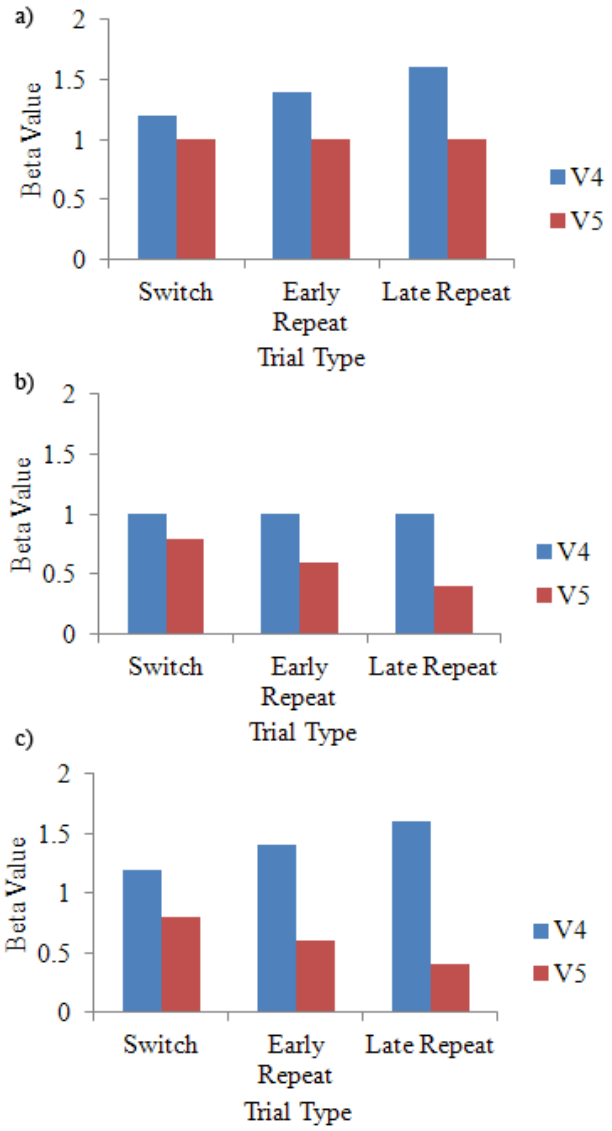

Figure 1. A visual depiction of three different ways in which competition between area V4 and area V5 may play out in the context of task switching on colour relevant trials. a) Enhancement of task-relevant information indexed by increased activation in V4, and no change in activation in V5. b) Suppression of task-irrelevant information indexed by no change in activity in V4, but a decrease in activity in V5. c) Both enhancement of task-relevant information and suppression of task-irrelevant information, indexed by an increase of activity in V4, and a decrease of activity in V5. Switch trials are trials in which a switch in dimension has occurred. Early repeat trials are the first and second trials following this switch in which the same dimension is repeated, and late repeat trials are the third, fourth and fifth trials in which the same stimulus dimension is repeated.

In addition to addressing the question of whether competition between V4 and V5 differed across trial type, differences in the degree of modulation within these extrastriate visual regions was examined. It is possible that differences in the level of competition between V4 and V5 would not be found between switch and repeat trials, but that differences in the degree of modulation across these different trial types would be found if activity within these regions was looked at independently. It was predicted that the smallest amount of modulation would occur on switch trials when top-down modulation is just beginning to modulate attention in the relevant extrastriate region, and the greatest amount of modulation would occur on later repeat trials as participants become better at honing in on the relevant stimulus.

Finally, the fourth hypothesis deals with the question of which brain areas may be responsible for implementing biasing signals and modulating area V4 and V5. It is expected that the PFC will play an important role in this top-down modulatory process. More specifically, it is expected that the IFJ will be involved in modulating both area V4 and area V5. The IFJ plays an important role in cognitive control, and is consistently activated in studies of task switching (Brass, Derrfuss, Forstmann, & von Cramon, 2005; Cole & Schneider, 2007; Derrfuss, Brass, Neumann, & von Cramon, 2005; Morton et al., 2009). In addition, this region has been shown to be involved in the modulation of both area V4 and area V5 in the context of a working memory task (Zanto et al., 2010; Zanto et al., 2011). Another brain region that is expected to play a role in the modulation of these extrastriate regions is the parietal cortex. This area of the brain has been implicated in the modulation of visual regions in the context of an attention shifting task in monkeys (Herrington & Assad, 2010) and in the context of working memory tasks in humans (Zanto et al., 2011) so it is expected that it will play an important role in the modulation of extrastriate regions in the present study. More

specifically, it is expected that the supramarginal gyrus and angular gyrus will be involved in modulating both area V4 and V5. These brain regions have been shown to play an important role in modulating these extrastriate regions in the context of working memory (Zanto et al., 2011).

Chapter 2 – Methods

2.1 Participants

Twenty-one adults ranging in age from 18-28 (mean 23.86; 10 males) were recruited from the undergraduate and graduate faculties at Western University to participate in this study. All participants were right-handed, had normal or corrected to normal vision and reported no history of neurological or psychiatric illness. Data from three participants were excluded from the analyses, one due to excessive motion (greater than 3mm), one because their behavioural accuracy performance was more than 4 SD below the group mean, and one due to an inability to localize area V4 or V5 with the functional localizer. Thus, the data presented here are from 18 participants. All participants provided informed consent consistent with the policies of the Human Subjects Research Ethics Board at Western University.

2.2 Stimuli

All stimuli in the task-switching runs were bivalent moving coloured dots presented on a black background. The stimuli consisted of a rectangular array of 290 dots. The dots moved in one of six directions (left, upper-left, lower-left, right, upper-right, lower-right), and were displayed in one of six different colours. The dots were either dark red (red, green, blue (RGB) value = 128, 0, 0), light red (RGB = 255, 0, 128), medium red (RGB = 255, 0, 0), dark blue (RGB = 0, 0, 255), light blue (RGB = 0, 128, 255), or medium blue (RGB = 0, 0, 255). Each of these different directions and colours were matched. This meant that 36 different bivalent stimuli were used in the experiment. A gray fixation cross was displayed in the centre of the screen throughout the runs and participants were instructed to maintain central fixation

throughout the experiment. The localizer task involved the presentation of univalent stimuli presented in different blocks. Some blocks contained stationary gray dots, other blocks contained stationary coloured dots (blue or red), and other blocks contained moving gray dots which moved either left or right.

2.3 Experimental Procedure

Participants completed two event-related task switching runs. Each trial within these runs involved the presentation of a bivalent stimulus. Participants had to attend to only one dimension of the stimulus (colour or direction of motion) on each trial however, the relevant dimension switched throughout the run. Participants were instructed to respond as quickly and accurately as possible to each trial based on an auditory cue that preceded the trial. The auditory cue was 600ms in length and was presented 500ms prior to the appearance of the stimulus. The cue instructed participants as to which aspect of the stimulus to attend to and consisted of the word "motion" preceding motion-relevant trials and "colour" preceding colour-relevant trials. Following the auditory cue, a bivalent stimulus was presented for 750ms and participants had up to 2000ms to respond. In the motion condition, participants responded to the direction of motion of the dots, pressing 1 if the dots were moving left and 2 if they were moving right. In the colour condition, participants responded to the colour of the dots indicating whether they were red or blue. This response was issued by pressing 1 or 2, the button assignment for the colour condition varied across subjects. Responses were given on a four button response box held in the right hand. The 2 buttons that were not utilized for this experiment were covered with tape to alleviate confusion regarding which buttons to press. See Figure 2 for a schematic depiction of the trial sequence.

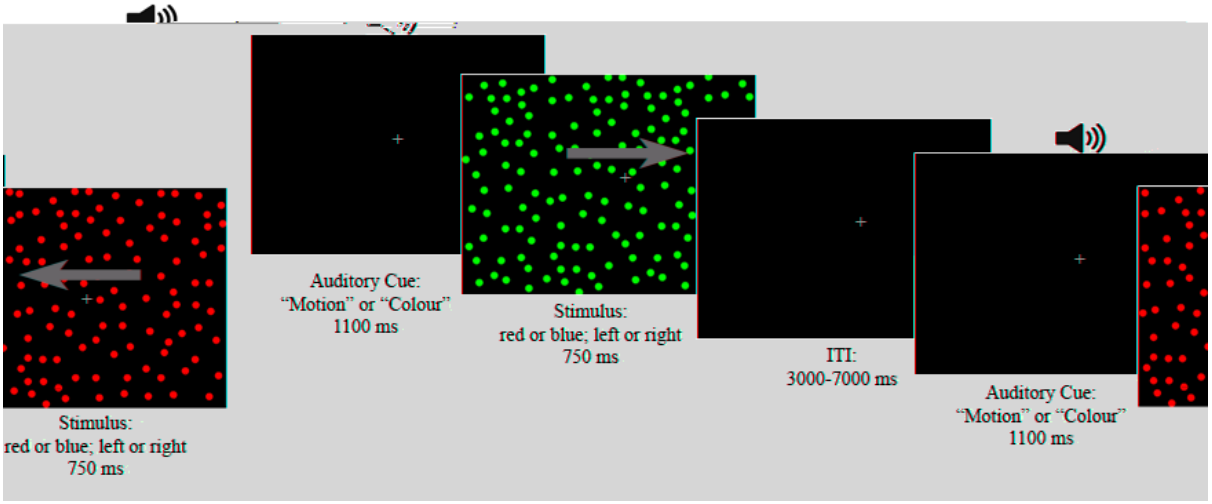

Figure 2. Schematic illustration of trial sequence. Participants attended to either colour or motion depending on the auditory cue preceding stimulus presentation. They were required to make a behavioural choice based on the dimension of relevance as quickly and as accurately as possible. Gray arrows simply indicate direction of stimulus motion, and were not part of the stimulus administered during the task.

The relevant dimension switched throughout the run so participants were required to remain alert for the occurrence of switch trials which would require them to shift their attention. A particular dimension was relevant for 3 to 5 trials before a switch occurred. In total, 6 different trial types were included in the experiment. Switch trials were trials in which the relevant dimension changed from what was previously relevant. Repeat 1 was the first trial following the switch in which the relevant dimension repeated for the first time. Trials in which the relevant dimension repeated for the second time were referred to as repeat 2, followed by repeat 3, repeat 4, and repeat 5 which was the fifth time that the relevant dimension repeated.

Participants completed two runs of the task-switching task with 655 volumes collected in each run. Each run consisted of 160 trials; for 80 of these trials, colour was relevant; for the remaining 80, motion was relevant. There were an equal number of congruent and incongruent trials in both attention conditions in both runs. There

were also an equal number of congruent and incongruent, and colour- and motion-relevant trials in each of the 6 trial types mentioned above. To desynchronize the timing of events with respect to the acquisition of brain slices and to ensure requisite variability in signal time courses to permit event-related modelling, inter-trial intervals (ITI) of different durations were included, ranging from 3000-7000ms with a mean ITI of 5000ms. An additional sixty-two null events, the timing of which equalled that of the task events, were distributed randomly across the two runs. During null events, participants maintained fixation and no response was required. These events were included to increase the variability in signal time courses to allow for event-related modelling.

Participants also completed a motion and colour localizer task during which 215 functional volumes were collected. The localizer was a block design consisting of 25 15s blocks. Six of these blocks were motion blocks which required participants to view 15 moving gray dot stimuli. Participants were instructed to respond to each stimulus by pressing 1 if the dots were moving left and 2 if they were moving right. There were also 6 colour blocks during which participants viewed stationary coloured dots which were either blue or red. They were instructed to respond to each stimulus by pressing 1 or 2. The assignment of the buttons varied across participants, but corresponded to the colour-response associations used for that particular participant in the task-switching runs. Each stimulus was presented for 750ms followed by a 250ms interstimulus interval (ISI). Each of these task blocks were separated by a rest block. There were 13 rest blocks in total which consisted of the presentation of stationary gray dots consistently throughout the 15s block. No response was required on rest blocks. A gray fixation cross was present in the centre of the screen throughout the localizer run and participants were instructed to maintain fixation.

Subjects practiced both the task switching and localizer tasks before the main experiment commenced and all reported that they understood the task and were ready to proceed. All stimuli were projected from a Windows PC running E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) at a resolution of 1024 x 768. Stimuli were projected onto the centre of a screen which was mounted outside of the magnet. Participants viewed the display through a mirror which was placed above the head coil. The visual display was 15cm in height and 20cm in width and was located 25cm away from the mirror, which subtends approximately 43.6° of visual angle.

2.4 fMRI Data Acquisition

Functional and structural images were collected using a 3-Tesla Siemens Tim Trio scanner, using a Siemens 32-channel head coil. T2*- weighted functional scans were acquired using an echo-planar imaging pulse sequence. Thirty seven slices per volume were collected using an ascending, interleaved slice acquisition order which provided coverage of the whole brain (repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, FOV = 210mm x 210mm, flip angle = 90 degrees, 70x70 matrix, 3x3x3mm voxel resolution). A high-resolution anatomical scan (192 slices, 256 x 256 matrix, 1 x 1 x 1 mm voxel resolution) was also obtained from each participant using a 3D pulse sequence weighted for T1 contrast.

2.5 fMRI Data Preprocessing

All functional images were preprocessed and analysed using BrainVoyager QX 2.3.0 (Brain Innovation, Maastricht, Netherlands). Data were motion corrected by aligning each functional volume with the first volume of the run for each participant (trilinear/sinc interpolation). Slice scan time correction (cubic spline interpolation),

and temporal high-pass filtering (GLM with Fourier basis set, 2 cycles) were also performed. T1-weighted anatomical scans were aligned to the ACPC axis, and normalized to Talairach and Tournoux (1998) stereotaxic space. Each functional image was then coregistered to the participant's anatomical image, transformed into Talairach space, and finally smoothed using an 8 mm full width at half maximum Gaussian smoothing kernel.

2.6 fMRI Analysis

2.6.1 Whole Brain Analysis

In order to test the first hypothesis, an initial analysis was run to determine which brain areas showed evidence of switch-related activity. A random-effects general linear model (GLM) analysis was applied to the functional data collected during the two task switching runs using separate regressors for colour switch trials, motion switch trials, colour repeat trials, and motion repeat trials. Separate regressors were also included for both error and post-error trials. Regions that showed switch-related activity were identified with the contrast of the estimates of the beta coefficients of switch and repeat predictors. The resulting map was corrected for multiple comparisons by means of a random-field theory based estimate of false-discovery rate (FDR), where q (FDR) < 0.03. For all event-related predictors, epochs spanning the entire duration of the stimulus presentation were convolved with a sum of two gammas model of the hemodynamic response function (HRF).

2.6.2 Region of Interest Analyses

In order to assess the second and third hypotheses regarding the existence of modulation in category specific regions V4 and V5, regions of interest (ROIs) were

identified subject-wise by means of a colour-motion localizer. In order to identify these ROIs, BOLD responses in the localizer were estimated by means of a GLM with separate regressors for motion blocks, colour blocks, and stationary gray dot rest blocks. To identify area V5, the beta coefficient estimate for motion was contrasted against the stationary dots. Regions of interest in the left and right hemisphere were defined as regions in which this difference was significantly greater than zero and whose Talairach coordinates corresponded with anatomical estimates of the localization of V5 (Dumoulin et al., 2000; Watson et al., 1993). Similarly, V4 was identified by contrasting the beta coefficient estimate for colour against the stationary gray dots. V4 ROIs in the left and right hemisphere were defined as regions in which this difference was significantly greater than zero, and whose Talairach coordinates corresponded with previous estimates of the localization of V4 (McKeefry & Zeki, 1997; Schoenfeld et al., 2007). Statistical thresholds for both of these contrasts were set at an individual subject level, but all thresholds were less than q (FDR) < 0.05. Activity within these ROIs formed the basis for subsequent analyses.

Separate regressors for all levels of trial type (repeat 1-5, switch), congruency (congruent/incongruent), and dimension (colour-relevant/motion-relevant) as well as variables of non-interest (error, post-errors trials) were created by convolving a vector of onsets for each predictor with a two-gamma model of the HRF. Estimates of the beta coefficients of these predictors were then computed in the context of a whole-brain RFX GLM. Beta coefficient estimates were then extracted from 4 subject-level ROIs (left V4, right V4, left V5, right V5) and compared offline by means of a 3 (trial type; early repeat, late repeat, switch) x 2 (congruency; congruent versus incongruent) x 2 (dimension; colour-relevant versus motion-relevant) repeated-measures analysis of variance (ANOVA). Early repeat trials were a combination of repeat 1 and repeat 2

trials while late repeat trials were a combination of repeat 3, 4, and 5 trials. Due to the similarity in beta values, betas extracted from V4 in the left and right hemisphere were collapsed, as were the betas extracted from the left and right hemispheres comprising area V5.

In order to assess the third hypothesis with regards to differences in the level of competition between area V4 and V5 across trial type, the beta weights of area V4 and V5 were normalized so that they could be directly compared. The beta weights from area V4 and area V5 were z-normalized, using the equation $z = \frac{x-\bar{x}}{sd}$, where x was the raw score to be standardized, $\bar{x}$ was the mean of the beta weights in the relevant brain region, and sd was the standard deviation of those beta weights. Before the difference scores were calculated, the relationship between these brain regions and their activation patterns based on which dimension was relevant was explored using a 3 (trial type; early repeat, late repeat, switch) x 2 (dimension; colour-relevant versus motion-relevant) x 2 (Brain Region; area V4 versus area V5) repeated measures ANOVA.

As an index of competition, difference scores were then calculated in order to determine whether the difference in brain activity between area V4 and V5 differed across trial types depending on whether colour or motion was relevant. When colour-relevant trials were investigated, difference scores were calculated as the beta weight from area V5 subtracted from the beta weight from area V4. When motion-relevant trials were investigated, difference scores were calculated as the beta weights in V4 subtracted from those beta weights extracted from V5. These difference scores were then subjected to a repeated-measures ANOVA to determine if the level of competition differed across trial type such that competition was greatest on switch trials when interference from the other dimension would be greatest.

Following this, the second part of hypothesis 3 was then investigated. In order to assess differences in the degree of modulation within a particular extrastriate region across trial type, difference scores were again calculated for each individual subject. Since these differences were between colour and motion relevant trials within a particular brain region, the non-normalized data was used. When difference scores were calculated in area V4, beta weights associated with trials in which the participant was to ignore colour were subtracted from those associated with trials in which the participants should attend to colour. Similarly, when difference scores were calculated in area V5, beta weights associated with trials in which the participant was to ignore motion were subtracted from those associated with trials in which they were to attend to motion. These difference scores were then subjected to a repeated-measures ANOVA to determine if the degree of modulation differed across trial type such that modulation was smallest on switch trials and largest on later repeat trials.

2.6.3 Follow-up Analyses

After finding a lack of modulation in area V5 which will be explored below, additional analyses were run to determine the reason for this finding. In order to determine if we could replicate the findings of previous switching studies, which had found modulation in V5, an additional analysis was run redefining the ROIs using an approach closer to that used in these earlier studies by using the task switching runs to define the ROIs (Liston et al., 2006; Liu et al., 2003). These new ROIs were identified subject-wise. BOLD responses in the task switching runs were estimated by means of a GLM with separate regressors for motion-relevant, colour-relevant, error, and post error trials. To identify area V5, the beta coefficient estimate for motion-relevant trials was contrasted against that for colour-relevant trials. Regions of interest in the left and

right hemisphere were defined as regions in which this difference was significantly greater than zero and whose Talairach coordinates corresponded with anatomical estimates of the localization of area V5 (Dumoulin et al., 2000; Watson et al., 1993). Statistical thresholds for this contrast were set at an individual subject level, but all thresholds were less than q (FDR) < 0.05. Activity within these ROIs formed the basis for subsequent analyses.

The separate regressors created for the original analysis for all levels of trial type (repeat 1-5, switch), congruency (congruent/incongruent), and dimension (colour-relevant/motion-relevant) as well as variables of non-interest (error, post-errors trials) were utilized once again. Estimates of the beta coefficients of these predictors were computed in the context of a whole-brain RFX GLM. Beta coefficient estimates were then extracted from the 2 subject-level ROIs created using the task switching runs (left V5 and right V5) and compared offline by means of a 3 (trial type; early repeat, late repeat, switch) x 2 (congruency; congruent versus incongruent) x 2 (dimension; colour-relevant versus motion-relevant) repeated-measures ANOVA. Due to the similarity in beta values, betas extracted from V5 in the left and right hemisphere were collapsed.

In order to determine if the V5 ROIs defined by the localizer analysis were in different locations than the V5 ROIs defined using the task switching runs, the Euclidean distance between the peak voxels of area V5 as defined by these two different methodologies was calculated. The equation used to calculate the Euclidean distance between the coordinates can be seen below.

$$\mathrm{d} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

2.6.4 Psychophysiological Interaction Analysis

One important question that remains is whether the enhanced response in area V4 to colour stimuli was a result of top-down modulation from frontal and parietal areas as suggested by hypothesis four. If this were the case, regions involved in top-down modulation would show increased connectivity with V4 when participants were attending to colour as compared to when they were ignoring colour. To address this, a psychophysiological interaction analysis (PPI) was conducted. A PPI analysis can determine whether the correlation in activity between distinct brain regions is different in different psychological contexts (Friston et al., 1997). Regions across the entire brain can be identified whose activity is more highly correlated with a specified seed region in one experimental condition compared to another.

To conduct this analysis, two seed regions were created in each subject; left V4 and right V4. These seed regions were defined using the peak coordinates of area V4 from each hemisphere yielded from the localizer analysis (coloured dots > stationary dots) on an individual subject level. A 5mm sphere was created around the peak of left V4 and right V4 using the VOI time series extraction utility. Signal time courses were extracted from these seed regions and used as physiological regressors. The main effect of attention condition (attend to colour > ignore colour) was defined as the psychological regressor. The design matrix for the first level analysis included the psychological regressor, the physiological regressor, and a third regressor which represented the cross product of the previous two (the psychophysiological interaction term). PPIs were carried out for each seed region in each subject separately and were then entered into a group analysis (thresholded at $p < 0.0001$, uncorrected with a cluster size of 5 voxels).

Chapter 3 – Results

3.1 Behaviour

Response time and accuracy data are displayed in Table 1. A 3 (trial type; early repeat, late repeat, switch) x 2 (congruency; congruent versus incongruent) x 2 (dimension; colour-relevant versus motion-relevant) repeated-measures ANOVA showed a significant switch cost for both reaction time, F (1.2, 19.8) = 40.97, p <.001, and accuracy, F (2, 34) = 10.39, p <.001. Bonferroni-corrected post-hoc tests revealed that participants were significantly faster and more accurate at responding to early and late repeat trials than to switch trials. They were also significantly faster at responding to late repeat trials than early repeat trials. There was a main effect of congruency for both reaction time, F (1, 17) = 34.71, p = .001, and accuracy, F (1, 17) = 42.77, p <.001, with participants responding more rapidly and more accurately to congruent trials relative to incongruent trials. While participants responded at a similar speed to both colour and motion-relevant trials, they were significantly more accurate on the motion-relevant trials (F (1, 17) = 4.66, p = .046). For accuracy, a significant trial type by congruency interaction was also found, F (2, 34) = 23.81, p <.001. Bonferroni-corrected simple effects tests revealed that responses to congruent stimuli were more accurate than responses to incongruent stimuli only on early repeat and switch trials. While there was no significant difference in accuracy across trial types for congruent trials, on incongruent trials, accuracy was higher on early and late repeat trials than it was on switch trials.

Table 1

Mean response times (ms) and accuracy (in %; in parentheses) across trial types, congruency, and relevant dimension.

	Switch		Early Repeat		Late Repeat	
	Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent
Colour Relevant Trials	541.99 (98.26)	596.35 (90.97)	497.88 (98.79)	545.55 (96.01)	490.68 (98.92)	533.34 (98.38)
Motion Relevant Trials	560.22 (99.63)	594.72 (94.07)	536.35 (99.65)	553.75 (97.74)	513.32 (98.43)	535.12 (98.81)

3.2 fMRI

3.2.1 Whole Brain Analysis

The first analysis of the imaging data sought to identify regions important in the performance of cognitive control. Regions that showed switch-related activity were identified using the contrast of activation during switch trials greater than repeat trials with a significance level of q (FDR) < 0.03. A full list of significant clusters identified in this contrast can be seen in Table 2. Consistent with the first hypothesis and with the results of other studies, we observed activation in regions that have previously been defined as the cognitive control network (Cole & Schneider, 2007). This included activation in the DLPFC, ACC/pSMA, AIC, dPMC, IFJ, and the PPC. These regions can be seen in Figure 3.

Table 2

Brain regions more activated during task switch trials than task repeat trials.

Region	BA	Hemisphere	*t*-value	Cluster Size	Talairach
DLPFC	9	R	4.114	537	32, 37, 18
IFJ	9	R	5.101	9338	41, 7, 39
dPMC	6	R	3.702	327	17, -5, 60
ACC/pSMA	6	L	4.071	2318	-4, 7, 51
Superior temporal gyrus*	22	R	6.946	196376	65, -26, 0
Claustrum**	-	R	4.407	522	23, 13, 15
Claustrum	-	L	5.126	634	-25, -17, 21
Inferior occipital gyrus	19	R	4.247	1364	41, -77, -3
Middle temporal gyrus	21	L	6.185	812	-46, -2, -12
Precentral gyrus	6	L	8.018	32382	-52, 1, 42

Talairach coordinates are for the peak voxel within each cluster. Cluster size is measured in mm^3.

* this was a large bilateral cluster also encompassing superior and medial parietal cortex.

** this cluster also contained the anterior insula.

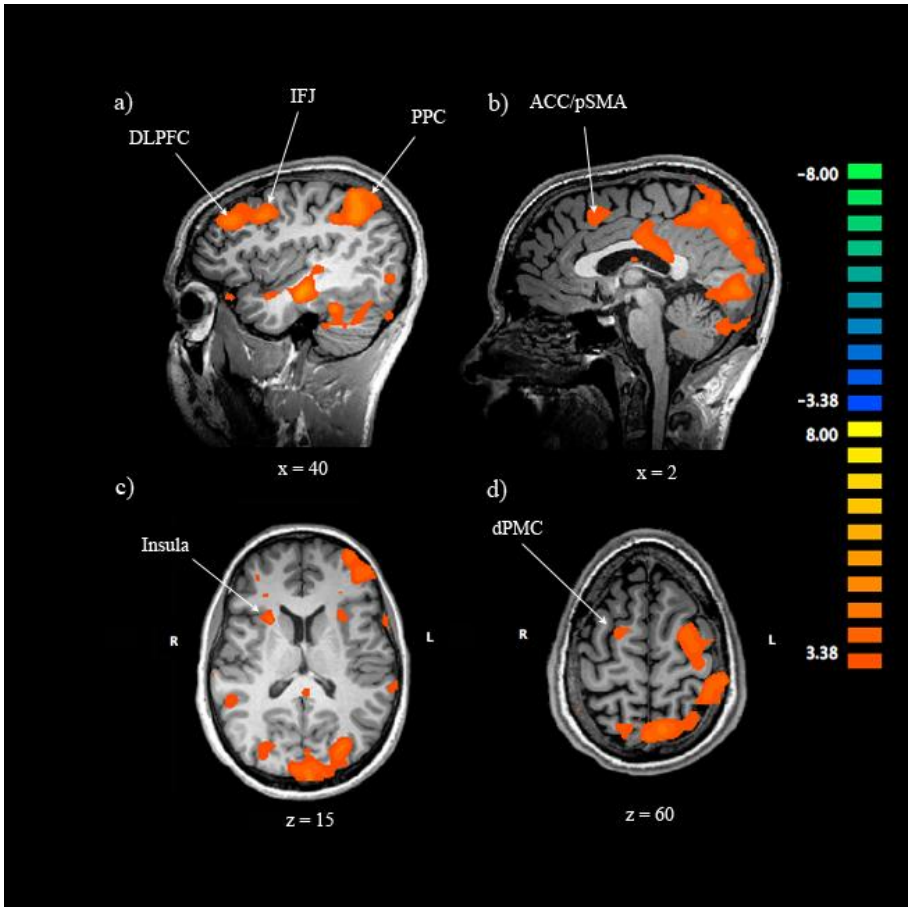

Figure 3. Neural regions showing greater activation during task switch trials than task repeat trials, *q* (FDR) < .03.

3.2.2 ROI Analyses

Area V4 and V5 were defined in each individual subject using the localizer scan. Area V4 was defined using the contrast of coloured stationary dots greater than gray stationary dots, and area V5 was defined using the contrast of moving gray dots greater than stationary gray dots. Statistical thresholds for both of these contrasts were set at an individual subject level, but all thresholds were less than *q* (FDR) < 0.05. The mean Talairach coordinates for area V5 in the left hemisphere were -48, -67, 2, and for the right hemisphere were 43, -66, 2. The mean Talairach coordinates for area V4 were -30, -72, -16 in the left hemisphere and 25, -68, -18 in the right hemisphere. These coordinates correspond well to those found in previous studies (Dumoulin et

al., 2000; McKeefry & Zeki, 1997; Watson et al., 1993). The location of each ROI in an example subject can be seen in Figure 4. When area V4 was examined using a 3 x 2 x 2 repeated measures ANOVA, a main effect of trial type emerged, F (2, 34) = 10.81, $p < .001$, such that activity was significantly greater on switch trials than early repeat trials, and activity was also significantly greater on late repeat trials than early repeat trials as determined by Bonferroni-corrected post-hoc tests (Figure 5a). A main effect of dimension was also observed in area V4, F (1, 17) = 10.20, $p = .005$. As expected, participants displayed significantly greater activation in this region on colour-relevant trials than on motion-relevant trials (Figure 6a).

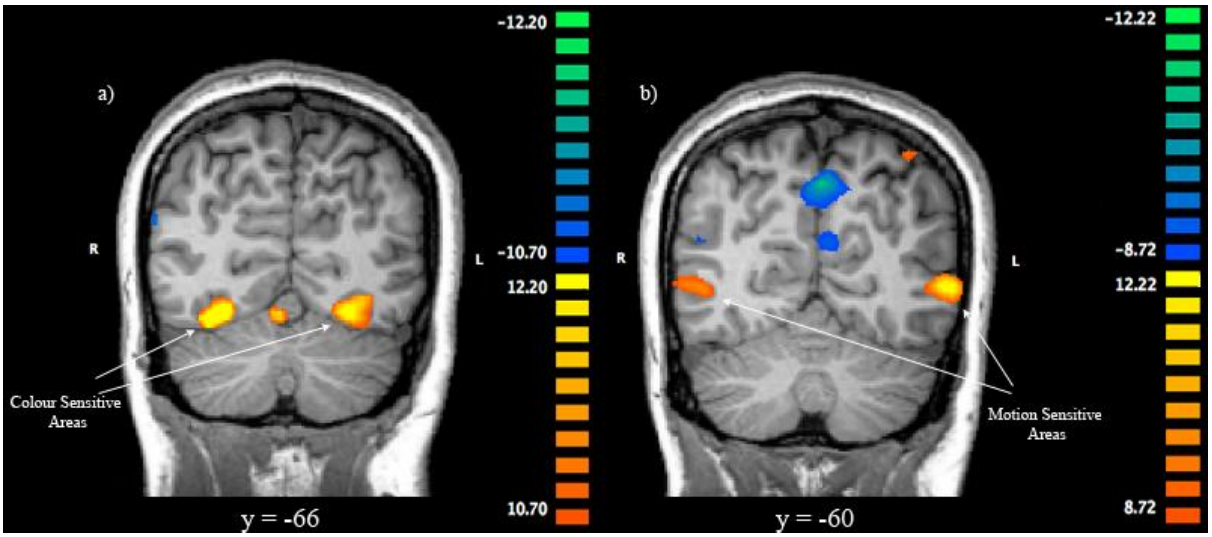

Figure 4. Four ROIs within category-specific extrastriate areas in an example subject. a) Left and right colour-specific area V4, the Talairach coordinates of the peak voxel in this cluster for this subject are (-22, -65, -15) for the left colour sensitive area and (38, -62, -21) for the right colour sensitive area, q (FDR) < .05. b) Left and right motion-specific area V5, the Talairach coordinates of the peak voxel within this cluster for this subject are (-52, -59, 3) for the left motion sensitive area and (53, -59, 3) for the right motion sensitive area, q (FDR) < .05.

The same 3 x 2 x 2 repeated measures ANOVA was run on the beta estimates extracted from area V5, and a main effect of trial type was found, F (2, 34) = 9.15, p = .001. Bonferroni-corrected post-hoc tests revealed that activation in area V5 was significantly higher on switch trials than early repeat trials (Figure 5b). There was however, no main effect of dimension in this area, F (1, 17) = .005, p = .944, and thus no modulation based on attention (Figure 6b). Similarly, no significant interactions were found. Congruency did not have an effect in either V4 or V5.

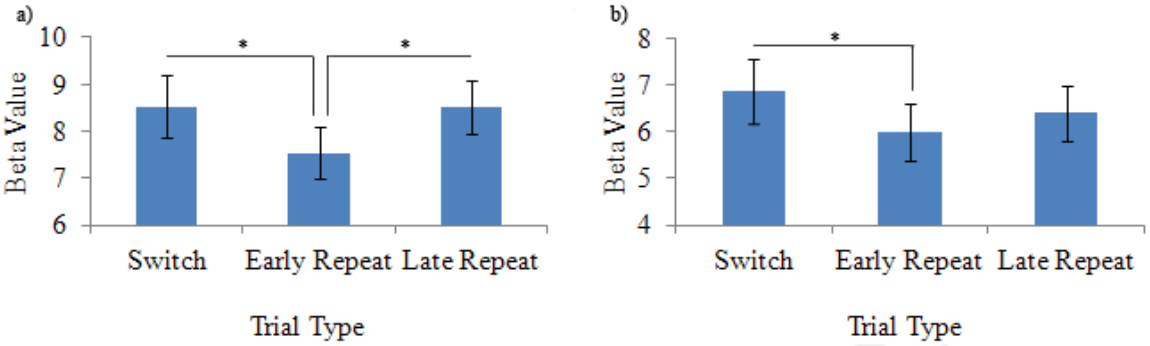

Figure 5. Mean beta weights from category specific extrastriate regions a) V4 and b) V5 depicting the main effect of trial type. Bars indicate standard error of the mean.

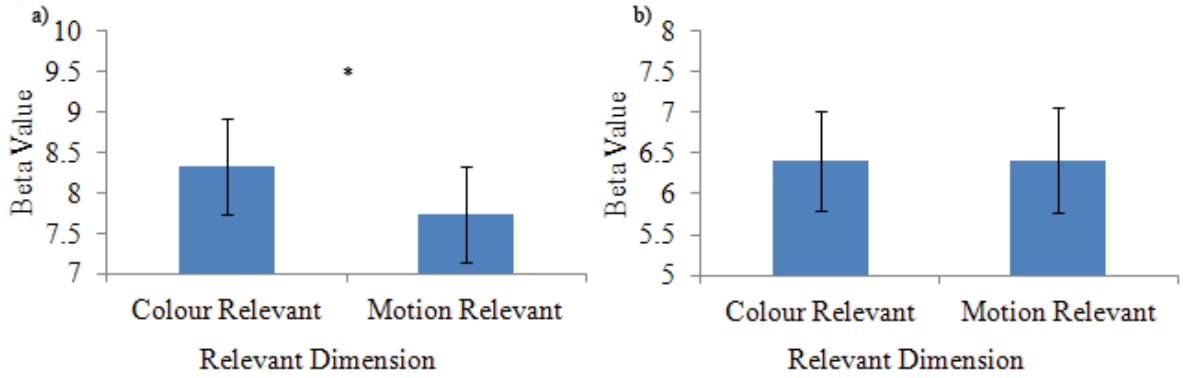

Figure 6. Mean beta weights from category specific extrastriate regions a) V4 and b) V5 depicting the main effect of dimension. Bars indicate standard error of the mean.

In order to examine the third hypothesis which concerned whether there would be greater competition between area V4 and V5 on the switch trials compared to the

repeat trials, the data were normalized so that activity from area V4 could be directly compared to that of area V5. Before getting to the question of whether competition between the regions differs across the trial types, these normalized beta weights were explored across the two brain regions to see how they interact. In order to explore the relationship between area V4 and V5 and their activation patterns based on which dimension was relevant, a 3 x 2 x 2 repeated measures ANOVA was conducted on the normalized beta weights. This analysis revealed a main effect of trial type, F (2, 34) = 11.39, p <.001. Bonferroni-corrected post-hoc tests revealed that activity was significantly higher on switch trials than early repeat trials, and activity was also significantly higher on late repeat than early repeat trials. This result was to be expected and merely replicates the findings from the non-normalized betas. This ANOVA also revealed a significant interaction between dimension and brain area, F (1, 17) = 20.09, p <.001. Bonferroni-corrected post-hoc simple effects tests revealed that for area V5, there was no significant difference in brain activity when motion was relevant versus when colour was relevant. In contrast, in area V4, this difference was significant. Participants showed significantly higher activity in area V4 when they were attending to colour than they did when they were attending to the motion of the stimulus. This interaction is depicted in Figure 7 and highlights the finding previously reported that while attentional modulation can be seen in area V4, it is not present in area V5.

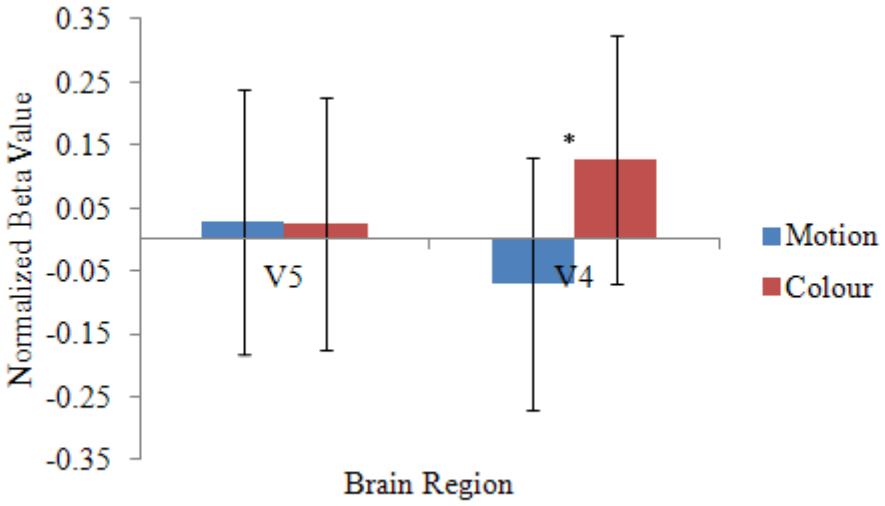

Figure 7. Normalized beta weights from category specific extrastriate regions, showing the significant interaction of trial type and dimension.

In order to determine whether there were differences in the level of activation between area V4 and area V5 across the different trial types, as an index of competition, difference scores were calculated on the normalized betas. The proposed hypotheses for this analysis are depicted in Figure 1. When motion was relevant, difference scores were calculated as the beta weight in area V4 subtracted from the beta weight in area V5. When colour was relevant, the difference score was calculated as the beta weight in area V5 subtracted from the beta weight in area V4. Such calculations allowed us to examine whether on colour relevant trials, for example, the difference between activation in area V4 and V5 was smaller on switch trials than repeat trials. If this were the case, this would indicate more competition between these regions on switch trials as predicted. The calculated difference scores for colour-relevant trials can be seen in Figure 8a. The repeated measures ANOVA conducted on these difference scores indicated that there were no significant differences between the scores across the different trial types, F (1, 24) = .25, p = .7. The calculated

difference scores for the motion-relevant trials can be seen in Figure 8b. The repeated measures ANOVA conducted on these difference scores also indicated that there were no significant differences between the difference scores across trial type, F (2, 34) = .99, p = .38. This analysis on the normalized beta weights from area V4 and V5 indicates that contrary to the third hypothesis, there does not seem to be any difference in the magnitude of competition between switch and repeat trials. Thus, none of the proposed hypotheses from Figure 1 appear to be supported. It seems instead that competition between area V4 and V5 does not play a role in the generation of switch costs since competition between these regions is similar regardless of whether the trial is a switch or a repeat trial.

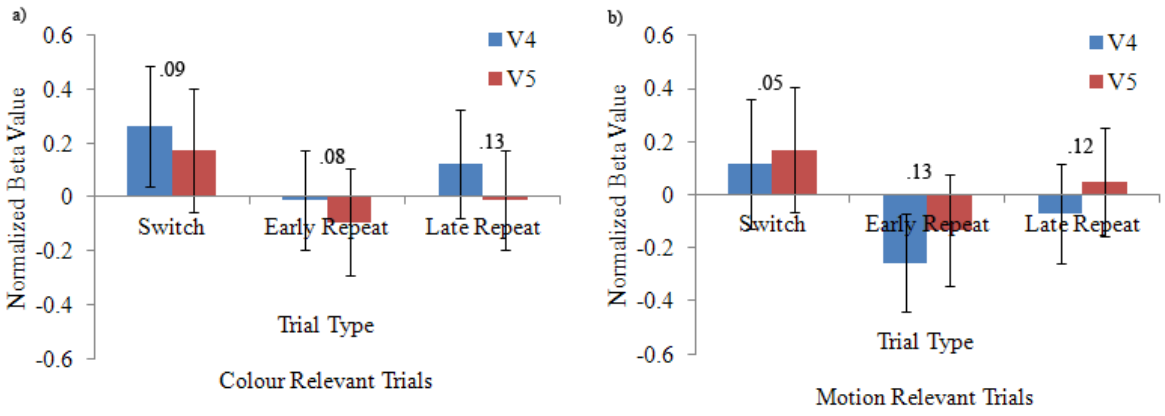

Figure 8. a) Normalized beta weights for the colour-relevant trials depicting the relationship between trial type and activity in area V4 and V5. The numerical values displayed in the graph indicate the difference in beta values between area V4 and area V5. b) Normalized beta weights for the motion-relevant trials depicting the relationship between trial type and activity in area V4 and V5. The numerical values displayed in the graph indicate the difference in beta values between area V5 and area V4. Bars indicate standard error of the mean.

The third hypothesis also postulated that if a difference in the degree of competition between V4 and V5 did not exist, perhaps differences in the level of modulation within these regions would differ across trial type, and perhaps this would shed some light on switch costs. Contrary to this hypothesis, no significant interaction of trial type by dimension was found in either area V4 or V5 as described above. This result indicated that there was no difference in modulation across the various trial types. In order to delve into this question further, difference scores were calculated on the beta weights from both area V4 and V5 to verify that there was indeed no difference in the magnitude of modulation between switch and repeat trials. These difference scores in area V5 were calculated as the beta value for colour-relevant trials subtracted from the beta for motion-relevant trials. For area V4, the difference score was calculated as the beta for motion-relevant trials subtracted from that for colour-relevant trials. Difference scores were calculated separately for each different level of trial type.

The calculated difference scores in area V4 for each trial type can be seen in Figure 9. The repeated measures ANOVA conducted on these difference scores indicated that there were no significant differences between the scores across the different trial types, F (2, 34) = .22, p = .8. While the smallest difference score did occur on the switch trial, this result was not statistically significant. The calculated difference scores in area V5 for each trial type can be seen in Figure 10. In this brain region as well, the repeated measures ANOVA conducted on the difference scores indicated that there were no significant differences between the difference scores across trial type, F (2, 34) = .31, p = .74. Thus, this analysis also indicates that there does not seem to be any difference in the magnitude of top-down modulation between switch and repeat trials.

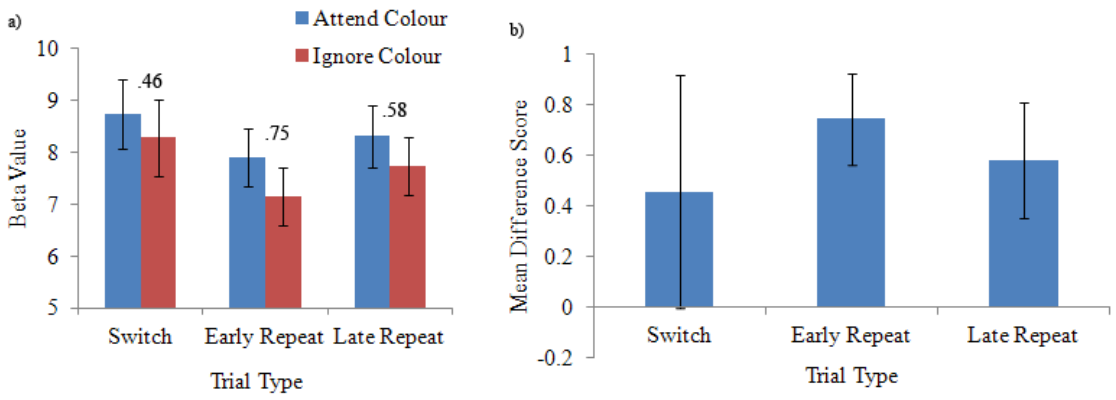

Figure 9.a) Mean beta weights from area V4 depicting the relationship between dimension and trial type. The numerical values displayed in the graph indicate the difference in beta values between attend colour and ignore colour conditions. b) Mean differences scores across the different trial types. These scores were not significantly different from each other. Bars indicate standard error of the mean.

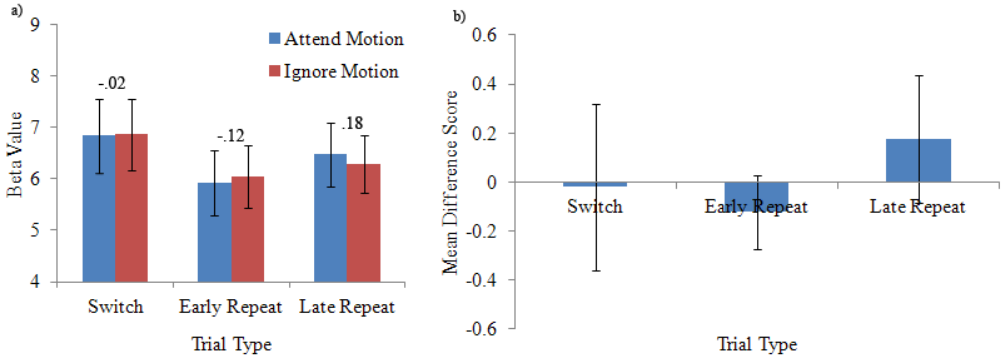

Figure 10.a) Mean beta weights from area V5 depicting the relationship between dimension and trial type. The numerical values displayed in the graph indicate the difference in beta values between attend colour and ignore colour conditions. b) Mean differences scores across the different trial types. These difference scores were not significantly different from one another. Bars indicate standard error of the mean.

3.2.3 Follow-up Analyses

Since no modulation was found in area V5 contrary to the second hypothesis, additional analyses were run to see if this was due to the way in which area V5 was defined in the current study. To determine if this was indeed the case, new V5 ROIs were defined using the task switching runs similar to the methodology used in previous studies (Liston et al., 2006; Liu et al., 2003). Using a statistical threshold of $q(\text{FDR}) < 0.05$, only 7 of the 18 participants showed activation of area V5 in the contrast of motion trials greater than colour trials during the switching task. The betas extracted from these 7 participants were examined in more depth using a 3 x 2 x 2 repeated measures ANOVA. A main effect of trial type emerged, $F(2, 12) = 20.6$, $p < .001$, such that activity was significantly higher on switch trials than early repeat trials, and activity was also significantly higher on late repeat trials than early repeat trials as determined by Bonferroni-corrected post-hoc tests (Figure 11b). This result replicates the main effect that was found when the localizer was used to define area V5. A main effect of dimension was also observed in area V5, $F(1, 6) = 87.06$, $p < .001$. In contrast to the results found when the localizer was used to define area V5, when the task switching runs were used to define the ROI, participants displayed significantly greater activation in this region on motion-relevant trials than on colour-relevant trials (Figure 11a).

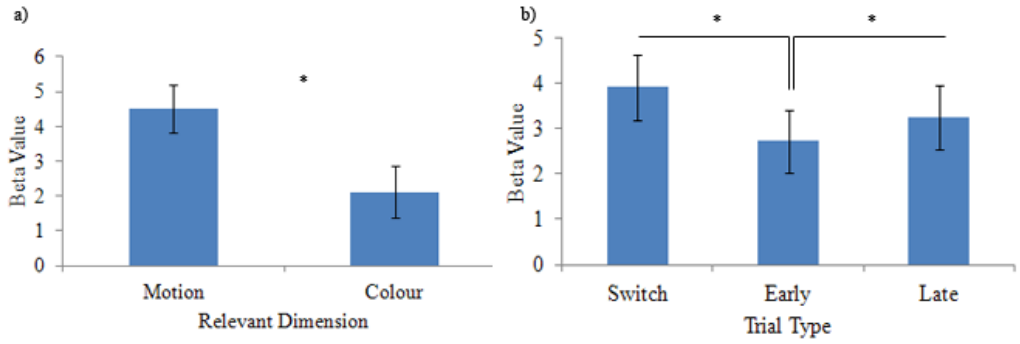

Figure 11. Mean beta weights from area V5 as defined using the task switching runs depicting the main effect of a) dimension and b) trial type. Bars indicate standard error of the mean.

In order to compare the locations of the two differentially defined V5 ROIs, the distance between the average peak voxel from the localizer analysis and the average peak voxel from the task switching analysis was calculated in each hemisphere. The Talairach coordinates for the average peak voxel from both ROI definition methodologies, and their distance from each other can be seen in Table 3. In addition to extracting the peak voxel from each of these clusters in each subject, the entire clusters generated from each analysis methodology were directly compared on an individual subject level. In the left hemisphere, the peaks are far from each other as indicated in Table 3, and in addition to this, these clusters do not overlap. In the right hemisphere, the two peaks are much closer, but still very little overlap is seen between the clusters defined using the localizer and those defined using the task switching runs. These two methodologies lead to the activation of distinct category-specific clusters.

Table 3

Comparison of the mean location of V5 activation from the localizer and task switching runs.

	Localizer Run	Task Switching Runs	Distance Between Peak Voxels (mm)
	Motion > Stationary	Motion > Colour	
Left V5	-48, -67, 2	-42, -59, 5	10.44
Right V5	43, -66, 1	42, -68, 2	2.45

Mean Talairach coordinates are for the peak voxel within each region.

3.2.4 Psychophysiological Interaction Analysis

In order to address hypothesis four, a PPI analysis was conducted to determine whether the enhanced response observed in area V4 when attending to colour was the result of top-down modulation from frontal and parietal regions. Results suggest that is indeed the case. A number of frontal and parietal brain regions showed enhanced functional connectivity with area V4 when participants were attending to colour compared to when they were ignoring colour. A complete list of these regions can be seen in Table 4. The IFJ, supramarginal gyrus, and middle frontal gyrus, which have all been implicated in issuing top-down control signals showed enhanced connectivity with area V4 when attending to colour (Figure 12). These results lend support to the idea that these frontal and parietal brain regions issue biasing signals to area V4 to bias processing towards information that is currently relevant.

Table 4

Brain areas showing significant connectivity with area V4 during the attend colour condition compared with the ignore colour condition.

Brain Region	BA	Hemisphere	Z Score	Cluster Size	Talairach
Supramarginal/Angular Gyrus	40	L	5.12	294	-40, -50, 36
Supramarginal/Angular Gyrus	39	R	4.29	78	45, -53, 31
Inferior Frontal Junction	6	R	4.56	15	30, 8, 43
Inferior Frontal Gyrus	44	L	4.16	22	-56, 17, 10
Middle Frontal Gyrus	46	R	4.33	26	54, 28, 25
Anterior Cingulate Cortex	32	L	4.32	19	-15, 17, 40
Anterior Cingulate Cortex	32	R	4.07	7	16, 24, 34
Precentral Gyrus	6	L	4.71	41	-37, -7, 34
Cingulate Gyrus	24	L	4.17	14	-1, -24, 36
Posterior Cingulate Cortex	30	L	4.03	8	-26, -66, 11
Substantia Nigra	-	R	5.08	52	7, -19, -13
Superior Temporal Gyrus	22	R	5.17	107	34, -54, 14
Cuneus	18	L	4.33	13	-18, -86, 21
Lingual Gyrus	17	L	5.24	115	-14, -81, 1
Lingual Gyrus	18	R	4.09	14	10, -81, 1

Talairach coordinates are for the peak voxel within each cluster. Cluster size is measured in mm. Thresholded at $p < 0.0001$, uncorrected.

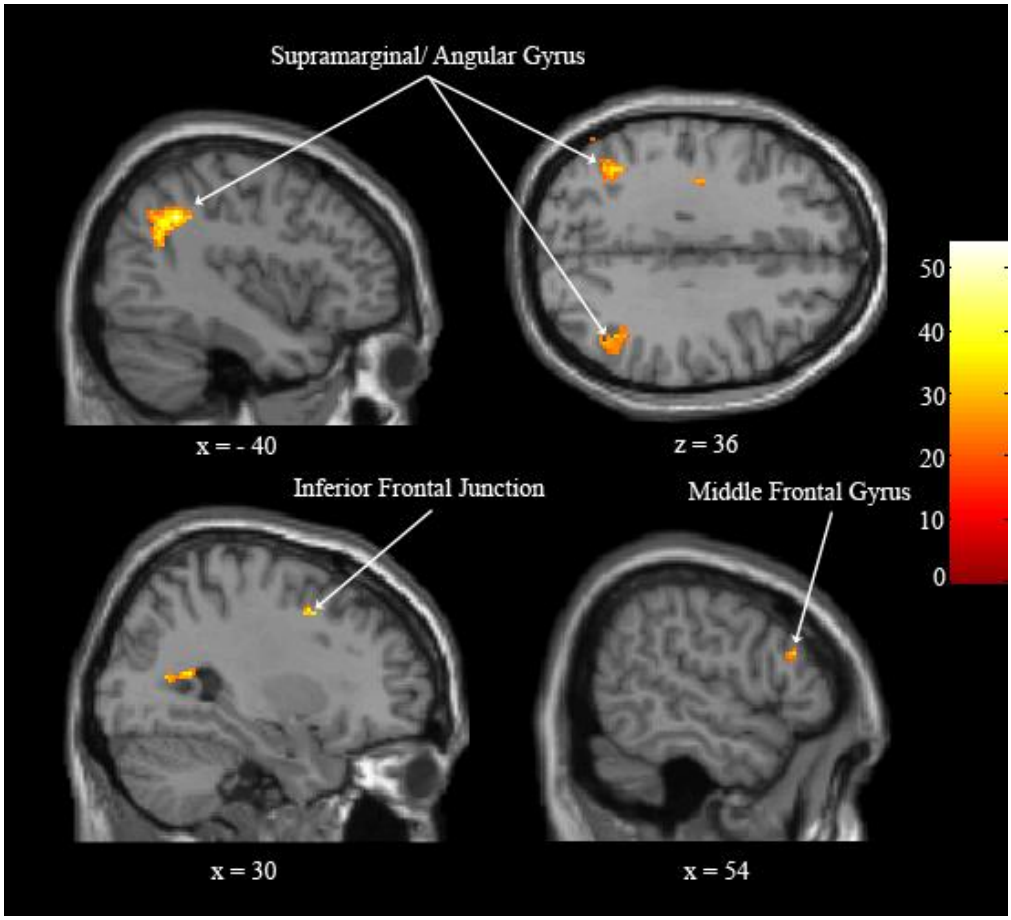

Figure 12. Neural regions whose time course was more highly correlated with area V4 in the attend colour condition compared to the ignore colour condition ($p < 0.0001$, uncorrected, minimum cluster size of 5).

Chapter 4 – Discussion

4.1 Task-Switching and the Cognitive Control Network

This study sought to examine whether attentional modulation could be observed in colour area V4 and motion area V5 in the context of task switching. Modulation in these category specific extrastriate regions has been found during selective attention tasks and during more cognitively demanding working memory tasks. However, to date, no study has examined modulation in area V4 and V5, as defined by an independent functional localizer in the context of task switching. In order to examine whether such modulation takes place, participants performed a switching task during fMRI scanning. Behaviourally, participants performed as expected, displaying the switch costs that are a hallmark of human performance on such tasks (Kiesel et al., 2010; Vandierendonck et al., 2010). Participants were significantly slower and more error prone on switch trials when they were required to shift attention from one feature dimension to another as compared to repeat trials when they attended to the same dimension across multiple trials.

The neuroimaging results complement these behavioural findings. In accordance with previous research, the implementation of cognitive control during switching engaged a network of brain regions including the DLPFC, ACC/pSMA, dPMC, AIC, IFJ, and PPC. These regions were all activated during switching, regardless of which feature dimension was attended. These results support the first hypothesis which suggested that greater activation would be found in these regions during switch trials compared to repeat trials. The results also fit well with the findings of previous studies that have shown that these brain regions are consistently activated in studies of task switching (Badre & Wagner, 2006; Braver et al., 2003;

Gold et al., 2010; Liston et al., 2006; Liu et al., 2003; Morton et al., 2009; Sohn et al., 2000; Yeung et al., 2006). This specific set of brain regions seem to be important for the implementation of cognitive control.

4.2 Top-Down Modulation of Area V4 and V5

In order to test the second hypothesis, category-specific extrastriate regions V4 and V5 were closely examined in order to determine whether activity in these regions was modulated based on which feature dimension was attended. Modulation was observed in colour area V4, as would be expected from the biased competition model of attention (Desimone & Duncan, 1995). When participants were instructed to attend to the colour of the stimulus, activity was enhanced in this region compared to when they were instructed to attend to the direction of motion the stimulus was moving in. This result supports the notion that during the performance of a cognitively demanding switching task, area V4 is subject to top-down modulation (Desimone & Duncan, 1995; Miller & Cohen, 2001). These data corroborate findings from other studies that have looked at modulation in V4 in the context of selective attention (Chawla et al., 1999; Corbetta et al., 1991; Schoenfeld et al., 2007; Shibata et al., 2008), and also working memory (Zanto et al., 2010; Zanto et al., 2011). This study also adds to these previous findings by showing that such modulation occurs even in the context of task switching. This is the first study to show such modulation in traditionally defined colour area V4 during switching.

In contrast to the task-related modulation observed in V4, no modulation was observed in motion area V5. Regardless of whether participants were attending to the colour or the direction of motion of the stimulus, activity in this region did not differ. This result was somewhat unexpected as based on Desimone and Duncan's (1995)

biased competition model of attention it was expected that top-down modulation would be seen in this region when participants attended to motion. Additionally, other task switching studies which have looked at attentional modulation in area V5 have found modulation in this region (Liston et al., 2006; Liu et al., 2003). Several possibilities for why the results found here do not corroborate those found in previous studies will be explored.

4.2.1 Defining Area V5

It is possible that modulation in area V5 was not found in the current study because an independent functional localizer was used to define the ROIs. There have been three previous studies which have looked at modulation in category specific motion areas of the brain in the context of task switching. One of these studies did indeed use an independent localizer, but they examined modulation in area V5 only during the preparatory cue period and not during stimulus presentation, so this study is not directly comparable (Wylie et al., 2006). The results of the present study do fit with their findings though. No preparatory competition was found in area V5 in their study, and similarly, the current study found no competition in area V5 during the stimulus period either. However, there are two studies that have found modulation in area V5 during stimulus presentation in the context of task switching (Liston et al., 2006; Liu et al., 2003). What these two studies have in common is that neither of them used a functional localizer to identify area V5 independently on an individual subject level. Instead, both studies used the task switching runs and contrasted motion trials against colour trials to determine motion-relevant brain regions. In both studies this contrast revealed that area V5 was indeed more activated on motion trials than

colour trials. Thus, methodological differences may contribute to the discrepancy between the results reported here and those found previously.

Some support for this idea comes from a study of visual attention to motion which showed that different subsections of V5 may respond to motion depending on whether the motion stimulus is passively viewed or actively attended (Buchel et al., 1998). This study revealed that activation of area V5 when comparing attention to motion and no attention to motion conditions was 10mm away from the corresponding peak from the comparison of passive motion viewing and stationary dot conditions. While both of these peak voxels fell within area V5, those voxels modulated by attention were located in a slightly different area of V5 than the peak voxels located in a contrast closer to the localizer scan used in the current study. It is possible that modulation in area V5 was not found in the current study because the region defined by the motion localizer scan is not the same region that is modulated by attention. If this were the case, this would explain why studies that used the task switching runs to define area V5, rather than a motion localizer scan, did find attentional modulation in V5 while we did not (Liston et al., 2006; Liu et al., 2003). They may have been looking at a slightly different area of V5 which does actually show attentional modulation.

In the current study, when data from the task switching runs was used to identify area V5, only 7 of the 18 participants showed activation of this region. Interestingly, in those 7 participants, attentional modulation was seen in area V5, such that activation was significantly higher in this area when motion was relevant compared to when colour was relevant. The exact location of the ROIs defined using the task switching run were indeed located in different areas of V5 just as previous findings had suggested (Buchel et al., 1998). It is clear that at least in the left

hemisphere, these ROIs are in different sections of area V5. However, it should be kept in mind that using the task switching runs to define V5 was a non-independent way of defining the ROI, and this could lead to biases in the results.

While this explanation carries some promise, it may not explain the entire story. While all participants in the current study were capable of successfully performing the switching task, fewer than half of them showed activation of area V5 in the additional analysis. This suggests that for most participants it was not modulation in a different region of area V5 that was leading to successful performance on the task. In addition, previous studies that have looked at attentional modulation in area V5 in a working memory paradigm have successfully found modulation within this region even when the region was defined using an independent functional localizer (Zanto et al., 2010; Zanto et al.,. 2011). So, while it is possible that the reason that no attentional modulation was found in V5 was because of the way it was defined, other potential reasons for this finding should also be explored.

4.2.2 Does Area V5 show feature selective modulation? Evidence from Electrophysiology

An alternative interpretation is that area V5 may not actually show modulation during task switching. Previous studies that have found modulation within this regions in the context of selective attention and working memory have used localizers similar to the one used in the present study, and have still managed to find attentional modulation in area V5 (Treue & Maunsell, 1996; Corbetta et al., 1991; Chawla et al., 1999; Zanto et al., 2010). This may be because these tasks involve performing the same attentional task for longer periods of time than is the case with task switching. In

a switching task, attention is constantly shifting on a rapid timescale, and under these conditions, it is possible that we do not see modulation of area V5.

Some support for this supposition comes from electrophysiology studies conducted in monkeys. In a study aiming to determine whether selective attention effects could be extended to a task switching paradigm, it was found that rule-based attentional modulation was not present in MT, which is the monkey equivalent of area V5 in humans (Sasaki & Uka, 2009). In this study, monkeys were trained to perform a depth discrimination task as well as a direction discrimination task, and to switch between these tasks based on a cue preceding stimulus presentation. Activity was recorded from MT neurons using single unit electrophysiological recording while the monkeys performed the task. They found that neuronal activity was virtually identical during the performance of the depth discrimination task and the direction discrimination task. Even though the monkeys could successfully switch between performing these two tasks, neural activity in MT did not reflect this switch. This is reminiscent of the findings from the current study. While participants in the current study were capable of performing both the colour and the motion tasks in the present study, activity in area V5 did not reflect which task was being performed at any given time. The constant shifting required in this type of task may eliminate any modulation of area V5. In contrast to the lack of modulation in V5 during task switching, attentional modulation has been found in area V4 during switching using electrophysiology in monkeys (Mirabella et al., 2007). These results fit well with the results found here, suggesting that V4 can indeed be modulated by attention during task switching.

A recent electrophysiological study which examined the effect of feature based attention on neural responses in area MT also offers some interesting ideas

(Chen, Hoffmann, Albright, & Thiele, 2012). In this study, monkeys performed either a selective attention task or a switching task in which they were to attend to stimulus colour on some trials, and stimulus direction on other trials. The relevant dimension on a particular trial was indicated by a cue preceding stimulus presentation. Monkeys had to respond with a saccade to indicate the direction of motion of the stimulus when motion was relevant, or the colour of the stimulus when colour was relevant. Extracellular single-unit activity was recorded from MT neurons using standard electrophysiological methods while the monkeys performed this task. It was hypothesized that the firing rate of MT neurons would increase when the monkey attended to motion, but not when they attended to colour since area MT is motion-selective. It was found that 22% of neurons in area MT were significantly affected by feature selective attention. These neurons fell into two different classes, which was unexpected. One class of neurons showed an up-modulation of neuronal firing when attention was directed to motion, while the other class of neurons showed the opposite, responding with higher firing rates when attention was directed to stimulus colour. Interestingly, what the results of this study show is that MT neurons do in fact change their activity depending on the feature dimension attended, but this is not restricted to the attention to motion condition as would be expected. Some MT neurons actually respond more when attention is directed to stimulus colour.

These results suggest that it is possible that top-down modulation was not seen within area V5 in the current study because some neurons in this region were modulated by the colour task, and others were modulated by the motion task. By averaging activation across a large area encompassing thousands of neurons, identifying subtle modulatory differences at the individual neuron level may not be possible. However, this still does not explain why the results of the current study are

so different from those of previous studies that have found modulation in area V5 during task switching (Liston et al., 2006; Liu et al., 2003). One final possible explanation for the lack of top-down modulation in area V5 relates to the experimental paradigm utilized in the current study.

4.2.3 The Role of Bottom-Up Mechanisms

The final suggestion for why modulation was not found in area V5 in the present study suggests that bottom-up mechanisms may have played an important role. As proposed by Desimone and Duncan (1995), stimuli in our visual field are constantly competing for processing capacity. This competition is biased by two different mechanisms. Up to this point, the focus of this paper has been directed exclusively on the biasing of attention towards stimuli that is task-relevant via top-down modulation but the role of bottom-up biases on this competition has been neglected. Exploring the role of these bottom-up mechanisms may assist in the understanding of why a lack of modulation was observed in area V5 despite the fact that participants were able to perform the motion task adequately.

Research has shown that bottom-up mechanisms can change the type of competitive interactions that take place in extrastriate visual regions. A common finding in the competitive attention literature is that when stimuli are presented simultaneously rather than sequentially, suppressive interactions among those stimuli take place despite the fact that the physical stimulation parameters are identical across time under both conditions. These competitive interactions manifest in reduced neural activation in the simultaneous condition because these stimuli are competing for neural representation in visual cortex (Beck & Kastner, 2005; McMains & Kastner, 2011). Such competitive interactions can be reduced in extrastriate cortex when

bottom-up features of the stimuli are manipulated (Beck & Kastner, 2005). When four stimuli are presented simultaneously, if one is particularly salient because it is a different colour than the other three stimuli, then competitive interactions in extrastriate regions are not seen. Bottom-up mechanisms draw attention to the salient stimuli, thus eliminating competition between visual regions. In contrast, this competition remains when heterogeneous displays are used in which all four stimuli are different colours. The results of this study suggest that bottom-up mechanisms can play a very important role in modulating competition in extrastriate regions.

While it is important to note that bottom-up mechanisms can play an important role, what is particularly relevant to the current study is how such bottom-up mechanisms interact with top-down attentional mechanisms to influence competition in extrastriate regions. While these two mechanisms are usually studied separately, a recent study set out to identify how these two biasing mechanisms work together as they would in real world situations (McMains & Kastner, 2011). This study isolated the effects of bottom-up processes on competition in extrastriate regions by manipulating the degree of perceptual grouping of a stimulus array presented peripherally. They manipulated perceptual grouping by using stimuli with differing degrees of illusory contours. When stimuli form a perceptual group, such that an illusory shape with clear defined boundaries is present, they are processed as one, thus reducing competition in extrastriate regions. The effects of top-down modulation were also explored by including trials which required participants to attend to the stimulus, and trials that required them to perform a letter discrimination task at fixation to prevent them from attending to the peripheral display. The amount of attention modulation found when looking at the contrast of attend versus un-attend varied linearly with the degree of competition left unresolved by bottom-up mechanisms.

Modulation of extrastriate regions was largest when neural competition was least influenced by bottom-up mechanisms (not perceptually grouped), and attention modulation was no longer seen when neural competition was strongly influenced by bottom-up mechanisms (perceptually grouped). These results suggest that attention is only beneficial, and only modulates extrastriate regions, when competition is left unresolved by bottom-up processes.

It is possible that modulation in area V5 was not observed in the current study because the motion of the stimuli was more salient than the colour, and thus bottom-up mechanisms resolved competition in area V5 without the need for top-down mechanisms to play a role. Indeed, participants were significantly more accurate at responding to motion trials than colour trials. Bottom-up mechanisms may have directed participant's attention to the motion of the dots immediately, without the need for any top-down modulation. However, in order to successfully perform the colour task, participants were required to overcome the bottom-up bias to motion, and use top-down modulation to redirect attention to colour. This would explain why modulation was found in area V4, but not area V5.

Studies have also shown that conditions which require the highest cognitive demand tend to show attentional enhancement in category specific extrastriate regions, while easier tasks do not show this same modulatory effect (Erickson et al., 2009). It is possible that the motion task administered in the current study was simply too easy, and this is why modulation was not observed in area V5. The task may have been so simple that it did not require sufficient demand on attention to actually lead to modulatory effects in area V5. The fact that participants were significantly more accurate on the motion task suggests that they did indeed find this task easier to complete than the colour task. It seems that the most apt explanation for why

modulation in area V5 was not found in the context of task switching in this experiment is because the motion task used in this study was simply too easy and the motion stimuli were particularly salient so any competition in extrastriate regions would have been resolved by bottom-up processes without the need for any top-down modulation. However, it should be kept in mind that it is possible that the motion task was easier for another reason. The motion task may have been easier because of the non-arbitrary stimulus-response mappings assigned to this condition. It is natural for participants to respond with the left button when a stimulus is moving left and the right button when it is moving right. In contrast, the assignment of the stimulus-response mappings in the colour condition was arbitrary. There is no natural inclination to press the left button when you see a blue stimulus or the right button when you see a red stimulus. Attempts were made to mitigate this problem by placing coloured bars on either side of the stimuli to remind participants of the stimulus-response mappings in the colour task. However, the possibility remains that participants may have had a more difficult time on the colour task because they needed to remember which button was to be pressed for each colour.

4.3 Competition during Switch and Repeat Trials

The third hypothesis was interested in exploring differences in the competition between area V4 and V5 across switch and repeat trials, and also in exploring differences in modulation within these regions across switch and repeat trials. Most studies of task switching have focussed exclusively on the contrast of switch trials versus repeat trials either during stimulus presentation or during the cue period in an attempt to figure out the mechanisms underlying our ability to switch between tasks (Monsell, 2003). In looking at this contrast, such studies collapse across all repeat

trials and compare that activity to switch trials. They do not look at whether differences also exist at the level of the repeat trial depending on whether a task has been repeated a small or large amount of times. This study sought to look at these differences by dividing repeat trials into early and late repeat depending on how many times a particular task had been repeated. Traditionally, switching studies have focussed on the role of a variety of prefrontal and parietal areas in switching, but have neglected to examine the role played by category specific extrastriate regions. So, in addressing the third hypothesis, activation differences in area V4 and V5 across trial type were identified, and an exploration of how both modulation and competition in these regions differed depending on trial type was examined.

In both area V4 and V5, brain activation was higher on switch trials than it was on early repeat trials. This result is not surprising and fits well with findings from previous studies. In switching studies, brain regions that are task-relevant tend to show greater activation on switch than repeat trials (Kimberg, Aguirre, & D'Esposito, 2000). The greater difficulty that switch trials entail likely elicits greater general arousal leading to higher activation in brain regions that are relevant to task performance (Monsell, 2003; Yeung et al., 2006). These results also fit well with findings from other studies that have examined whether switch trials elicit greater activity than repeat trials in other category specific extrastriate regions. This effect has been found in the inferior temporal gyrus during a word switching task and also in the FFA during a face switching task (Yeung et al., 2006). The finding of greater activation in area V4 and V5 on switch trials relative to repeat trials fits well with the results of other studies.

In area V4, participants showed significantly higher activation on late repeat compared to early repeat trials. This trend was seen in area V5 as well. This result was

somewhat unexpected, as one would anticipate that activation in this region would actually be lower on the late repeat trials than the early repeat trials due to adaptation (De Baene, Kuhn, & Brass, 2012). Well initially surprising, these results do fit with findings from studies using the Wisconsin card sorting task (WCST). The WCST is a task switching paradigm which assesses ones' ability to flexibly shift their attention. An ERP study using this paradigm has demonstrated that during performance of the WCST, the amplitude of the P3b component changes depending on trial type (Barcelo, Munoz-Cespedes, Pozo, & Rubia, 2000). The amplitude of this component is smallest in the initial trial following a switch trial, and it then gets progressively larger with subsequent repeat trials. Anatomical sources for this P3b component have been proposed to be in medial temporal lobe regions. The findings in the current study of increased activation in area V4 on later repeat trials fit well with these findings. It has been suggested that this rise in amplitude across repeat trials may be due to an increase in the strength of the currently relevant task set growing over successive repeats of the same trial. These results have also been replicated in another ERP study of task switching (Wylie et al., 2003b). It seems that the increases seen in activity over area V4 on late repeat trials may reflect a strengthening of the newly established task set as it continues to be repeated.

The third hypothesis specifically explored how competition between area V4 and V5 would differ across trial type in order to determine whether the biased competition model of attention offers any insight into why we see switch costs during task switching. It was expected that the largest amount of competition between these brain regions would be seen on switch trials when the now irrelevant stimulus was relevant on the previous trial. Previous studies have suggested that competition between motion and colour sensitive regions is greater on switch trials relative to

repeat trials (Liston et al., 2006). It was also expected that this competition would then decrease with subsequent repeat trials as participants got used to performing a particular task. Behaviourally, participants did indeed get better at performing the task across subsequent repeat trials. They were significantly faster at responding to early and late repeat trials than to switch trials and they were also faster at responding to the late repeat trials than the early repeat trials. Since these behavioural results show a gradual improvement in performance across trials, it was expected that this improvement would also be reflected in changes in the level of competition between area V4 and V5. Contrary to this hypothesis, when normalized betas were examined to compare competition between area V4 and V5 across the different trials types, no differences in the level of competition were observed. While suggestions had been made about whether this competition would have been reflected as an enhancement of task-relevant information, a suppression of task-irrelevant information, or both, the current study does not provide support for any of these hypotheses as no differences in competition between the regions were observed.

These results are surprising as they conflict with the findings of Liston et al. (2006) and with the competition hypothesis (Wylie et al., 2004a, 2004b). The competition hypothesis suggested that competition between stimulus-response mappings would take place on all trials when more than one response was associated with a given stimulus, but that competition would be more pronounced on switch trials because the competing task would have just been carried out and will thus be a stronger competitor. However, the results found here do not lend support to this supposition.

Similarly, it was expected that we would have seen differences in the degree of modulation across the different trial types with modulation smallest on the switch

trial, and increasing with each subsequent repeat trial. No evidence for this hypothesis was found. In area V5, no attentional modulation was observed, and in area V4, where significant modulation was found, that modulation did not differ across trial type.

It is possible that we did not find the results that we had anticipated because competitive differences across switch and repeat trials may not occur in the extrastriate regions responsible for processing the stimuli, namely area V4 and V5. This is the first study to actually examine competition between these regions during task switching. While Liston et al. (2006) did look at competition between motion and colour processing regions, they did not look specifically within area V4 as we did in the present study. These results suggest that the examination of competition in category-specific extrastriate regions may not be particularly useful in helping us understand switch costs.

While very little research has been done to look at the direct relationship between task switching and selective attention, it has been suggested that there are two basic hypotheses. The first is the independence hypothesis which suggests that switching attention and selectively attending are two independent abilities without much overlap. The alternate hypothesis is the shared central resource hypothesis which suggests that selective attention and task switching are intimately linked such that they utilise the same limited resources during task performance (Meiran et al., 2012). Research on task switching in pre-schoolers provides support for this second hypothesis as when attempts are made to simplify selective attention components of a task, switch costs are reduced (Diamond, Carlson, & Beck, 2005). In contrast, research in adults, which has looked at the ability of participants to ignore irrelevant distracters during task switching provided support for the first hypothesis which suggests that selective attention and task switching are independent abilities (Meiran

et al., 2012). This study provides support for the idea that in adults, selective attention and task switching are two independent processes. The biased competition model of attention is not a useful model to adopt in an attempt to explain switch costs since the results of this study suggest that selective attention acts similarly on both switch and repeat trials. However, this does not rule out the possibility that in children selective attention and task switching may be more closely linked. In this younger, still developing population, it is possible that an examination of selective attention processes in extrastriate regions during task switching may assist in understanding the perseveration and large switch costs seen in pre-school aged children (Hanania & Smith, 2010). However, the results of this study suggest that this is not the case in adults.

4.4 The Role of Prefrontal and Parietal Regions in Top-Down Modulation

Since attentional modulation was observed in area V4, the fourth and final hypothesis was interested in exploring which brain regions were involved in providing top-down signals to this region to bias processing towards task-relevant information. The PPI analysis revealed a number of brain regions which showed stronger functional connectivity to area V4 while participants were attending to colour compared to when they were ignoring colour. This included activation in the IFJ, the middle frontal gyrus, and the supramarginal/angular gyrus, suggesting that these regions may provide top-down signals to area V4 to bias processing towards task-relevant information.

In the present study, signals biasing processing in area V4 appeared to originate in the IFJ, and this fits well with findings from previous studies of working memory which have also implicated this region in such modulatory processes (Zanto

et al., 2010). TMS research has even shown that the IFJ appears to play a causal role in the attentional modulation of area V4 (Zanto et al., 2011). The middle frontal gyrus was also implicated in providing bias signals to area V4. Previous working memory studies have found evidence suggesting that this brain region does appear to bias extrastriate cortex, specifically, the middle frontal gyrus seems to bias activity in the PPA towards scene stimuli when it is task-relevant (Gazzaley et al., 2007). Our results suggest that this brain region is also implicated in providing such attentional biasing signals to area V4 when colour is a feature dimension of interest. Activity in the supramarginal/angular gyrus was also found to be significantly more correlated with activity in area V4 when participants were attending to colour versus ignoring colour, and this too fits with the results of previous studies. This region has been shown to be involved in the modulation of area V4 when participants are attending to colour versus ignoring colour in the context of working memory (Zanto et al., 2011). Our results replicate the results of working memory studies that have used functional connectivity analyses to investigate the source of top-down modulatory signals, and they extend these findings to task switching. These findings fit well with theoretical models (Corbetta & Shulman, 2002), and suggest that a network of fronto-parietal regions are involved in providing top-down signals to area V4 which bias processing in this region towards information that is task-relevant.

4.5 Future Directions

This study is one of the first to examine category specific extrastriate cortex activity in the context of a task switching paradigm. While it has begun to address the question of whether top-down modulation of extrastriate regions is important for the completion of such tasks, there are still a number of avenues of research that remain

to be explored in developing an understanding of the role that neural competition plays in task switching. The majority of single-unit studies looking at selective attention properties have focussed on the role that individual neurons in extrastriate regions V4 and V5 play in spatial attention, fewer studies have looked at the role that they play in feature-based attention (Maunsell & Treue, 2006). More studies are needed on this topic in order to resolve what exactly is going on in category specific regions like area V4 and V5 when attention is directed to different aspects of a stimulus feature. Preliminary research suggests that neurons in area MT, which have been shown to be motion selective, can be modulated by an attentional task in which colour is relevant (Chen et al., 2012). More studies are required to replicate this effect and explore other extrastriate regions such as area V4 using a feature based attention task such as that used by Chen et al. (2012). Such findings could really change the way that we think about area V4 and area V5, thus more research is needed to truly elucidate their role in feature selective attention at the single neuron level.

It would be useful for a future study to examine this same question, but with stimuli that are better matched for bottom-up processing. A pilot study should be completed to ensure that the stimuli used for the colour task and the stimuli used for the motion task are equated for bottom-up processes. In order to do this, the pilot study should ensure that response times and accuracy on the motion task are equivalent to those on the colour task. If one task emerges as easier, steps should be taken to increase the difficulty of that task until equivalent performance is achieved. It is clear that both bottom-up and top-down mechanisms interact to influence competition in visual regions of the brain, thus any study hoping to isolate the role of top-down mechanisms needs to control for bottom-up mechanisms. In this study it seems that the motion task was too easy for participants, thus future studies should

keep this in mind, and have participants detect subtle changes in stimulus direction, or use different coherence levels for the moving dots. Using a more challenging task may actually lead to different findings in terms of whether attentional modulation can be found in area V5 in the context of switching.

Once all of these methodological challenges are addressed, it would be interesting to perform a similar study in children. Studies of working memory that have shown modulation in these extrastriate regions have shown that the magnitude of such modulation differs in children compared to adults (Wendelken, Baym, Gazzaley, & Bunge, 2011). Children really struggle when it comes to task switching, showing larger switch costs and higher error rates than adults (Cepeda et al., 2001). Once the methodological glitches that were discovered in the current study are amended, and the role of modulation in area V4 and V5 during task switching is identified, it would be interesting to use the same paradigm in children. It is possible that their poor performance on switching tasks will be reflected in differences in the degree of competition between area V4 and V5 on switch and repeat trials. While the results of this study suggest that this is not the case in adults, it may be true in children as it seems that in this younger population task switching and selective attention are more closely linked (Diamond et al., 2005; Meiran et al., 2012). More research is required to truly understand the role that area V4 and V5 play in task switching.

Chapter 5 - Summary and Conclusions

This study set out to investigate whether top-down modulation of area V4 and area V5 could be observed in the context of a task switching paradigm which involved bivalent coloured and moving stimuli. In addition to this, this study sought to determine whether the magnitude of such attentional modulation or competition between area V4 and V5 would shed any light on switch costs which are a hallmark behavioural effect found in task switching studies. Results revealed a network of fronto-parietal regions that were involved in the performance of task switching. It was found that colour sensitive area V4 did indeed show signs of attentional modulation in the context of task switching. Motion sensitive area V5 did not show this same attentional modulation. While participants were able to successfully switch between the motion and the colour task, activity in area V5 did not reflect this switch. This result presents the possibility that not all extrastriate visual regions are modulated by attention in the context of a switching paradigm. Alternatively, this finding may be a reflection of the particular task utilized in the present experiment. It is possible that since the motion task used in this study was particularly simple, bottom-up mechanisms may have driven attention towards the motion of the stimuli without the need for any top-down attentional mechanisms to bias area V5. Future studies will be needed to tease apart these two explanations and identify whether attentional modulation can be found in area V5 even in the context of an attention switching task.

Results of the present study indicated that competition between area V4 and V5 did not differ across switch and repeat trials, nor did the degree of modulation within area V4 or V5. These results suggest that the biased competition model of selective attention is not a useful model for explaining switch costs. Instead, our

results suggest that selective attention and task switching are independent processes and that the mechanisms involved in task switching cannot be identified solely by examining the effects of selective attention in extrastriate visual regions.

Finally, this study also sought out to determine which brain regions may be responsible for issuing top-down signals to area V4 to bias processing in that region to information that is task-relevant. Our results revealed that biasing signals appear to originate in a network of fronto-parietal regions.

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Appendix 1 – Ethics Approval

Office of Research Ethics
The University of Western Ontario
Room 4180 Support Services Building, London, ON, Canada N6A 5C1
Telephone: (519) 661-3036 Fax: (519) 850-2466 Email: ethics@uwo.ca
Website: www.uwo.ca/research/ethics

Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. J.B. Morton
Review Number: 17547 **Review Level:** Full Board
Review Date: November 09, 2010 **Approved Local # of Participants:** 50
Protocol Title: Age related differences in top-down modulation of extrastriate cortex activity in a task-switching paradigm
Department and Institution: Psychology, University of Western Ontario
Sponsor: NSERC-NATURAL SCIENCES ENGINEERING RSRCH COU
Ethics Approval Date: December 03, 2010 **Expiry Date:** November 30, 2011
Documents Reviewed and Approved: UWO Protocol (including instruments noted in Section 8.1), Assent Letter, Letter of Information and Consent Form - Parent dated 16 Nov 2010 and Adult dated 16 Nov 2010, and Poster
Documents Received for Information:

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced study on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

During the course of the research, no deviations from, or changes to, the protocol or consent form may be initiated without prior written approval from the HSREB except when necessary to eliminate immediate hazards to the subject or when the change(s) involve only logistical or administrative aspects of the study (e.g. change of monitor, telephone number). Expedited review of minor change(s) in ongoing studies will be considered. Subjects must receive a copy of the signed information/consent documentation.

Investigators must promptly also report to the HSREB:

a) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) all adverse and unexpected experiences or events that are both serious and unexpected;
c) new information that may adversely affect the safety of the subjects or the conduct of the study.

If these changes/adverse events require a change to the information/consent documentation, and/or recruitment advertisement, the newly revised information/consent documentation, and/or advertisement, must be submitted to this office for approval.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

Chair of HSREB: Dr. Joseph Gilbert
FDA Ref. #: IRB 00000940

Ethics Officer to Contact for Further Information			
☐ Janice Sutherland (jsutherl@uwo.ca)	☑ Elizabeth Wambolt (ewambolt@uwo.ca)	☐ Grace Kelly (grace.kelly@uwo.ca)	

This is an official document. Please retain the original in your files. cc: ORE File

Research Western

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Prof. Bruce Morton
Review Number: 17547
Review Level: Delegated
Approved Local Adult Participants: 50
Approved Local Minor Participants: 0
Protocol Title: Age related difference in top-down modulation of extrastriate cortex activity in a task-switching paragram
Department & Institution: Psychology, University of Western Ontario
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: November 29, 2011 **Expiry Date:** April 30, 2012
Documents Reviewed & Approved & Documents Received for Information:

Document Name	Comments	Version Date
Revised Study End Date		

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The UWO HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Ethics Officer to Contact for Further Information

✓ Janice Sutherland (jsutherl@uwo.ca)	___ Grace Kelly (grace.kelly@uwo.ca)	___ Shantel Walcott (swalcot@uwo.ca)

This is an official document. Please retain the original in your files.

Curriculum Vitae

KATIE KNAPP

EDUCATION

2010-2012	Master of Science Neuroscience The University of Western Ontario, Canada
2009	Bachelor of Arts (Honours) Psychology University of Auckland, New Zealand
2006-2008	Bachelor of Arts Psychology Massey University, New Zealand

HONOURS AND AWARDS

2011-2012	NSERC Alexander Graham Bell Canada Graduate Scholarship – Masters Award
2011	Ontario Graduate Scholarship – Masters Award (Declined)
2011	Western Graduate Student Teaching Award Nomination
2010-2012	Western Graduate Research Scholarship
2009	University of Auckland Honours Scholarship
2009	Merit Award University of Auckland Psychology Poster Competition
2008	Massey University Scholar (Declined)
2008	Hesketh Prize in Psychology
2007	Massey University Undergraduate Scholarship
2007	The Longman Paul Prize in History
2006	Sir Robert Jones Undergraduate Scholarship

PUBLICATIONS

Addis, D. R., **Knapp, K**., Roberts, R. P., & Schacter, D. L. (2012). Routes to the past: Neural substrates of direct and generative autobiographical memory retrieval. *Neuroimage*, *59*, 2908-2922.

POSTER PRESENTATIONS

Addis, D. R., **Knapp, K.,** Inger, M., & Schacter, D. L. (2010). *Common and distinct neural substrates of direct and generative autobiographical memory retrieval.* Poster presented at Theoretical Perspectives on Autobiographical Memory Conference, Aarhus, Denmark.

Knapp, K., & Addis, D. R. (2009). *Temporal and spatial differences in the core brain network supporting direct and generative retrieval of autobiographical memories.* Poster presented at The University of Auckland Psychology Poster Competition in Auckland, New Zealand.

RELEVANT WORK EXPERIENCE

2010-2012	Teaching Assistant Research Methods and Statistical Analysis in Psychology The University of Western Ontario.
2010	Research Assistant for Dr. J. Bruce Morton Cognitive Development and Neuroimaging Laboratory The University of Western Ontario
2010	Research Assistant for Dr. Stephen Lomber Cerebral Systems Laboratory The University of Western Ontario