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SELECTING AND INHIBITING RESPONSES: COMMON COGNITIVE AND NEURAL SUBSTRATES?

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Abstract

Despite the brain receiving a constant influx of sensory information in ever-changing environments, humans are nonetheless able to flexibly guide their behaviour in accordance with higher goals and plans. The cognitive system achieves this by implementing executive control processes that monitor, regulate and alter the settings of lower level cognitive processes that are involved in analyzing incoming sensory information and executing motor plans. At the core of goal-directed behaviour are the abilities to *select appropriate responses* and *inhibit planned actions* in response to changes in the environment or internal states. While there have been considerable advancements made in understanding the behavioural and neural substrates of response selection and response inhibition, we currently know relatively little about the relationship and possible interplay between these two key cognitive operations. The experiments in this thesis investigate the behavioural and neural overlap in response selection and response inhibition processes by identifying the latent structure that underpins performance in a wide range of action control tasks, exploring the causal role of a brain region that has been implicated in both processes, and by inspecting the degree to which response selection training transfers to other response selection and inhibitory control tasks.

Study 1 describes a behavioural study that employed an individual differences approach to investigate the underlying relationships across a battery of common response selection tasks (as measured by the psychological refractory period paradigm (PRP), single response selection task, and attentional blink (AB) task), and response inhibition tasks (as measured by the stop-signal task (SST), Go-Nogo tasks, Stroop, and Flanker task). In order to avoid task impurity and construct validity problems that can seriously undermine the utility of correlational and exploratory factor analytic studies, I used confirmatory factor analysis to statistically extract only what is common about the tasks. Using this approach, I found that response inhibition and response selection were separable, with SST and Go-Nogo task performance related to response inhibition, and the PRP, Stroop, Single Response Selection, and AB tasks related to response selection. These findings suggest that response selection and response inhibition reflect two distinct cognitive operations.

As neurocognitive work has implicated the superior medial frontal cortex (SMFC) in both response selection and the proactive modulation of response tendencies when stopping is occasionally required (inhibitory response selection control), it suggests that the neural substrates for these two cognitive operations overlap in this brain region. In

Study 2, I used transcranial direct current stimulation (tDCS) to investigate this hypothesis. In Experiment 1, using the same behavioural paradigm and tDCS protocol that causally demonstrated left posterior lateral prefrontal cortex involvement in response selection and training processes (Filmer et al., 2013a), I found that anodal (excitatory) and cathodal (inhibitory) tDCS of SMFC did not modify response selection and training processes relative to sham stimulation. However, when introducing an inhibitory context to the paradigm where occasional response inhibition was required (Experiments 2 and 3), I found that cathodal stimulation of the SMFC modulated response selection by increasing reaction times in the context of proactive response inhibition. Collectively, these results suggest a context-dependent role of the SMFC in response selection and response inhibition and further indicate that task set can influence the interaction between the brain and behaviour.

Response selection performance is typically compromised due to the processing limitations associated with cognitive control and decision-making when completing two tasks together relative to when completing the component tasks in isolation. While these multitasking performance decrements can be improved with training, it is currently not known whether training-related benefits can transfer to new tasks. In Study 3, I tested whether training on a dual-task can benefit performance on other tasks that are theoretically related to the trained construct. Given reports that training on video action games that requires continuous, dynamic multitasking in a demanding environment can lead to positive transfer effects on aspects of cognition, I asked a group of participants to train on a combined dynamic, continuous visuomotor tracking task and perceptual discrimination task, while an active control group practiced the two component tasks in isolation. Performance on the practiced tasks and on a battery of tests measuring response selection (PRP, Single Response Selection Task, and AB), inhibition (SST, Go-Nogo task, and Stroop) and spatial attention (Flanker) was examined pre- and post-training. Consistent with the dual-task training literature, multitasking training resulted in substantial, task-specific gains in multitasking, but this benefit did not transfer to other untrained tasks. These results suggest that training on a fast paced visuomotor tracking and discrimination task results in task-specific benefits but this benefit does not extend to untrained tasks that are theoretically related to the trained construct.

Taken together, the studies reported in this thesis offer novel insights into our understanding of the cognitive and neural substrates of response selection and response inhibition. These findings have implications for current theoretical accounts of response

selection and response inhibition processes and contribute to models of how the executive control of action should be operationalized.

Declaration by Author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Peer-reviewed publications

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Publications included in this thesis

This thesis contains three empirical studies (Studies 1-3) that have been published or submitted to peer-review journals. The empirical studies are contextualized with a General Introduction and a General Discussion. Contributions for each of the relevant articles are listed below.

Bender, A. D., Filmer, H. L., Garner, K. G., Naughtin, C. K., & Dux, P. E. (in press). On the relationship between response selection and response inhibition: an individual differences approach. *Attention Perception & Psychophysics,* DOI 10.3758/s13414-016-1158-8. Incorporated in Study 1.

Contributor	Statement of contribution
Angela D. Bender	Conceptualized & designed experiments (50%) Data collection, analysis & interpretation (70%) Wrote the paper (50%)
Hannah L. Filmer	Conceptualized & designed experiments (10%) Data analysis & interpretation (10%) Wrote the paper (20%)
Kelly G. Garner	Conceptualized & designed experiments (10%) Wrote the paper (5%)
Claire K. Naughtin	Conceptualized & designed experiments (10%) Wrote the paper (5%)
Paul E. Dux	Conceptualized & designed experiments (20%) Data interpretation (20%) Wrote the paper (20%)

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Contributor	Statement of contribution
Angela D. Bender	Conceptualized & designed experiments (50%) Data collection, analysis & interpretation (60%) Wrote the paper (60%)
Hannah L. Filmer	Conceptualized & designed experiments (25%) Data collection, analysis & interpretation (20%) Wrote the paper (20%)
Paul E. Dux	Conceptualized & designed experiments (25%)

	Data collection, analysis & interpretation (25%) Wrote the paper (20%)

Contributions by Others to this Thesis

Paul E. Dux (Primary supervisor) and Hannah L. Filmer (Associate supervisor) were key contributors to this thesis and assisted with conceptualisation, design and interpretation of all three experiments, along with proofreading manuscripts and thesis drafts. Claire K. Naughtin was integral to designing the experimental tasks in Study 1 and 3. Kelly G. Garner was a key contributor to designing Study 1. Kristina Horne and Ashley York (research assistants) assisted in behavioural data collection for Study 3.

Statement of Parts of the Thesis Submitted to Qualify for the Award of Another Degree

None.

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cognitive control, response selection, response inhibition, multitasking, attention, individual differences, transcranial direct current stimulation

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List of Abbreviations Used in the Thesis

AB: Attentional blink
AFC: Alternative force choice
AIC: Akaike's information criterion
ANOVA: Analysis of variance
AUD: Australian dollar
BF: Bayes factor
BOLD: Blood oxygen level dependent
CFA: Confirmatory factor analysis
CFI: Comparative fit index
dLPFC: Dorsolateral prefrontal cortex
DMC: Dual mechanisms of control
EPIC: Executive-process interactive control
ECTVA: Executive control of the theory of visual attention
fMRI: Functional magnetic resonance imaging
GPe: External segment of the globus pallidus
GPi: Internal segment of the globus pallidus
HRF: Hemodynamic response function
IFC: Inferior frontal cortex
IFG: Inferior frontal gyrus
IFJ: Inferior frontal junction
ITI: Inter-trial interval
LPFC: Lateral prefrontal cortex
M: Mean
MD: Multiple demand
PFC: Prefrontal cortex
pLPFC: Posterior lateral prefrontal cortex
PRP: Psychological refractory period
Pre-SMA: pre-supplementary motor cortex
RSVP: Rapid serial visual presentation
RT: Reaction time
RT1: Reaction time to task 1
RT2: Reaction time to task 2
rTMS: Repetitive transcranial magnetic stimulation

rIFG: Right inferior frontal gyrus

SD: Standard deviation

SMA: Supplementary motor area

SMFC: Superior medial frontal cortex

SOA: Stimulus onset asynchrony

SRMR: Standardized root-mean-square residual

SSD: Stop-signal delay

SST: Stop-signal task

SSRT: Stop-signal reaction time

T1: Task 1

T2: Task 2

tDCS: Transcranial direct current stimulation

TMS: Transcranial magnetic stimulation

GENERAL INTRODUCTION

"THINKING IS EASY, ACTING IS DIFFICULT, AND TO PUT ONE'S THOUGHTS INTO ACTION IS THE MOST DIFFICULT THING IN THE WORLD"

Johann Wolfgang von Goethe

How the brain flexibly adapts behaviour in a constantly changing environment has been a central question in cognitive psychology and neuroscience since research began in these fields. Yet we are still puzzled how executive control, an umbrella term which refers to a broad range of cognitive operations that allow people to strategically adjust their behaviour in a goal-directed fashion, is exercised. In the realm of action control, response selection requires the intentional selection of a response from several alternatives when a signal changes or a cue is detected. However, the selection of a task-relevant action also necessitates response inhibition - the ability to suppress automatic response tendencies, task-irrelevant information or task sets when a context changes (e.g., hitting the car's brake when a traffic light switches to red). Historically, these two functions have been considered as largely independent processes but there is increasing evidence of overlap between these two cognitive operations (Mostofsky & Simmonds, 2008; Verbruggen, McLaren, & Chambers, 2014). However, the extent to which these two functions interact and draw on a common process remains to be definitely determined.

This thesis examines the relationship and interaction between these two key executive functions that are critical for the control of actions. Understanding whether a general action control mechanism or two distinct mechanisms underpins performance in response selection and inhibition is of relevance, not only for fully characterising the human cognitive architecture but because impaired executive function is linked with a range of clinical conditions. Indeed, impaired response selection has been shown to contribute to processing speed impairments in schizophrenia (Krieger, Lis, & Gallhofer, 2001; Luck et al., 2009; Pellizzer & Stephane, 2007; Woodward, Duffy, & Karbasforoushan, 2013; Woodward et al., 2009) and an age-related decline in multitasking (Anguera et al., 2013), whereas impaired inhibitory control has been shown to contribute to several clinical and neurological conditions, including attention-deficit hyperactivity disorder (Nigg, 2001), obsessive-compulsive disorder (Penades et al., 2007), schizophrenia (Thakkar, Schall, Boucher, Logan, & Park, 2011), addiction and eating disorders (Crews & Boettiger, 2009; Houben, 2011; Noel, Brevers, & Bechara, 2013) and decreased physical health, poor school and job outcomes (Diamond, 2013; Moffitt et al., 2011). To wit, detailing the processes underlying response selection and inhibition may lead to more targeted and efficacious interventions.

In this General Introduction, I first outline the theoretical and empriciral work on response selection and response inhibition. Along the way, I highlight key experimental paradigms that have been employed to measure response selection and inhibition and further discuss how the observed behavioural effects in these paradigms led researchers to propose theoretical frameworks and computational models. Here I also discuss the neural substrates that are involved in response selection and inhibition, focusing on the localization of these operations in neuro-typical and neuro-atypical human and animal samples. Furthermore, I will present evidence from behavioural and cognitive neuroscience studies that argue for and against a unitary model of action control. Finally, I outline three outstanding questions in the field that will form the basis of my empirical investigations: 1) Can an individual differences approach shed light on the underlying mechanism(s) that contribute to performance outcomes in a wide range of response selection and response inhibition tasks? 2) What is the role of the superior medial frontal cortex in response selection and response inhibition? And, 3) does dual-task training improve performance, and if so, do training benefits transfer to other action control tasks that are theoretically related? I employ a range of behavioural approaches and a non-invasive stimulation technique to address these questions.

Executive Control

Over the last decades, considerable effort has been made to explore the system-level neural processes that underlie executive control (Koechlin, Ody, & Kouneiher, 2003). However, the systems-level neural architecture associated with this collection of cognitive operations remains to be definitely characterised. One perspective commonly ascribes top-down control to anatomically distinct regions of the prefrontal cortex (PFC), with executive control recruited by multiple functionally organised systems when different executive control operations are required. These theories posit that the rostro-caudal axis of PFC supports hierarchically arrayed levels of control, whereby increased activity in progressively anterior subregions of the PFC but not lower, more posterior regions, is associated with increasingly abstract control requirements and temporally extended, abstract representations (Badre & Wagner, 2004; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Fuster, 2004; Hazy, Frank, & O'Reilly, 2006; Koechlin & Jubault, 2006; Koechlin et al., 2003; Koechlin & Summerfield, 2007; O'Reilly & Frank, 2006; O'Reilly, Noelle, Braver, & Cohen, 2002; Petrides, 2005; Petrides & Pandya, 2006). Such a representational hierarchy is thought to be expressed through the passing of control signals from different functionally specialised anterior PFC regions to lower posterior regions to reduce

uncertainty during action selection (Koechlin et al., 2003; Koechlin & Summerfield, 2007), or to activate and coordinate tasks sets among more posterior regions (Sakai & Passingham, 2006). Indeed, anatomical evidence supports an asymmetry in the corticocortical connections within the PFC (Barbas & Pandya, 1987; Petrides & Pandya, 2007) and support from animal lesion data and functional magnetic resonance imaging (fMRI; a neuroimaging technique that assesses neuronal activity by measuring the blood oxygen level-dependent (BOLD) signal) studies have demonstrated functionally selective PFC subregions associated with executive control. For example, the dorsolateral prefrontal cortex (dLPFC) has been identified to play a key role in maintaining and manipulating information within working memory (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2004; Bunge, Wendelken, Badre, & Wagner, 2005; MacDonald, Cohen, Stenger, & Carter, 2000; Miller & Cohen, 2001), while lateral prefrontal cortex (LPFC) is recruited during reward-based and cue-based decisions (Fuster, 1990; Goldman-Rakic, 1987). However, a series of clinical observations, functional neuroimaging data, and animal lesion studies have also shown that medial frontal and subcortical regions play an important role in executive control, with the dorsal anterior cingulate/ pre-supplementary motor area (pre-SMA) critical for the monitoring and detection of response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001) and the basal ganglia important in action selection (Diamond, 2013). Taken together, the neuroscientific studies provide support for a specialization of functions within the PFC and further highlight the importance of posterior and subcortical regions for the successful implementation of goal-directed behaviour.

In contrast, a second view posits that executive control is not functionally restricted to cognitive domains or anatomically distinct brain regions. Instead, this account argues that executive processes underlie a unitary mechanism that actively enables the representation and maintenance of goal-directed representations online. This framework postulates that a common network of brain regions is recruited whenever task difficulty increases, regardless of the exact cognitive process, stimulus, or response that is manipulated. A typical approach taken in studies that look for the neural substrate of action control, is to locate brain regions that show increased acitivity across a wide range of executive control tasks. Indeed, neuroimaging data accord well with the later theoretical framework, as goal-directed behaviour has been consistently associated with a system of frontal and parietal activations in neuroimaging (Cabeza & Nyberg, 2000; Cole & Schneider, 2007; Dosenbach et al., 2006; Duncan, 2010; Duncan & Owen, 2000; Fox et al., 2005). This so-called “multiple-demand” (MD) network (Duncan, 2010; Duncan &

Owen, 2000) plays a central role in executive control, as it is commonly activated across a diverse range of cognitive requirements and has been shown to recruit part of the LPFC, dorsal anterior cingulate, the pre-SMA and the inferior parietal cortex.

However, one potential alternative explanation for such co-activation of a common executive control network (Duncan & Owen, 2000) might stem from studies that underestimate the important role of proactive (preparatory) and reactive (online) control functions (Braver, 2012) because these models are often based on fMRI designs that do not have the temporal resolution to disentangle target-related and preparation-related BOLD activation (see Ruge, Jamadar, Zimmermann, & Karayanidis, 2013 for discussion). According to the Dual Mechanisms of Control (DMC; Braver, 2012) framework, goal-directed behaviour can be achieved through both proactive and reactive mechanisms. A proactive control strategy can be defined as a form of “early selection”, which requires sustained active maintenance of goal representations during the preparatory stage of a cognitively demanding task, so that attention, perception, and action domains can be biased appropriately to enable task-relevant outcomes. In contrast, reactive processes can be defined as a form of “late correction”, where executive control is involved after the occurrence of a high-interfering situation and may be equated to bottom-up reactivation of task goals (Braver, 2012). Thus, task designs that do not differentiate between preparatory and response–related mechanisms at different times during a trial may confound the localisation of distinct cognitive processes and their neuroanatomical counterparts (Goghari & MacDonald, 2009). The question remains therefore, whether executive control of action is supported by one or multiple systems.

Selecting Responses

The ability to select the most appropriate response out of several response alternatives is thought to result from the interplay between three separable stages (Sternberg, 1969): a perceptual stage, where task-relevant stimuli (e.g., a traffic light switching from green to orange) are analysed and attended to, a central response selection stage where an appropriate response is selected and mapped on to a motor action plan (e.g., the decision to decelerate and stop the car), and the final response execution stage where the generated motor response is performed.

Modeling response selection

Converging evidence from neuroimaging (Forstmann et al., 2010; Heekeren, Marrett, & Ungerleider, 2008), primate neurophysiology (Mazurek, Roitman, Ditterich, &

Shadlen, 2003; Shadlen & Newsome, 2001), behavioural studies and sequential sampling models (Brown & Heathcote, 2008; Ratcliff & Smith, 2004; Smith & Ratcliff, 2004) indicate that the brain employs accumulation-to-threshold mechanims when deciding between alternative actions.

Sequential sampling models provide a mathematical framework to understand the dynamics of human decision-making because they reveal the latent psychological step involved that lead to an observed choice (Brown & Heathcote, 2008; Ratcliff & Smith, 2004; Smith & Ratcliff, 2004). These models are based on the assumption that information about stimuli is intrinsically noisy in the cognitive system (e.g., neuronal states produced by different processes ocurring at the same time) and in the environment (e.g., salience of stimuli may be perceptually degraded). Information about such noisy states is sequentially accumulated and integrated into sensory evidence until a decision criterion is reached. The lower the quality of a stimulus, the longer until the accumulation process reaches the response threshold, thus resulting in longer reaction times and higher error rates. The key parameters of the response selection process are the response criterion (i.e., the amount of information required for a response to be selected) and drift/accumulation rate (i.e., how quickly information accumulates). A low response criterion (i.e., a liberal response criterion) results in more impulsive decision making and higher error rates, whereas a high response criterion gives rise to slower responding and less choice errors (Ratcliff & Smith, 2004; Smith & Ratcliff, 2004). These models have been successfully applied to a range of simple response selection tasks (White, Ratcliff, Vasey, & McKoon, 2010), with further support coming from studies that show accumulation to response selection threshold to resemble activity in specific neurons (Hanes & Schall, 1996; Purcell et al., 2010).

Response selection in response to changes in the enviroment is often studied in tasks such as the psychological refractory period (PRP; De Jong, 1993; Pashler, 1994b; Pashler & Johnston, 1989; Welford, 1952) and other dual and single-response selection tasks that place temporal response limitations on central selection processes. For example, in the PRP task, participants are instructed to make speeded responses to two stimuli where the interval between the two targets, known as the stimulus onset asynchrony (SOA) is either temporally short (e.g., 150 ms) or long (e.g., 1000 ms). A common finding is that reaction time (RT) to the second stimulus (Task 2) increases as SOA decreases, while RT to the first stimulus (Task 1) is relatively unaffected by SOA. This robust PRP effect that tends to occur across all classes of stimulus and response modalities led Welford (1952) to propose the presence of a bottleneck in human information processing. However, it is currently not known whether the observed

multitasking limitations are reflective of a bottleneck that is predominantly structural in nature or a cognitive architecture that is subserved by a central executive system which strategically allocates capacity-limited information processing resources in a flexible manner.

The structural central bottleneck model

One of the most influential theoretical framework of dual-task interference is the central bottleneck account (Pashler, 1984). The key assumption of this theory implies a discrete view of dual-task interference. Namely, interference occurs because the central response selection stage can only process incoming sensorimotor information in a strictly serial manner, such that only one decision can be processed at any given moment. Consequently, when two tasks need to be performed in quick succession (~400 ms or less), response selection for the second task is delayed until the decision-making process for the first task has been finalised. In contrast, perceptual- and response execution stages are thought to operate without such constraints, meaning that the processing of multiple tasks concurrently is possible.

The central bottleneck account makes several testable predictions. First, any lengthening of the time to process Task 1 at the precentral or central response selection stage will lead to an increase in response times for both Task 1 and Task 2. Second, the locus of slack logic predicts that the effect of lengthening the duration of Task 2 processing at the precentral stage (e.g., increased perceptual difficulty to identify stimulus 2) will affect RT2 less at shorter relative to longer SOAs. This is because its effects will be absorbed into the cognitive slack that occurs while Task 2 waits for access to the central resource during Task 1 analysis. Third, any effects of a factor lengthening the duration of Task 1 that occur after the bottleneck requiring central stage, should only increase RT1 due to the fact that RT2 does not wait for access to this processing module. Likewise, any factor slowing Task 2 post bottleneck will only influence RT2. Indeed, research over several decades has confirmed these predictions in a number of emprical studies (e.g., McCann & Johnston, 1992; Pashler, 1984; Pashler, & Johnston, 1989; Schweizer, Jolicoeur, Vogel-Sprott, & Dixon, 2004). For example, using the locus of slack technique, Pashler (1984) and Pashler and Johnston (1989) varied Task 2 encoding difficulty by manipulating the stimulus 2 intensity. In line with the locus of slack logic, increased difficulty to identify stimulus 2 increased RT2, with the effect strongest at longer SOAs relative to shorter SOAs.

Taken together, these findings suggests that humans ability to multitask efficiently may be limited by an inflexible, structural, serial information processing bottleneck at the

central response selection stage. Indeed, evidence for a strictly serial execution of response selection stages can still be observed when importance for Task 1 and 2 is equally emphasised. For example, the response time interval between both tasks has been shown to remain similar to the time that is required to process Task 2 at the response selection stage, even if parallel processing of the two tasks is encouraged (Pashler, 1994a; Ruthruff, Pashler, & Hazeltine, 2003). However, subsequent research has challenged the validity of an inflexible and structural information processing bottleneck.

Capacity sharing models

While the serial central bottleneck model (Pashler, 1984) successfully accounts for many Task 2 effects, a number of empirical observations have casted some doubt on its strictly serial nature. For example, the central bottleneck model is unable to account for findings that show increased Task 2 response selection demands to also affect Task 1 response selection with short SOAs (Tombu & Jolicoeur, 2003, 2005). This discrepancy raises the question whether resources can be flexibly allocated to multiple tasks in a graded fashion (McLeod, 1977; Navon & Miller, 2002; Tombu & Jolicoeur, 2002; 2003, 2005). To account for such findings, Tombu and Jolicoeur (2003) proposed the central capacity sharing model, which assumes that capacity sharing between tasks at the central response selection stage is possible, but capacity-limited. Thus, when two tasks require access to the central processor simultaneously, resources can be divided equally between both tasks, yet performance will not be as efficient if tasks require more resources than are available. According to this model, the classic PRP effect results from initially allocating more resources to Task 1, with little or no capacity available for Task 2 processing. In contrast, when response selection demands for Task 2 are high, central capacity-limited resources are withdrawn from Task 1, resulting in the observed RT1 increases at short SOAs.

Further support of at least partial parallel processing of central operations comes from several studies, which have shown that intertask response compatibility between Task 1 and Task 2 can influence RT to Task 1 (i.e., backwards crosstalk effect). For example, a study by Hommel (1998) observed that participants were faster in responding to the colour of a green or red rectangle when the vocal colour-naming response (i.e., red or green) for Task 2 corresponded to the colour of Task 1.

the backwards crosstalk effect is evident when responding to Task 1 (RT1) and to Task 2 (RT2), Hommel (1998) proposed that such effect is consistent with the hypothesis

that activation of response codes for Task 2 occurs prior to the completion of Task 1 response selection, indicating that response selection can occur at least partially in parallel. Converging evidence comes from an electrophysiological study that showed that the lateralized readiness potential activation for Task 2 coincided temporally with response selection processing of Task 1 (Lien, Ruthruff, Hsieh, & Yu, 2007). Similar backwards crosstalk effects have been reported in mental rotation operations (Pannebakker, Band, & Ridderinkhof, 2009), episodic memory (Logan & Delheimer, 2001), response outputs (Miller, 2006), and when response congruency for Task 1 and Task 2 is manipulated with different categories (Fischer, Miller, & Shubert, 2007; Logan & Schulkind, 2000).

On the other hand, several other theoretical models posit that limited processing resources can be shared but are instead strategically scheduled by a central executive system to meet task demands. Meyer and Kieras (1997) developed the executive-process interactive control (EPIC) framework, which proposes no limit on central-processing capacity. Instead, dual-task slowing results from limitations at sensory and motor stages when both tasks require the same processors (e.g., it is not possible to move the eyes to read a text message while simultaneously attending to ongoing traffic). Consequently, this framework argues that the PRP effect arises when task operations are adaptively scheduled (e.g., making sure that tasks are responded to in the instructed order) to alleviate the delays in sensory and motor systems.

Similarly to the EPIC framework, the executive control of the theory of visual attention (ECTVA) theory (Logan & Gordon, 2001) assumes that in order to complete two tasks, an executive controller sets the parameters to bias attention based on current task sets. These parameters are then used to perform successive perceptual categorizations until there is enough support for the mental representations of the targets. Once the accumulated evidence reaches a certain threshold, a signal is sent to a response selection stage where stochastic evidence accumulates until the response criteria threshold for a goal-related motor response is reached. According to this model, these limited processing resources can run in parallel, however, in order to minimize between-task crosstalk the processing system employs strategic, serial resource scheduling that is based on current task goals.

The threaded cognition account (Salvucci & Taatgen, 2008, 2011) posits that cognition can be represented as threads of information processing, coordinated by a central procedural resource and executed by peripheral processing modules. These modules can operate in parallel due to their independent nature, however dual-task interference occurs when multiple tasks require access to the same resource as each

resource can only process information for one task at a time.

In sum, although there is evidence that indicates a structural bottleneck at the response selection information processing stage, there have been many findings that indicate a more flexible mechanism. The notion of a strategic versus structural bottleneck has been further investigated in a number of studies that looked at the influence training has on dual-task performance. Evidence for complete or partial parallel processing would imply that the response selection bottleneck is not absolutely structural, and hence could indicate that dual-task interference can be attenuated with extensive training.

Can response selection improve with training?

Early investigations into the effects of dual-task practice on performance showed little effect of practice on interference after extensive PRP training (e.g., Karlin & Kestenbaum, 1968; Van Selst & Jolicoeur, 1997). However, given that the trained PRP tasks in these studies required manual responses to both tasks, which increases the probability of output interference between the two responses (De Jong, 1993), Van Selst, Ruthruff, and Johnston (1999) investigated whether dual-task interference in the PRP can be reduced with training by using task pairs that shared no output overlap between sensory-input or response-output modalities. During training, participants were required to first respond to a task that mapped auditory to vocal responses and a second task that mapped visual to manual responses. In contrast to previous findings, training resulted in a significant reduction in the PRP effect (from 353 ms to 40 ms). Since then, a strong practice-related reduction in dual-tasks costs has been consistently observed in a wide range of dual-task studies (e.g., Hazeltine, Teague, & Ivry, 2002; Hirst, Spelke, Reaves, Caharack, & Neisser, 1980; Liepelt, Strobach, Frensch, & Schubert, 2011; Ruthruff, Johnston, & Van Selst, 2001; Ruthruff, Van Selst, Johnston, & Remington, 2006; Schumacher et al., 2001) and thus provide broad support that dual-task interference can be attenuated with training. However, the exact underlying mechanisms that drive such training-related performance benefits are currently not fully understood.

Two main accounts have been proposed that center around the debate whether training bypasses or reduces the central bottleneck. The stage shortening account posits that dual-task training may accelerate existing information processing computations of Task 1 (Pashler & Johnston, 1989; Ruthruff, Van Selst, Johnston, & Remington, 2006; Van Selst et al., 1999). Evidence for a temporal reduction of information processing at the central bottleneck comes from studies that showed the PRP effect to remain attenuated when a highly trained first task is combined with a novel second task, but not when the first

task is replaced with a novel task and combined with a highly trained second task (Ruthruff, Johnston, & Van Selst, 2001).

According to the task automatisation account, the repeated exposure to consistent stimulus-response mappings in each task results in the formation of memory traces that enable the development of direct associations between stimuli and responses (Logan, 1988; Palmeri, 1999). Consequently, the automatisation of either task is thought to eliminate the conflict for limited central resources and hence, completely bypasses the bottleneck (i.e., allow for parallel processing) following either single task or dual task practice. Key evidence for an automatisation of both tasks after practice was established in a study by Schumacher et al. (2001) that trained participants on blocks of trials that required responding to either single-task trials or simultaneously presented dual-task trials (mixed trial type condition), and blocks that only required the completion of the single-task. Capturing dual-task efficiency by comparing the extent to which dual-task RTs were not statistically different to single-task RTs from both mixed and single-task blocks, the authors showed that a complete elimination of the dual-task cost was achieved after only five training sessions. However, while the results were prosed to indicate perfect time-sharing, the involvement of a task switching requirement between single- and dual-task trials in the mixed trial type condition may have resulted in proactive slowing due to uncertainty with respect to the task requirements of the next trial. Thus, the absence of a statistically significant difference may have occurred due to slowed learning of the single task under mixed trial conditions, rather than performing two tasks simultaneously more quickly. Indeed, when Tombu and Jolicoeur (2004) controlled for these confounding conditions, a statistically significant difference was observed between dual-task and single-task RTs.

In sum, the above-mentioned theoretical accounts and empirical studies provide a broad understanding of the cognitive architecture underpinning response selection performance and suggest a response selection bottleneck that can at least partially process incoming information in parallel.

Neural substrates of response selection and training

Within the response selection literature, functional magnetic resonance imaging has been widely empolyed to investigate the underlying neuronal architecture that maps onto response selection limitations. In order to locate brain regions that are involved in the response selection process, researchers commonly manipulate response selection demands (e.g., high versus low response selection load or dual versus single response selection trials) to identify how these manipulations influence the BOLD signal. Data from

these studies indicate that response selection activates an interconnected network of fronto-parietal and subcortical brain regions, such as the lateral prefrontal cortex (LPFC), anterior cingulate cortex, superior medial frontal cortex (SMFC), parietal cortex, and subcortical regions (Dreher & Grafman, 2003; Garner & Dux, 2015; Schubert & Szameitat, 2003; Szameitat, Schubert, Muller, & Von Cramon, 2002; Tombu et al., 2011) – regions resembling the multiple-demand network (Duncan, 2010). In a prominant study, Marois et al. (2006) manipulated response selection demands by varying the number of stimulus response mappings under both dual-task and single-task conditions in order to identify brain regions that positively correlate with response selection limitations. The authors observed increased peak BOLD amplitude in dorsal pre-motor cortex and the LPFC, when central response selection demands were high. Importantly, a perceptual difficulty manipulation that increased RT2 latency without having an effect on response selection demands did not influence hemodynamic activity, indicating that activation within these regions of the brain is reflective of capacity-limited response selection processing.

In addition, the frontoparietal network, and especially the left LPFC has also been implicated as a neural substrate for the response selection bottleneck when using a time-resolved fMRI technique – a technique that is able to detect spatio-temporal patterns of BOLD activity across brain regions (Formisano & Goebel, 2003). Dux et al. (2006) engaged participants in single- and dual-tasks that induced sufficiently long responding delays to bring the dual-task limitation within the temporal resolution of fMRI. In line with the response selection bottleneck framework which reasons that regions underpinning a neural substrate of the response selection bottleneck should demonstrate longer task-processing under dual-task conditions compared to single-task conditions, the authors showed an increased duration of the hemodynamic response function (HRF) of the BOLD signal for dual-task situations relative to single-task situations in the left LPFC and, albeit to a lesser degree, the SMFC. Similarly, using a time-resolved fMRI combined with a a time-sensitive analytical approach, Sigman and Dehaene (2008) found delayed activity in the frontoparietal network that correlated with increased response selection requirements in a PRP paradigm.

Frontoparietal regions and the left posterior LPFC have been also implicated in training-related reductions of dual-task interference (Dux et al., 2009; Erickson et al., 2007; Schumacher & D'Esposito, 2002), with activations of the left posterior LPFC (Dux et al., 2009) and dorsomedial frontal and parietal cortex decreasing after dual-task training (Garner & Dux, 2015). Currently, it is not fully understood what drives such training-related reductions of dual-task costs. However, a recent neuroimaging study by Garner and Dux

(2016) showed that a decrease in multitasking cost after training was associated with increased differentiation of voxelwise activity patterns (a statistical analysis that assesses, in a multivariate manner, the distribution of category-specific fMRI activity patterns) for the two tasks in the frontoparietal-subcortical network, indicating that training led to increased neural specialization of task representations.

While the above mentioned studies suggest a key role for the left pLPFC and to a lesser degree the SMFC in response selection, fMRI designs (where the BOLD signal is the dependent variable) provide only correlational evidence. On the other hand, the use of a non-invasive neuromodulation technique such as transcranial direct current stimulation (tDCS) can be employed to establish a causal relationship between specific brain regions and behaviour. Unlike other stimulation techniques such as transcranial magnetic stimulation (TMS), which uses targeted magnetic fields to activate or suppress activity in cortical regions, tDCS uses direct electrical currents that produce polarity-specific effects via anodal (exitatory) and cathodal (inhibitory) stimulation by modulating neuronal excitability in a region without eliciting action potentials (Filmer, Dux, & Mattingley, 2014).

According to animal studies (Bindman, Lippold, & Redfearn, 1964; Purpura & McMurtry, 1965), anodal stimulation applied directly to the cortex leads to a depolarisation of cells, causing the resting membrane to become more positive and thus making it more likely for an action potential to occur. In contrast, cathodal stimulation hyperpolerises cells, making it less likely for an action potential to occur. Further evidence for the modulatory effects of tDCS comes from studies that applied tDCS to the primary motor cortex in humans. As reflected in TMS evoked potentials (Antal, Kincses, Nitsche, & Paulus, 2003) and motor evoked potentials (Antal et al., 2003; Nitsche et al., 2007; Nitsche & Paulus, 2000, 2001; Pellicciari et al., 2013), cathodal stimulation caused a decrease in neuronal excitability, whereas anodal stimulation led to increased neuronal excitability. Thus, by altering neural activity, tDCS has the potential to make an important contribution to our understanding of the neural basis of action control.

Despite its obvious advantages, it must also be noted that tDCS has some important limitations. For example, models of tDCS current flow (Bai, Dokos, Ho, & Loo, 2014; Bikson, Rahman, & Datta, 2012; Faria, Hallett, & Miranda, 2011; Russell et al., 2013; Wagner et al., 2014) suggest that the effects of tDCS are relatively broad in the brain. While tDCS-induced neural changes occur closest to the regions underlying the electrodes (Wagner et al., 2014), research indicates that the neural modulation may result in recruitment of broader networks of functionally connected regions (Antal, Polania, Schmidt-Samoa, Dechent, & Paulus, 2011; Polania, Paulus, & Nitsche, 2012; Saiote, Turi,

Paulus, & Antal, 2013; Turi, Paulus, & Antal, 2012). Moreover, given that a constant current is passed from one electrode to the other, with one electrode placed over the target area (target electrode) and one positioned over another cranial or extracranial region (return electrode), it is also possible that any observed effects are due to stimulation at the return electrode. Nonetheless, one can alleviate doubts about the influence of the return electrode by conducting control experiments that use a different return electrode location.

To date, tDCS has been successfully applied to investigate the causal role of the pLPFC, a region that has previously been implicated in response selection and training operations (Dux et al., 2006; Tombu et al., 2011). In two studies, applying tDCS over the left pLPFC influenced single-task (Filmer, Mattingley, Marois, & Dux, 2013) and dual-task response selection and training processes (Filmer, Mattingley, & Dux, 2013), whereas tDCS over the right pLPFC did not affect performance, providing causal evidence for the involvement of the left pLPFC in response selection and training processes. Considered alongside a substantial body of neuroimaging research (Dux et al., 2006; Hesselmann, Hebart, & Malach, 2011; Jiang & Kanwisher, 2003; Marois & Ivanoff, 2005; Marois, Larson, Chun, & Shima, 2006; Miller & Cohen, 2001; Schubert & Szameitat, 2003; Sigman & Dehaene, 2008; Szameitat et al., 2002), these observations suggest that response selection and response selection training is mediated by a left-hemisphere network in which the LPFC is a cruicial node.

Inhibiting Responses

Another key component of action control is the ability to supress inappropriate or automatic response tendencies (Aron & Poldrack, 2006; Logan & Cowan, 1984; Verbruggen, Liefooghe, & Vandierendonck, 2004). Investigations of response inhibition have employed a variety of tasks and it is generally assumed that inhibitory control can be parsed into at least two different mechanisms: task-irrelevant and task-relevant inhibition. The Eriksen Flanker task (Eriksen & Schultz, 1979) and Stroop task (Stroop, 1935) are often employed to probe the successful inhibition of distractor stimuli where task-irrelevant information needs to be ignored. For example, in the Stroop task, participants need to respond to the ink colour of colour words (e.g., “Red”; “Green”) and ignore the more automatic written word responses. A typical finding is that naming the ink colour of a word is slowed when the ink colour is incongruent to the colour word (e.g., the word “Red” written in blue). In contrast, in the Go-Nogo paradigm (Donders, 1969; Robertson, Manly,

Andrade, Baddeley, & Yiend, 1997) participants are required to inhibit task-relevant, prepotent response tendencies on a subset of trials.

Another widely employed paradigm used to understand how people inhibit their responses in the face of changing task goals is the stop-signal paradigm (SST; Logan & Cowan, 1984). In this task-relevant form of inhibition, participants perform a simple choice reaction task (i.e., the primary go task) which requires a speeded response. On a small subset of trials (e.g., 25%) the primary go stimulus is followed by an auditory (Lappin & Eriksen, 1966; Verbruggen, Aron, Stevens, & Chambers, 2010), visual (Verbruggen et al., 2010), or tactile (Akerfelt, Colonius, & Diederich, 2006) stop signal (i.e., stop-signal trials; Verbruggen & Logan, 2008) that instructs participants to inhibit their previously planned response. A ubiquitous finding is that the probability of successfully witholding a response decreases markedly if the time between the go stimulus and the onset of the stop-signal (stop signal delay, SSD) is delayed and increases when the SSD is short.

Modeling response inhibition

To account for these observations, Logan and Cowan (1984) proposed that performance in the stop-signal task can be modeled as an independent ”race” that starts with the onset of the primary go stimulus, which races in parallel against the stop process (triggered by the onset of the stop-signal). The behavioural outcome is determined by the process that finishes the race first - response inhibition succeeds (i.e., no response occurs) if the stop process finishes before the go process, whereas response inhibition fails (i.e., a response is initiated) if the go process finishes the race before the stop process. The independent race model (Logan & Cowan, 1984) makes two key assumptions of independence between the stop process and the go process: stochastic independence and context independence. Stochastic independence assumes that the go process and stop process have independent finishing times, while context independence assumes that the finishing time for the go process is not influenced by the presentation of a stop-signal. The assumption of context independence is supported by the findings that the mean RTs on failed stop-signal trials are faster than the mean no-signal RTs (Band, Ridderinkhof, & van der Molen, 2003; Logan & Cowan, 1984). Based on these assumptions, the stop-signal reaction time (SSRT; an estimate of the latency of the stop process) can therefore be estimated from the observed no-signal RT distribution and the observed probability of responding on a given SSD. Hence, a common method to compute the SSRT is to subtract the mean SSD from the mean no-signal RT (for a review of SSRT estimation methods see also Band et al., 2003).

SSRT estimates have been employed to investigate inhibitory control across a wide variety of literatures, including developmental psychology (Huizinga, Dolan, & van der Molen, 2006; Williams, Ponesse, Schachar, Logan, & Tannock, 1999), neuropsychology (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Dimitrov et al., 2003), psychopathology (Chambers, Garavan, & Bellgrove, 2009; Schachar & Logan, 1990), and individual differences (Friedman & Miyake, 2004; Miyake et al., 2000). The independent race model applies to ongoing behaviours such as typing (Logan, 1982), speech (Slevc & Ferreira, 2006; Xue, Aron, & Poldrack, 2008) movement tracking (Morein-Zamir, Nagelkerke, Chua, Franks, & Kingstone, 2004) and discrete tasks such as alternative choice RT tasks (Logan, Cowan, & Davis, 1984).

However, while the assumptions of a race between the go and stop process seems plausible and the SSRT has face validity in psychology and neuroscience, the independent race model fails to specify the exact mechanisms that cause stopping and is unable to explain the underlying physiology. Moreover, the model's assumption that the go process and the stop process are stochastically independent appears unlikely as the stop process must at some point interact with the ongoing go process. Based on a study which found the control of eye movement inititation to be generated by the interaction of fixation- and movement-related neurons, Boucher, Palmeri, Logan, and Schall (2007) proposed a modification to the independent race model. In their interactive horse race model, the authors still assume a race between the go and stop process, but challenge the assumption of complete stochastic independence. Instead, Boucher et al. (2007) propose a two-stage stopping process. The first (afferent) stage encodes the occurrence of the stop signal and analyses its significance, whereas the second (interactive) stage inhibits all go responses by rising activation in neurons that control the stopping process. The rising activation of inhibitory neurons consequently prevents the activation of movement-related neurons that control the go process from reaching threshold. Based on this model, inhibition is successful if the rise in go process activation is suppressed before an irrevocable ballistic process is initiated.

The interactive horse race model was tested by fitting the model to data obtained from single cell recordings from two monkeys. The authors were able to demonstrate that the interactive stage at which activation in the go process neurons are inhibited and activation in the stopping process neurons begin to rise, was very strong and brief. The findings approximate the independent race model (Logan & Cowan, 1984) by demonstrating that go and stop processes are independent for the majority of time (i.e., during the afferent phase) and interact briefly in the interactive stage where the go

response is stopped by preventing the process to reach threshold (but see Salinas & Stanford, 2013).

Neural substrates of response inhibition

Theoretical models and extensive evidence from lesion, stimulation and neuroimaging studies suggest that the conceptual independent race between the go and stop process (Logan & Cowan, 1984) resembles a literal race between two main pathways, linking frontal cortex with the basal ganglia output nuclei that provide tonic inhibition of actions (Aron & Poldrack, 2006; Schmidt, Leventhal, Mallet, Chen, & Berke, 2013). Specifically, the cortico-striatal direct pathway is thought to be involved in the initiation of a response and includes involvement of the LPFC, SMFC, anterior cingulate cortex, the striatum, globus pallidus, thalamus and M1. Activation of the "respond" cells in the striatum inhibit the internal segment of the globus pallidus (GPi), which in turn reduces inhibition of the thalamus, leading to the execution of a motor response. However, this motor execution can be stopped via activation of the indirect or hyperdirect pathways. The indirect pathway links the right inferior frontal cortex (IFC), pre-SMA, thalamus, striatum and the globus pallidus pars interna (Aron & Poldrack, 2006; Schmidt et al., 2013). Activation of "stop" striatal cells activates the external part of the globus pallidus (GPe), leading to a reduction of tonic inhibition between the GPi and GPe, resulting in increased GPi activity, which consequently suppresses activity in the thalamus. Research indicates that inhibition via the indirect pathway may be relatively slow and may be employed for proactive slowing and stopping of a particular response (Aron & Verbruggen, 2008; Smittenaar, Guitart-Masip, Lutti, & Dolan, 2013). In contrast, reactive stopping (as required in the stop-signal task) is thought to be implemented via a hyperdirect stopping network, in which the stopping process is thought to recruit the rIFG and pre-SMA to trigger the STN for a broad suppressive effect on basal ganglia output (Aron, Herz, Brown, Forstmann, & Zaghloul, 2016).

Indeed, neuroimaging research shows that the right inferior frontal gyrus (rIFG) is consistently activated when participants successfully inhibit an already initiated response, with the magnitude of activation correlating negatively with SSRT (Aron, Behrens, Smith, Frank, & Poldrack, 2007; Aron & Poldrack, 2006; Rubia et al., 2000). Human lesion and temporal lesion studies using TMS provide converging evidence for the critical role of the rIFG in response inhibition, with response inhibition impaired in patients with lesions to the rIFG (Aron et al., 2003; Aron, Monsell, Sahakian, & Robbins, 2004; Obeso, Robles, Marron, & Redolar-Ripoll, 2013; Verbruggen et al., 2010; Zandbelt, Bloemendaal,

Hoogendam, Kahn, & Vink, 2013). Furthermore, using repetitive transcranial magnetic stimulation (rTMS) over rIFG but not left IFG has been shown to cause impairments in stopping but not going (Chambers et al., 2007), thus further supporting the rIFG's critical role in response inhibition.

Outside the PFC, TMS (Cai, George, Verbruggen, Chambers, & Aron, 2012; Chen, Muggleton, Tzeng, Hung, & Juan, 2009; Floden & Stuss, 2006; Obeso, Cho, et al., 2013; Obeso, Robles, et al., 2013) and tDCS (Hsu et al., 2011) over pre-SMA has also been shown to disrupt inhibitory performance, while neuroimaging studies have found successful inhibition to be associated with activity in the pre-SMA (Aron et al., 2007; Aron & Poldrack, 2006; Swann et al., 2012), STN (Alegre et al., 2013; Aron et al., 2007; Aron & Poldrack, 2006; Isoda & Hikosaka, 2008; Li, Yan, Sinha, & Lee, 2008), striatum (Watanabe & Munoz, 2011; Zandbelt & Vink, 2010), and globus pallidus pars interna (Aron et al., 2007; Aron & Poldrack, 2006).

Together, these findings indicate that the right IFG, pre-SMA, and basal ganglia are part of a right lateralized fronto-basal ganglia inhibition network, with the right IFG and pre-SMA thought to be key nodes in the induction of response inhibition.

Do Response Selection and Inhibition Processes Reflect One Common Action Control Mechanism?

The research discussed thus far indicates the involvement of common neural substrates for both response selection and response inhibition, with a frontoparietal-subcortical network commonly activated during tasks that require the selection and inhibition of responses (Duncan & Owen, 2000; Duncan, 2010). On the other hand, there is evidence that these two processes also recruit distinct regions of the brain, with increasing response selection demands commonly activating the left LPFC (Dux et al., 2006; Tombu et al., 2011), whereas the right IFC appears to be a critical node for the successful implementation of inhibitory control (Aron et al., 2003; Aron, Robbins, & Poldrack, 2014). Behavioural evidence for the indpendence of these two processe comes also from several studies that showed SSRT to be unaffected by the demands of the go task (Middlebrooks & Schall, 2014) or by the number of response mappings used (Logan, van Zandt, Verbruggen, & Wagenmakers, 2014; Rae, Hughes, Weaver, Anderson, & Rowe, 2014). A study by Yamaguchi, Logan, and Bissett (2012) examined SSRT in a PRP task, in which participants had to correctly inhibit the first (condition 1) or second (condition 2) response in a dual task setting while stopping one response in a single task setting (condition 3). In line with the independence assumption, SSRTs did not differ in all three

conditions, supporting the notion that inhibitory control does not share central capacity resources. Taken together, the findings thus far suggest that response selection and response inhibition operations may reflect different elements of action control, with both processes recruiting the function of an underlying frontoparietal network (Duncan & Owen, 2000).

However, although the above-mentioned studies have shed some useful light onto the neural and cognitive substrates of action control, the discrepant findings further highlight that it is currently still not known whether the performance in a wide range of response selection and inhibitory control tasks is subserved by one general action control mechanism, or whether the observed performance differences in these tasks reflect two distinct underlying processes. While empirical research on response selection and inhibition has been driven by very concrete paradigms, such as the PRP, dual response selection tasks (common response selection tasks) and the SST, Go-Nogo, Stroop, and Flanker tasks (common response inhibition tasks), it is difficult to infer a general fundamental underlying mechanism or construct that drives/impairs performance on these types of tasks. Thus, an outstanding question is how different classic action control paradigms are related to each other: Does a battery of response selection and response inhibition tasks share a common underlying action control mechanism or are these two processes dissociable?

One way to address this question is by employing an individual differences approach to explore the relationships between several action control paradigms. The rationale is if participants' performances on paradigms A and B are correlated, but these performances are not strongly correlated with performances on paradigm C, then it can be concluded that performance in paradigms A and B is at least partly driven by a common underlying mechanism, whereas performance in paradigm C is most likely underpinned by a different mechanism (Huang, Mo, & Li, 2012). Thus, using this individual differences approach allows one to test whether performances in a wide range of executive control paradigms are strongly related.

Confirmatory factor analysis (CFA) is a latent variable analysis of individual differences that statistically extracts what is common among a set of tasks selected to tap the same putative executive mechanism, and then uses the extracted purer latent variable factor to determine the interrelations between the different executive mechanisms. Thus, the latent variable approach minimizes the task impurity problem by excluding the systematic variance from non-cognitive control processes such as perceptual colour and sound processing (Miyake et al., 2000). A typical CFA analysis of individual differences

approach statistically extracts what is common among the tasks selected to tap the same putative executive mechanism and then uses that purer latent variable factor to determine the interrelations between the different executive mechanisms. CFA has been widely applied in social psychology but has been also successfully employed in the cognitive domain to explore the underlying mechanisms that subserve executive abilities in school-aged children (eg., Garcia-Barrera, Kamphaus, & Bandalos, 2011; Garcia-Barrera, Karr, & Kamphaus, 2013), young adults (e.g., Friedman & Miyake, 2004; Friedman et al., 2008; Miyake et al., 2000) and older adults (Hull, Martin, Beier, Lane, & Hamilton, 2008).

Indeed, using this approach, Miyake et al. (2000) successfully demonstrated that the performance on a battery of cognitive control tasks, tapped three related, yet distinct cognitive constructs: inhibition (suppressing goal-irrelevant responses), shifting (switching attention toward goal-relevant stimuli), and updating (updating contents of working memory). Thus, the correlational evidence by Miyake and colleagues (2000) suggests that there is diversity and unity in executive functions, with at least three distinct executive functions. In my first paper, I present an individual differences study that aimed to test the relationship between response selection and response inhibition. To do so, I presented participants with a battery of common action control tasks that varied in response selection and inhibition requirements and employed a latent variable approach similar to Miyake et al. (2000) to investigate the underlying mechanisms involved.

The Contextual Influence of the Superior Medial Frontal Cortex in Response Selection and Inhibition

Neuroscientific investigations so far suggest that the selection of responses and the stopping of inappropriate responses are partially supported by distinct brain regions, but intriguingly, neuroimaging, lesion and stimulation studies also demonstrate that these two operations share some common neural substrates. In particular, the pre-SMA is considered to be a key node in the executive control of action that requires the selection and inhibition of responses. In humans, the pre-SMA is part of the prefrontal-basal ganglia circuit and is located in the superior medial frontal cortex (SMFC), dorsal to the cingulate motor areas and rostral to the supplementary motor area (SMA), with extensive connections projecting to dorsolateral prefrontal cortex and basal ganglia (Nachev, Kennard, & Husain, 2008).

To date, converging evidence from fMRI (Dux et al., 2006; Tombu et al., 2011), electrophysiological recordings in monkeys (Hoshi & Tanji, 2004; Isoda & Hikosaka, 2007; Matsuzaka, Aizawa, & Tanji, 1992), tDCS and TMS studies have implicated the pre-SMA

in response selection processes when switching between tasks (Rushworth, Hadland, Paus, & Sipila, 2002), or when response tendencies need to be overridden with an incongruent response (Duque, Olivier, & Rushworth, 2013; Herz et al., 2014; Soutschek, Taylor, Muller, & Schubert, 2013; Spieser, van den Wildenberg, Hasbroucq, Ridderinkhof, & Burle, 2015). Similarly, fMRI, TMS, lesion studies (Aron & Poldrack, 2006; Cai et al., 2012; Chen et al., 2009; Floden & Stuss, 2006; Nachev, Wydell, O'Neill, Husain, & Kennard, 2007; Obeso, Cho, et al., 2013; Watanabe et al., 2015), and tDCS (Hsu et al., 2011) have demonstrated that the pre-SMA plays an important role in response inhibition. Moreover, the modulation of response tendencies under an inhibitory context (proactive control) has also been proposed as a function of this region (Boulinguez, Ballanger, Granjon, & Benraiss, 2009; Chikazoe et al., 2009; Jahfari, Stinear, Claffey, Verbruggen, & Aron, 2010; Obeso, Robles, et al., 2013; Reinhart & Woodman, 2014; Zandbelt & Vink, 2010).

While the above-mentioned studies implicate the SMFC separately in both response selection, response inhibition and proactive inhibitory control processes, in tasks using different stimuli and experimental protocols, we do not currently have causal evidence whether this region is involved in both operations. A key objective therefore is to distinguish the function of the pre-SMA within the neural circuitry of action control. Thus, the application of tDCS is especially useful because of its ability to interfer the neural processing during response selection and inhibition demands. In my second paper, I ran three tDCS studies that carefully varied in response selection and response inhibition requirements while holding stimulus-processing demands constant. Separating response inhibition and selection operations allowed me to further investigate the SMFC's role in proactive, context-dependent slowing and with it, the interplay between response selection and inhibition in goal-directed behaviour.

Does Dual-Task Training Transfer to Other Theoretically Related Action Control Tasks?

When it comes to multitasking ability, evidence thus far suggests that intensive training attenuates dual-task interference on the task itself (Garner, Tombu, & Dux, 2014; Hazeltine et al., 2002; Liepelt et al., 2011; Schumacher et al., 2001; Strobach, Frensch, Soutschek, & Schubert, 2012; Van Selst et al., 1999). But the extent to which training can transfer to benefit new measures is currently fiercely debated. If response selection training induces efficient time-sharing between tasks (Schumacher et al., 2001) or shortens the capacity-limited response selection stage (Dux et al., 2009), then training

benefits may generalize to other response selection tasks. Moreover, the neuronal overlap framework posits that the probability of transfer to new tasks is increased when the transfer measures are underpinned by tasks that draw on the same overlapping neural substrates (Kuwajima & Sawaguchi, 2010; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009; Thorell, Lindqvist, Bergman Nutley, Bohlin, & Klingberg, 2009). So far, only a small number of laboratory-based dual-task training studies have reported training-related enhancements to untrained tasks (Liepelt et al., 2011; Lussier, Gagnon, & Bherer, 2012), while the majority of studies show little to no transfer (Garner, Matthews, Remington, & Dux, 2015; Liepelt et al., 2011; Owen et al., 2010; 2006; Strobach, Liepelt, Pashler, Frensch, & Schubert, 2013).

Similarly, such training and transfer effects have also been assessed in response inhibition training tasks with the results here also ambiguous. Although several of these studies have failed to find a significant training-related improvement in inhibitory control ability after intensive training (Cohen & Poldrack, 2008; Enge et al., 2014), others have found decreases in SSRTs (Berkman, Kahn, & Merchant, 2014; Manuel, Bernasconi, & Spierer, 2013) or commission errors (i.e., correctly withholding a response on stop-signal trials) and Go RTs after training inhibitory control with go-nogo and stop-signal tasks (Benikos, Johnstone, & Roodenrys, 2013; Johnstone et al., 2012; Schapkin, Falkenstein, Marks, & Griefahn, 2007).

Functional neuroimaging studies have revealed that these training-induced benefits in inhibitory control are underpinned by BOLD changes within the inhibitory control brain network (Berkman et al., 2014; Chavan, Mouthon, Draganski, van der Zwaag, & Spierer, 2015; Manuel et al., 2013). For example, Berkman and colleagues (2014) observed that training-related improvements in inhibitory control (i.e., a reduction in SSRT from pre- versus post-training) correlated with increased activation in the right IFG after three weeks of training on the SST. Collectively, the mixed findings in this field of investigation indicate that while performance on inhibitory control tasks may improve with training, the reported improvements are usually small and evidence for training-related enhancements to untrained tasks remains elusive (Enge et al., 2014; Thorell et al., 2009).

In contrast, numerous studies have reported improved performance on a variety of cognitive and perceptual tasks that tap attention, task switching and visual processing after participants train for 10-50 hours on fast paced, visually demanding video action games (Green & Bavelier, 2003, 2007; Green, Sugarman, Medford, Klobusicky, & Daphne, 2012; Strobach, Frensch, & Schubert, 2012). These behavioural studies suggest that the possibility of transfer to other new tasks may occur when executive functions are

repeatedly taxed in a high interference, fast paced environment. Indeed, Anguera et al. (2013) trained a sample of older participants on a dual-task video game for twelve hours, in which participants had to keep a moving car in the center of the road, while simultaneously detecting and responding to a speeded shape discrimination task (multitasking condition) or train on the two component tasks in isolation (single-task condition). In line with the dual-task training literature, task-specific multitasking improvements were observed after multitasking training relative to single-task training. Critically, multitasking training resulted in performance benefits that extended to measures of sustained attention and working memory. These findings support the notion that benefits from tasks that require fast decision-making within a demanding environment may extend to untrained cognitive control abilities.

However, in order to draw strong conclusions about any observed training-related improvement, several standards need to be adhered to (e.g., Melby-Lervåg & Hulme, 2013; Mishra, Anguera, & Gazzaley, 2016; Noack, Lovden, & Schmiedek, 2014; Redick et al., 2013; Shipstead, Redick, & Engle, 2012). Key examples are that the performance changes in the treatment group should always be compared to an active control group, to ensure that observed changes cannot be attributed to potential treatment confounds such as a placebo effect. Therefore it is essential to minimize group differences in expectations of improvement and equal task engagement. Highly related to this concept is the factor of using adaptive training to ensure high motivation settings. Moreover, only outcome measures with a clear targeted theorectical construct should be employed, as this ensures that it is the cognitive target under study that continues to be trained. In addition, transfer tasks should be restricted to tasks that are related to the trained construct, as this allows assessment of whether or not the underlying mechanism has been improved by training or whether training benefits remain task specific. Last but not least, baseline differences should be carefully assessed as these imbalances can result in biased effect sizes. Collectively, adhering to these guidelines allows for more definite conclusions to be drawn when interpreting training-related performance benefits.

Given that relatively few dual-task training studies conducted to date have employed appropriate active controls (Liepelt et al., 2011; Strobach, Frensch, Soutschek, et al., 2012), nor taxed response selection processes in a fast paced and dynamic environment, it is currently not clear whether training-related performance benefits extend to other response selection measures that are theoretically related to the trained construct. In the third and final paper of this thesis, I report a dual-task training study that employed a continuous visuomotor tracking and perceptual discrimination task to assess whether or

not decision-making in a high-interference environment leads to task-specific multitasking benefits. To determine whether training-related benefits extend to other theoretically related transfer tasks, I administered a battery of closely related action control measures.

Summary

The selection of task-relevant responses and the inhibition of task-irrelevant, but often highly automatic behaviour is a vital requirement for the adaptive and goal- directed control of actions. Although these two processes have received a great deal of theoretical and empirical interest over the last decades, it is currently not clear whether these two cognitive operations tap a common action control resource or reflect two distinct processes, whether dual-task training benefits can transfer to other response selection and inhibition tasks that are theoretically related, or the extent to which these two processes interact and draw on overlapping neural substrates. In Study 1, I report a large-scale individual differences study and provide correlational evidence in support of the hypothesis that response selection and response inhibition reflect two distinct cognitive operations. This finding contrasts recent theoretical frameworks that propose a general action control mechanism (Mostofsky & Simmonds, 2008; Verbruggen et al., 2014).

Given that the SMFC has been implicated separately in both response selection and response inhibition processes, the tDCS study reported in Study 2 aimed to investigate the causal role of SMFC in response selection, response selection training, and inhibitory response selection control when occasional response inhibition was occasionally required. Contrary to previous neuroimaging findings that have implicated the SMFC in single and dual-task response selection and training, I found no evidence for the involvement of SMFC in single-task response selection and training processes. However, when adding an inhibitory context that required occasional stopping of a response, cathodal stimulation of the SMFC modulated response selection by increasing reaction times. The results are suggestive of a context-dependent role of the SMFC in response selection and further illustrate the interplay between response selection and inhibition processes.

As noted above, while dual-task training clearly improves task-specific multitasking ability, it is currently not known whether dual-task training benefits transfer to action control tasks that rely on common underlying neural substrates and are theoretically related. The final paper of this thesis (Study 3) investigated this issue by examining whether training-related benefits extend to other response selection and response inhibition tasks. I demonstrate that multitasking training resulted in task-specific benefits but I found no

evidence of positive transfer to untrained tasks that are theoretically related to the trained construct.

Together, this work extends our knowledge about the cognitive and neural substrates of two key executive functions that are critical for the implementation of behavioural change - response selection and response inhibition, and further characterizes the diversity and unity that underlies the executive control of actions.

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Study 1: On the Relationship Between Response Selection and Response Inhibition: An Individual Differences Approach

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Abstract

The ability to select appropriate responses and suppress unwanted actions are key executive functions that enable flexible and goal-directed behaviour. However, to date it is unclear whether these two cognitive operations tap a common action control resource or reflect two distinct processes. In the present study, we used an individual differences approach to examine the underlying relationships across seven paradigms that varied in response selection and response inhibition requirements: Stop-Signal, Go-Nogo, Stroop, Flanker, Single Response Selection Task, Psychological Refractory Period, and Attentional Blink. A confirmatory factor analysis suggested that response inhibition and response selection were separable with Stop-Signal and Go-Nogo task performance related to response inhibition, and the Psychological Refractory Period, Stroop, Single Response Selection, and AB tasks related to response selection. The findings provide evidence in support of the hypothesis that response selection and response inhibition reflect two distinct cognitive operations.

The abilities to select responses to specific stimuli (i.e., response selection) and to override a prepotent tendency to respond to other stimuli (i.e., response inhibition) have been attributed to core executive action control processes (Norman, 1986). These functions are critical in everyday life, as they allow people to flexibly adjust their behaviour according to their goals. Indeed, deficits in these cognitive operations contribute to several psychopathological conditions, including obsessive-compulsive disorder (Penades et al., 2007), attention-deficit hyperactivity disorder (Nigg, 2001), addiction and eating disorders (Crews & Boettiger, 2009; Houben, 2011; Noel, Brevers, & Bechara, 2013). However, despite the similarities between response selection and inhibition (i.e. both require the selection or non-selection of a response), the extent to which these processes relate and interact with one another is still unknown.

Response selection is a central decision-making process that maps incoming perceptual information to goal-appropriate motor output (Pashler, 1984; Welford, 1952). One theoretical framework that explicitly illustrates the various steps involved in the decision-making process are sequential sampling models. According to these models, simple decision-making involves the accumulation of information from the environment until a certain response criteria threshold (i.e., the amount of information needed to select a response) has been reached (Brown & Heathcote, 2008; Ratcliff & Smith, 2004; Smith & Ratcliff, 2004; Usher & McClelland, 2001). The option that reaches the response criteria threshold first is selected and then executed. While information at the perceptual and motor stages are thought to operate in parallel, it is the central response selection stage that is proposed to be capacity limited - only capable of acting on a single-task at any given time. This sensory-motor translation stage is therefore often studied using paradigms such as the psychological refractory period (PRP; Pashler 1984; Welford, 1952), dual-task (Dux, Ivanoff, Asplund, & Marois, 2006; Dux et al., 2009; Schumacher et al., 2001; Sigman & Dehaene, 2008), and high response load single-task tests, as these measures place strong demands on the response selection system. While conditions differ across these paradigms, they all require participants to encode sensory information and make a decision, and in paradigms with two tasks, participants must make simple response selections for items that occur simultaneously or in close succession.

In contrast, response inhibition is thought to be a heterogeneous construct that can be parsed into at least two different forms: task-relevant and task-irrelevant inhibition (Harnishfeger, 1995; Nigg, 2000). Successful inhibition of distractor stimuli is often measured in tasks where task-irrelevant information needs to be ignored, such as the Eriksen Flanker task (Eriksen & Schultz, 1979) and Stroop task (Stroop, 1935). Task-

relevant response inhibition, however, is often measured in tasks such as the Stop-Signal task (Lappin, 1966; Verbruggen & Logan, 2008) and Go-Nogo paradigms (Donders, 1969), that require the inhibition of task-relevant, prepotent response tendencies on a subset of trials. According to the popular race model account (Logan & Cowan, 1984), successful inhibition in the Stop-Signal task relies on the outcome of a race between the independent go and stop processes. Inhibitory control succeeds when the stop process finishes the race before the go process, whereas response inhibition fails if the go process reaches the response threshold first.

The attentional blink (AB) is another dual-task paradigm worth noting as it is thought to tap both response selection and inhibition operations. The AB is a perceptual limitation that is reflected in the inability to consciously perceive and report the second of two targets presented in close succession (Jolicoeur & Dell'Acqua, 1998; Raymond, Shapiro, & Arnell, 1992). While impaired attention to the second target is thought to partly occur because of attention-demanding memory encoding processes (Chun & Potter, 1995; Bowman & Wyble, 2007), research also indicates that the AB occurs due to capacity limitations at the central response selection stage of information processing (Jolicœur, 1998, 1999; Jolicœur & Dell'Acqua, 1998). Specifically, Jolicoeur (1998) investigated the extent to which drawing on the central response selection stage influenced the magnitude of the AB. In his experiments, he included a speeded Target 1 task that required an immediate rather than a delayed response on some of the trials, whereas responding to Target 2 was always offline. Performing response selection to Target 1 online created a processing overlap between Target 1 response selection and Target 2 working memory encoding at short lags. Results revealed a larger AB magnitude in speeded relative to un-speeded Target 1 trials, thus supporting the notion that both response selection and working memory encoding draw on the central capacity-limited processing stage. In addition, studies using time-resolved fMRI (Tombu et al., 2011) and MEG (Marti, Sigman, & Dehaene, 2012) have shown that the PRP and AB tap similar neural substrates. Although most explanations of the AB invoke a consolidation/response-selection bottleneck or cognitive-control mechanism(s) (Dux & Marois, 2009), research suggests that a suppressive mechanism that inhibits the deployment of attentional resources to irrelevant distractor stimuli may also play an important role in target selection (Dux & Harris, 2007; Dux & Marois, 2008; Raymond et al., 1992; Wyble, Bowman, & Nieuwenstein, 2009).

Traditionally, response selection and response inhibition processes have been investigated separately but there is increasing evidence suggesting that these two operations may draw on a common resource (Mostofsky & Simmonds, 2008; van Gaal,

Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; Verbruggen, McLaren, & Chambers, 2014). For example, neuroimaging and transcranial magnetic stimulation (TMS) studies have found that mid-dorsolateral, ventrolateral prefrontal areas (Bunge, 2004; Duncan & Owen, 2000) and pre-supplementary motor area (pre-SMA; Buch, Mars, Boorman, & Rushworth, 2010) are activated by tasks that require the selection and inhibition of responses. For instance, Verbruggen, Aron, Stevens, and Chambers (2010) demonstrated that transcranial magnetic stimulation (TMS) of the right IFG impaired performance on both a stop-signal task and a dual-task task, suggesting that this region supports both response selection and inhibition processes. Taken together, these findings indicate that response inhibition and response selection protocols might tap at least in part, a common mechanism of action control.

While response selection and response inhibition processes may partially overlap at the neural level, there is also evidence, which suggests that response selection and response inhibition tasks recruit distinct brain regions. Indeed, neuroimaging studies have observed greater activity in the left hemisphere posterior lateral prefrontal cortex (pLPFC) during dual-task compared to single-task trials, suggesting its role in response selection (Dux et al., 2006; Dux et al., 2009; Jiang & Kanwisher, 2003; Miller & Cohen, 2001). Similarly, Filmer and colleagues demonstrated that transcranial direct current stimulation of the left but not right pLPFC disrupts response selection for single- and dual-tasks and its associated training effects for both single and dual tasks (Filmer, Mattingley, & Dux, 2013a; Filmer, Mattingley, Marois, & Dux, 2013b). In contrast, right IFG appears to be crucial for the successful inhibition of an inappropriate motor response (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003), as it shows greater activity during successfully inhibited trials compared to failed inhibition trials (Aron, Robbins, & Poldrack, 2014) . Moreover, TMS of the right IFG has been found to temporarily increase stop-signal RTs (SSRTs) – an index of poorer inhibitory control – but TMS of other cortical regions, including the left IFG, right middle frontal gyrus and right angular gyrus had no impact on SSRTs (Chambers et al., 2007; Chambers et al., 2006). These studies suggest process-specific functional differences and converge with the idea that response selection and response inhibition produce distinct neural signatures; namely the left pLPFC is involved in response selection whereas the right IFG is involved in response inhibition. Although no study has directly assessed whether these two processes can be fully dissociated in the brain, these neural findings do at least suggest that these two processes could reflect distinct forms of action control.

The independence of response selection and response inhibition processes is further suggested by behavioural studies. While dual-task contexts typically result in performance decrements when central response selection processes overlap in time, performance in various inhibitory control tasks indicates that the 'go' process can occur independently from the 'stop' process (activated by the appearance of the stop signal; Logan & Burkell, 1986; Verbruggen & Logan, 2009; but see Verbruggen & Logan, 2015). For example, a recent study by Yamaguchi, Logan, and Bissett (2012) directly examined stop-signal performance in a PRP task, in which participants were required to correctly inhibit one response while carrying out the other response in a dual-task setting. In line with the independence assumption, response inhibition performance was not influenced by dual-task interference, supporting the notion that response inhibition is distinct from response selection demands. In agreement with the aforementioned neural work, these findings further suggest that response selection and response inhibition operations reflect different elements of action control.

While the above-mentioned studies provide valuable insight into the cognitive and neural substrates of action control, they also highlight that it is still unclear whether there is a general action control mechanism, which underpins performance in a wide range of response selection and inhibitory control paradigms, or whether the differences we observe in these tasks reflect distinct underlying processes. The previous work has been unable to resolve this conflict as these studies only compared single examples of response selection and inhibition tasks to test for a possible overlap or dissociation between these two processes. A drawback of this approach is that it is impossible to infer the specific nature of the process (which is independent of the paradigm used) that leads to any observed overlap or dissociation. This problem can be overcome by employing a latent variable approach to better understand the relations among commonly used measures of response selection and response inhibition (Miyake et al., 2000). Confirmatory factor analysis (CFA) is a latent variable analysis that statistically extracts the common variance among tasks that are expected to tap the same putative function. By only analyzing what is common among the tasks and excluding the systematic variance attributable to non-cognitive control processes (e.g., sound and colour processing), the 'purer' latent variable (Miyake et al., 2000) can be extracted to examine how different cognitive control functions relate to one another. Importantly, CFA allows the evaluation of different models on an *a priori* basis, utilizing knowledge from previous research about hypothesized task demands (i.e., tasks that are thought to share the same underlying

construct should load on the same latent factor and are specified before the different models are run).

The application of CFA to explore the relations among executive functions was successfully demonstrated in a series of studies by Miyake and colleagues (Friedman & Miyake, 2004; Miyake et al., 2000). Specifically, Miyake et al. (2000) used a battery of tasks thought to tap three core cognitive control functions - shifting, updating contents of working memory and inhibition of automatic responses. While CFA results revealed that the three cognitive operations shared some common overlap, a three-factor model provided the best fit to the obtained data, suggesting that all three functions represent distinct cognitive constructs that are qualified by shared variance between the executive control factors. The diversity of cognitive control is further supported by Friedman and Miyake's (2004) study that investigated the extent to which various measures of inhibitory control were related to one another and how these functions contribute to other cognitive control demanding tasks. The authors focused primarily on three potentially distinct inhibitory control functions: Prepotent response inhibition (the ability to override an automatic response); resistance to distractor interference (the ability to suppress irrelevant information); and resistance to proactive interference (the ability to suppress memory interference from previously relevant task information). CFA revealed that prepotent response inhibition and resistance to distractor interference were closely related to each other while resistance to proactive interference was unrelated to response and distractor inhibition.

Here, we employed a latent variable approach similar to Miyake et al. (2000) and Friedman and Miyake (2004), to understand the relations among response selection and response inhibition. This approach not only provides insights into how performance varies between individuals but it can also identify the extent to which indicators of action control relate to each other. If response selection and response inhibition processes reflect two distinct aspects of action control, then we would expect response selection tasks to load on one latent factor, and response inhibition tasks to load on a second factor. If, on the other hand, these two processes reflect "two sides of the same coin" (Mostofsky & Simmonds, 2008), then we would expect each paradigm to load highly on a single action control factor.

Method

Participants

Eighty-seven participants (mean age = 20 years, range = 17-39 years, 69 females) from The University of Queensland participated in this study for course credit. All participants had normal or corrected-to-normal vision. The University of Queensland Human Research Ethics Committee approved the study and all participants gave informed, written consent. The target sample and participant exclusion criteria were determined before data collection and was based on a 5:1 ratio of sample size to number of free parameters (Bentler & Chou, 1987). Participants were removed from final analysis if they did not reach the behavioural cut-off for one or more tasks. In total, data from 21 participants were excluded from final analysis due to failure to attend a testing session (4 participants) or because of poor performance (more than three standard deviations above the **overall mean** RT or accuracy mean) in one or several of the seven tasks (17 participants).

Apparatus

The experiment was run on an Apple Mac Mini and programmed in MATLAB (The MathWorks, Natick, MA) with the Psychophysics toolbox extension (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 21” CRT monitor (100 Hz refresh rate) and participants viewed the monitor from a distance of approximately 57 cm for all the tasks used in the two sessions.

Procedure

Participants took part in two 2-hour sessions that were administered seven days apart from each other. During each session, participants completed the following tasks, with task order randomized across participants and sessions: Stop-Signal Task (SST), Go-Nogo task, Stroop task, Flanker task, Single vs. Dual Response Selection paradigm, PRP, and AB. In all seven measures, each trial began with a black fixation cross that was presented in the center of a grey screen (RGB 128 128 128) for a variable interval (200-600 ms). At the end of each block, the mean RT and accuracy were displayed (with the exception of the AB task, as participants are usually very poor at identifying the second target). Following the tasks in the first session, participants provided demographic information about their age, gender, handedness, years of education, history of any neuropsychiatric illness and current neuropsychiatric medication.

Tasks

Response inhibition tasks

***Stop-signal task* (Verbruggen & Logan, 2008).** Participants completed go-signal and stop-signal trials. On go-signal trials, participants were required to discriminate between two different 2D abstract shapes (grey with a black outline, see Figure 1) by pressing the relevant response key ("F" or "J") as quickly and as accurately as possible. On stop trials (25% of trials), the primary go stimulus was followed by an auditory stop-signal (750 Hz sine wave tone, 200 ms duration), which instructed participants to inhibit their response. The stop-signal delay (SSD, the time between the onset of the go stimulus and stop-signal) was initially set at 250 ms and continuously adjusted with an adaptive staircase procedure to obtain a stopping probability of 50%. If a participant failed to inhibit their response in a stop-signal trial, SSD decreased by 50 ms, but if they succeeded, SSD increased by 50 ms. The fixation cross was replaced by the go stimulus, which remained on screen for 200 ms. Participants completed one practice block of 24 trials and four test blocks of 36 trials. The dependent variable was the stop-signal RT (SSRT), calculated by subtracting each participant's mean SSD from the mean Go RT (Verbruggen & Logan, 2009) . Better inhibitory performance was indicated by lower SSRTs.

***Go-Nogo task* (Donders, 1969).** On each trial of this task, participants were instructed to make a speeded response to the go stimulus (white abstract 3D shape, see Figure 1 for an example) by pressing the "G" key, but to withhold from responding if the no-go stimulus appeared (white abstract 3D shape, 25% of trials). Go and no-go stimuli were counterbalanced across participants. On each trial, a fixation square appeared (200 ms), followed by one of the two target stimuli and an 1800 ms response window. Participants completed a block of 24 practice trials and four test blocks of 36 trials. The dependent variable of interest was the number of commission errors on no-go trials (i.e., failure to inhibit a response). Better inhibitory control was indicated by fewer commission errors.

***Stroop task* (Stroop, 1935).** In this task, participants had to report the ink colour (red: RGB 237 32 36, green: RGB 10 130 65, yellow: RGB 250 250 0, and blue: RGB 44 71 151) of colour ("red", "green", "yellow" and "blue") and non-colour ("cup", "fork", "spoon", "saucer") words as quickly and as accurately as possible via key press. At the beginning of each trial, the fixation cross was replaced by a word target for 500 ms. The word target was equally likely to either be congruent (the printed colour word matched the ink colour, e.g., "blue" printed in blue), incongruent (e.g., "blue" printed in red ink colour), or neutral (i.e., a non-colour word printed in any of the four colours, e.g., "cup" printed in green ink

colour). Each of the four possible ink colours were mapped onto a corresponding response key and participants completed a practice block of 24 trials to familiarize themselves with these stimulus-response mappings. The experimental phase consisted of four blocks of 36 trials and the order of trial types was randomized. The dependent variable was the "Stroop congruency effect," which was calculated as the difference in RTs between congruent and incongruent trials. A smaller congruency effect reflects better performance.

Flanker task **(Eriksen & Schultz, 1979)**. Participants had to respond to the direction of a central arrow target (> or <) as quickly and as accurately as possible by pressing the "<" key for leftward-pointing arrows and the ">" key for rightward-pointing arrows. On congruent trials the target was flanked by two arrows on each side that pointed in the same direction as the target arrow (e.g., >>>>>). On incongruent trials, the target was flanked by two arrows on each side that pointed in the opposite direction as the target arrow (e.g., >><>>). On neutral trials, the flankers were two horizontal lines that appeared on each side (e.g., --<-). The fixation cross was replaced by the concurrent onset of the target and flankers, which remained on the screen for 200 ms. Participants completed 24 practice trials followed by four blocks of 36 test trials. There were an equal number of trials per condition and the order of trial types was randomized. The dependent variable was the "flanker congruency effect," which was calculated as the difference in RTs between the congruent and incongruent trials. Lower RT difference scores represented better performance.

Response Selection tasks

Single vs. dual response selection task **(Dux et al., 2006; Dux et al., 2009)*.*** Participants first practiced on three blocks of the two different, two-alternative force choice (AFC) RT tasks. Block 1 was a visual task in which participants discriminated between two different coloured circles (red: RGB 237 32 36, and blue: RGB 44 71 151, 12 trials), and block 2 was an auditory discrimination task (Filmer et al., 2013b). Each stimulus was mapped to specific response key and hand (A or S for left-hand responses and K or L for right hand responses), with the mapping of hand to task counterbalanced across participants. After learning the specific stimulus-response mappings of each task, participants completed a third practice block where one visual and one auditory stimulus were presented simultaneously on each trial. The experimental phase included four blocks of 36 trials, with each trial type randomly intermixed within blocks. In each test trial, the central fixation cross was followed by a visual stimulus only, an auditory stimulus only, or the simultaneous presentation of both for 200 ms. Participants were instructed to respond

as quickly and as accurately as possible via key press to the stimulus or stimuli. Of key interest was the reaction time to the single-tasks trials (averaged across the two tasks) as a pure measure of response selection and the difference in reaction time when tasks were performed with and without a concurrent task to measure dual-task executive function. Lower RTs/difference scores indicated better performance.

Psychological refractory period **(Pashler, 1984).** Participants first trained on three blocks of 20 trials of the two different four-AFC tasks. Each task was assigned a response hand and a specific key for each stimulus (A, S, D, or F for left hand responses and J, K, L, or ";" for right hand responses), with the mapping of hand to task counterbalanced across participants. In block 1, participants trained on the visual task (Task 1), which required a manual key press response to one of four different symbols (%, &, @, or #). Block 2 was an auditory task (Task 2) that required participants to make a manual key press response to four different complex tones. After learning the specific stimulus-response mappings of each task, participants completed a third practice block that was identical to the trials used in the experimental phase. Here, participants were presented with the visual Task 1 (T1) stimulus, which was presented centrally for a variable interval between 200-600 ms (randomly selected at the beginning of each trial)[1]. After either a long (1000 ms) or short (200 ms) stimulus onset asynchrony (SOA), the second task (T2) auditory target was presented for 200 ms. Participants were instructed to respond as quickly and as accurately as possible to the two tasks. The experimental phase consisted of four blocks, each containing 40 trials, with the two SOA conditions presented equally often across each block. The dependent variable was the PRP effect, which was calculated by subtracting the T2 RT under the 1000 ms condition from the 200 ms condition (Van Selst, Ruthruff, & Johnston, 1999). Lower differences scores indicated better performance.

Attentional blink **(Jolicoeur & Dell'Acqua, 1998; Raymond, Shapiro, & Arnell, 1992).** Here, on each trial, participants were presented with a rapid serial visual presentation (RSVP) stream containing two targets (black letters of the alphabet, excluding I, L, O, Q, U, V, X) and eight distractors (black digits ranging from 2-9). The participants' task was to report the identity of both targets at the end of the stream. There were no time constraints for responding and participants were encouraged to guess if they were unsure. The fixation cross was replaced by the first stimulus in the RSVP stream. Each item was presented for 100 ms. Target 1 (T1) always appeared at serial position 3, and Target 2 (T2) appeared either 200 ms (lag 2), 300 ms (lag 3), 500 ms

[1] Due to a programming error, presentation duration of the first target varied between 200-600 ms in the

(lag 5), or 700 ms (lag 7) after T1. Participants completed 24 practice trials and four test blocks of 24 trials. The dependent variable was AB magnitude, which was calculated as the difference in T2|T1 accuracy at lags 2 and 3 from lags 5 and 7 (Kelly & Dux, 2011). A smaller AB magnitude indicated better performance.

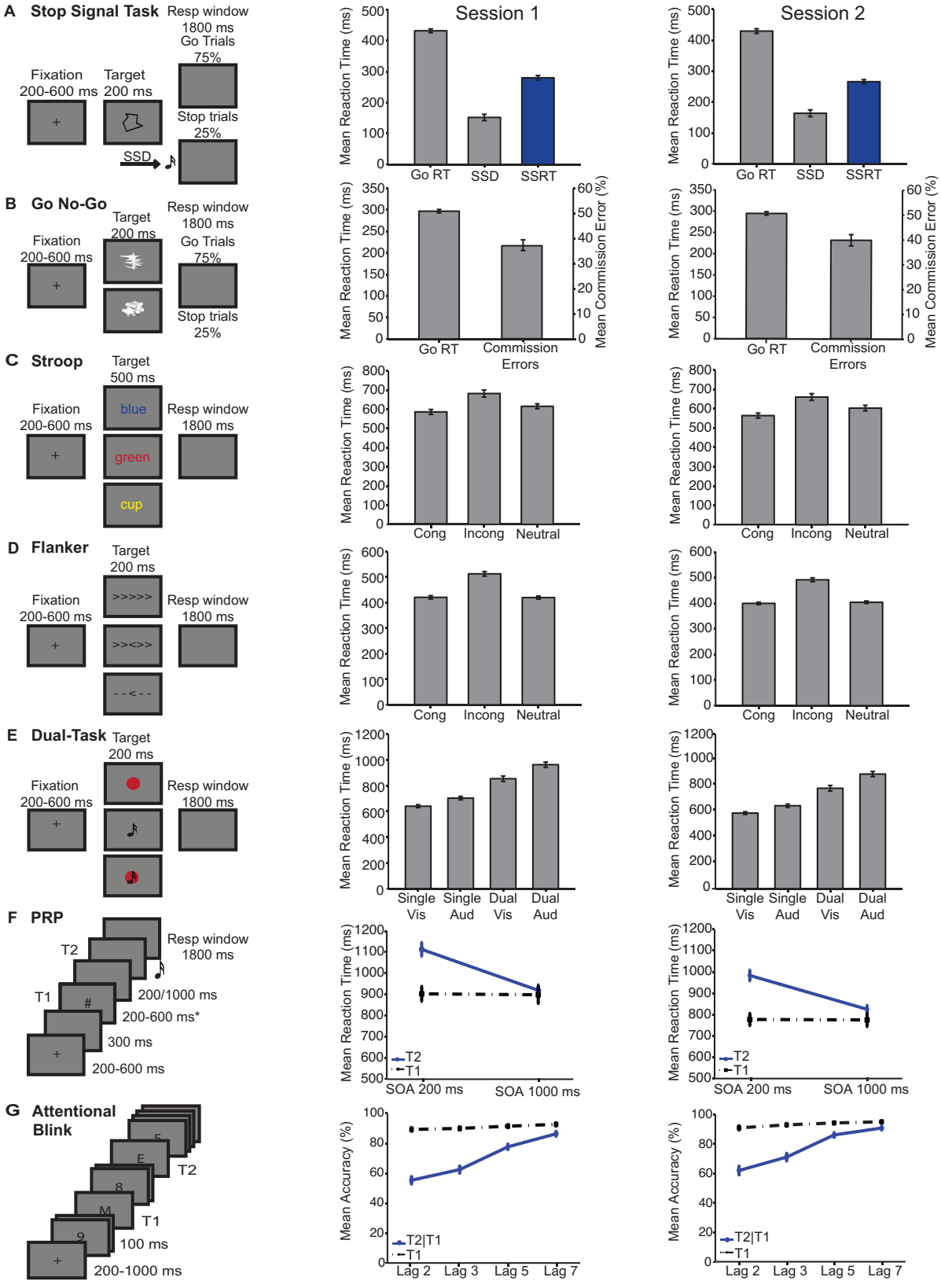


Figure 1. Schematic representation of the paradigms and task performance on the seven measures of interest across Session 1 and 2. Task performance: (A) shows the mean go response time (RT), the mean stop-signal delay (SSD) and mean stop-signal RT (SSRT) in the Stop-Signal task. (B) Task performance in the Go No-go task (B) shows the mean

go RTs and commission errors (failed no-go trials). (C) and (D) show the mean RTs for the congruent, incongruent and neutral condition in the Stroop and Flanker tasks, respectively. (E) shows the mean RTs for the single and dual visual stimulus condition and single and dual auditory condition in the Single vs. Dual Response Selection task. (F) shows the mean RTs as a function of stimulus onset asynchrony (SOA) for target 1 (T1) and target 2 (T2) in the Psychological Refractory Period, whereas (G) shows the mean accuracy as a function of lag for target 2 accuracy, given target 1 is correct (T1|T2) and T1 accuracy in the Attentional Blink task. The error bars represent the standard error of the mean (SEM).

Results

Outlier screening was performed for each participant, in each session and for each task separately. Trials greater than three standard deviations above the mean were removed.

Test-Retest Reliability

In order to assess the stability of performance for each measure, we first calculated test-retest reliability between Session 1 and 2 for each paradigm. As can be seen in Figure 2, all seven paradigms were shown to have moderate to strong test-retest reliability (*r*s range = .42 - .69), demonstrating that individual task performance remained relatively stable across the seven days. It was therefore appropriate to use these measures in inter-correlation analyses with the other tasks.

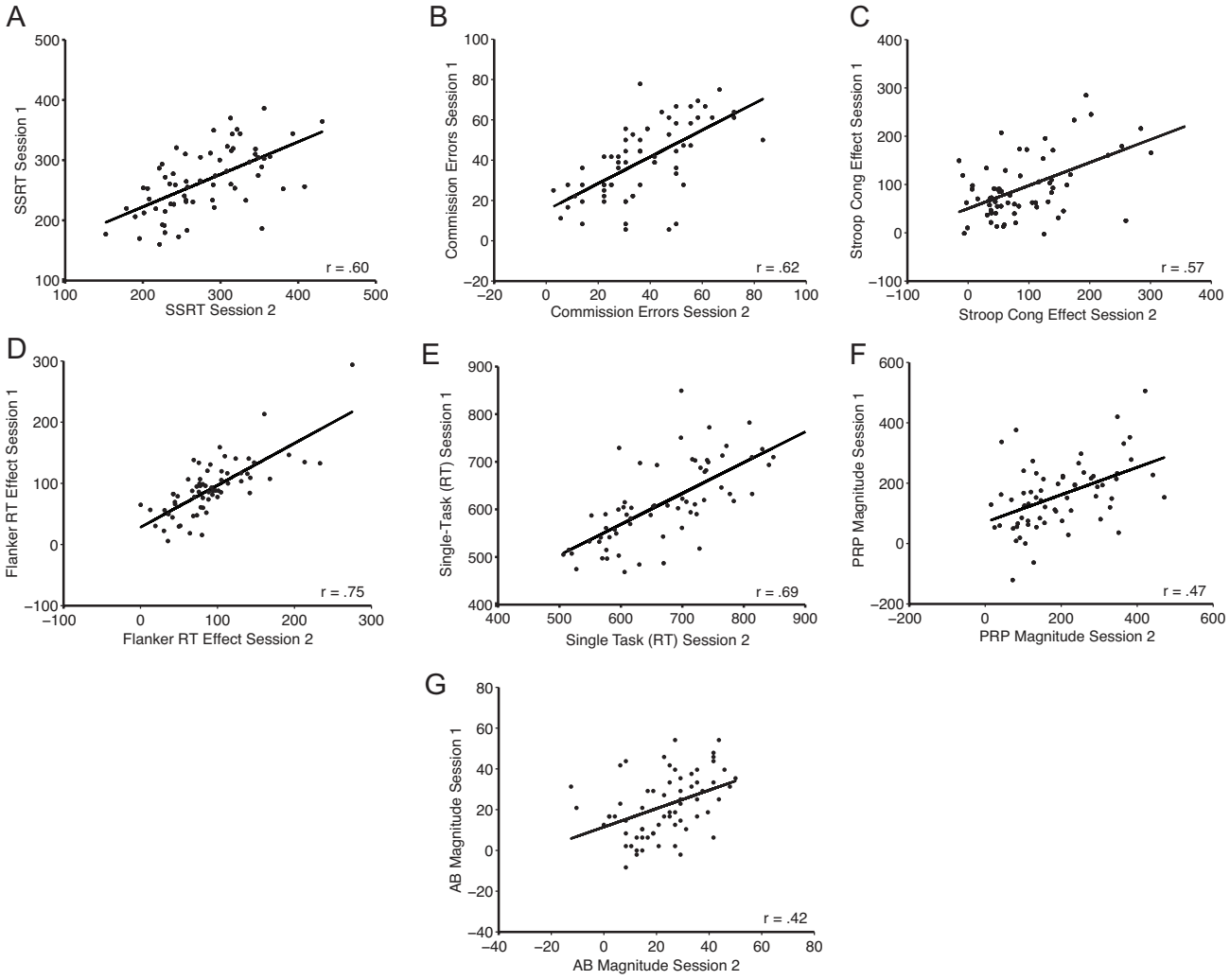


Figure 2. Scatterplots of the relationship between individual's (A) Stop-signal response time (SSRT), (B) Go No-go commission errors, (C) Stroop Congruency Effect (Stroop Cong Effect), (D) Flanker response time (RT) effect, (E) Single-Task response time (RT), (F) Psychological Refractory Period magnitude (PRP Magnitude), (G) Attentional Blink magnitude (AB Magnitude) across Session 1 and 2.

Relationships Among the Tasks

In order to assess whether the data contains clusters of interrelated variables that are in line with our a priori predictions, we first explored the relationships between the different tasks. The measures of interest (SST: SSRT, Go-Nogo: commission errors (%), Stroop: congruency effect, Flanker: congruency effect[2], Dual vs. Single Response Selection Task: Dual Task cost and Single-Task Response Selection RT, PRP: PRP magnitude, AB: AB magnitude) were first collapsed across sessions for each paradigm to

[2] We chose the Incongruent minus Congruent contrast instead of Incongruent minus Neutral or Neutral minus Congruent as our main Flanker and Stroop interference measure, as it resulted in the largest interference effect.

obtain an overall score. An attenuation correction[3] (Hunter & Schmidt, 1990) was applied to each correlation (r_c) to control for differences in reliability due to measurement error (see Table 1, and Supplemental Figure 1). Out of the response selection measures, the PRP correlated positively with other measures of response selection, such as the Single-Response Selection (r_c = .53, p < .01) task and only marginally with the AB (r_c = .36, p = .06) measure. Interestingly, the Stroop task, often employed to measure inhibition-related processes, did not significantly correlate with any of the inhibitory control tasks but instead correlated significantly positively with the PRP (r_c = .57, p < .01). The PRP also correlated significantly positively with the SST (r_c = .38, p < .05) response inhibition measure. In addition, the SST significantly positively correlated with the Go-Nogo (r_c = .88, p < .01) paradigm. Of interest, the Flanker paradigm did not correlate with any of the other measures and was therefore removed from further analysis.

Table 1. *Attenuated Pearson r correlations (Hunter & Schmidt, 1990) between the Stop-Signal task (SST), Go-Nogo task (NoGo), Stroop, Flanker, Dual vs. Single response selection task (Single-Task), Psychological Refractory Period (PRP), and Attentional Blink (AB). * p < .05 (critical r value = .374); ** p < .01 (critical r value = .479).*

	SST	NoGo	Stroop	Flanker	Single-Task	PRP	AB
1. SST	-						
2. NoGo	.88**	-					
3. Stroop	.10	.21	-				
4. Flanker	.15	-.08	.03	-			
5. Single-RS	-.10	-.13	.31	.14	-		
6. PRP	.38*	.25	.57**	-.09	.53**	-	
7. AB	.30	.22	.21	-.16	.11	.36	-

[3] Attenuation correction formula: rxy,corrected = rxy /sqrt(rxx)*sqrt(ryy) [sqrt = square root] where rxy is the uncorrected correlation taken from the correlation matrix and rxx and ryy is the test-retest reliability measure for measure 1 and 2 (Hunter & Schmidt, 1990).

Confirmatory Factor Analysis. To examine how response inhibition and response selection processes are related, we performed a series of CFAs. Using the well-established tasks that are known to differ in their response selection and inhibition requirements, we first empirically compared a set of different models (see Table 2) and selected the best fitting model via multiple appropriate fit indices. The fit of each model was evaluated with the chi-square statistic, the standardized root-mean-square residual (SRMR) and Akaike's information criterion (AIC). The chi-square statistic (non-significant values indicating a satisfactory fit) and AIC (lower AIC values indicate better fit) both measure the fit between the observed and predicted covariances. The SRMR represents the square root of the average covariance residuals between the observed and predicted model, with SRMR values less than .08 indicating an acceptable fit and values less .05 indicating a good fit (Hu & Bentler, 1998). In addition, we examined the models with the Bentler's comparative fit index (CFI), which compares each model to an independent baseline model (i.e., a model where all covariances are set to zero). Here, values between .95 and 1.00 are indicative of a good model fit (Hu & Bentler, 1998).

To examine whether one model significantly improved model fit compared to another, chi-square difference tests were performed on nested, more restrictive models. For these calculations the chi-square value (as well as the degrees of freedom) of the full model is subtracted from the smaller, more restricted model. If the chi-square difference is non-significant, then the more restrictive model represents a significantly better fit. The factor models (see Figure 3) include the standardized factor loadings (standardized regression coefficients), the error variance for each task (including measurement error and idiosyncratic task requirements), and the correlations between the latent variables.

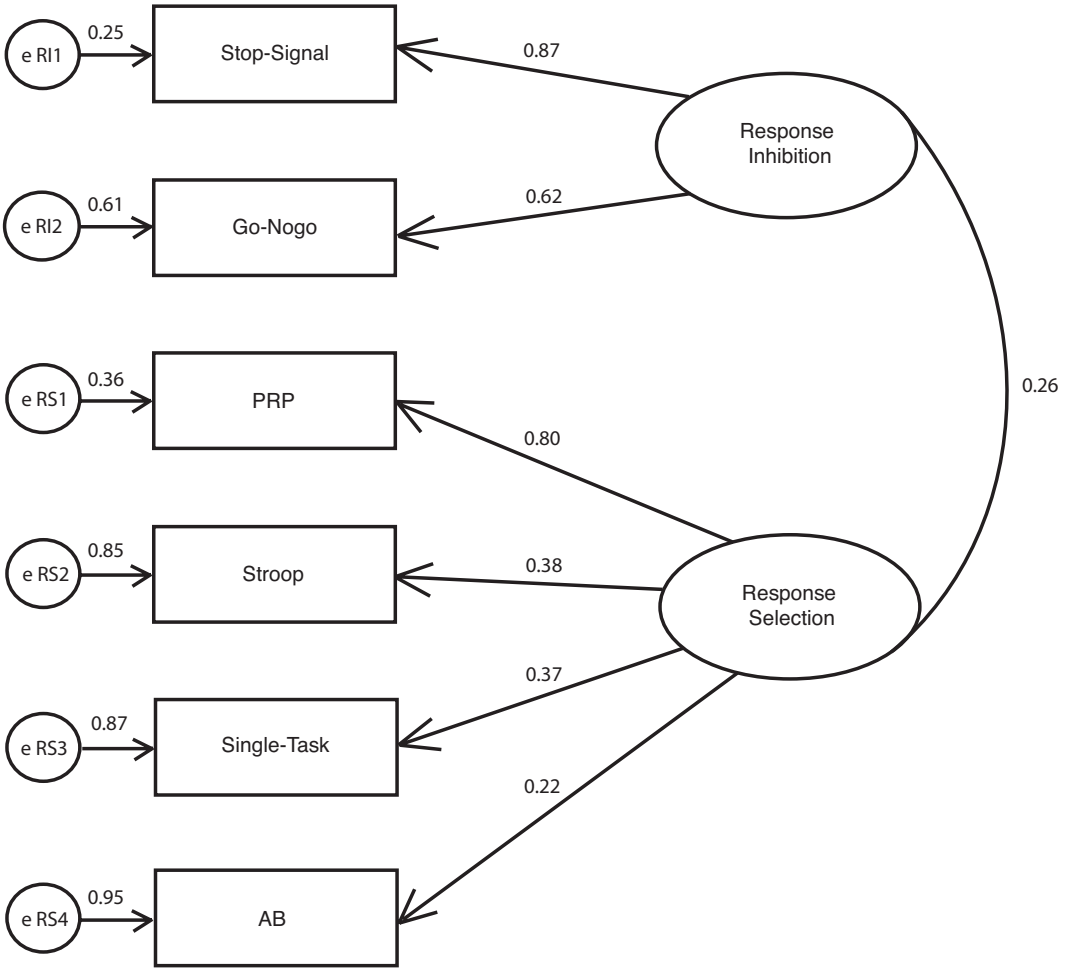


Figure 3. Best fitting model (Model 1) of the action control functions. Standardized factor loadings are given next to the straight arrows, leading from the latent factors to the indicators. Standardized residual variances for each task are listed within the error term circles. The number next to the double-headed arrows is the correlation between the two latent factors. Stop-Signal = Stop-Signal task; Go-Nogo = Go No-go task; PRP = Psychological Refractory Period; Stroop = Stroop task; Single-Task = Single vs. Dual Response Selection task; AB = Attentional Blink.

First, we constructed a two-factor model of response selection and response inhibition by selecting the key performance measure for each task as an indicator (e.g., AB represents AB magnitude). Given that the Stroop task only significantly correlated with response selection measures and not with any inhibitory control measures as anticipated, performance on the PRP, Stroop, Single-Task Response Selection and AB served as indicators of the response selection factor. We specifically chose Single-Task Response Selection performance instead of Dual-Task cost as a response selection indicator to

ensure that the latent response selection variable is not merely driven by dual-task measures (i.e., multitasking). Please note however, that using Dual-Task cost as a response selection indicator still resulted in an acceptable fit (see Table 2, Model 4). The stop-signal task and Go-Nogo task served as indicators of the response inhibition factor. The fit between the hypothesized model and the data was acceptable, with a non-significant chi-square value ($\chi 2$ (8) = 4.32, p = 0.83; SMRI = .057, CFI = 1.00. and an AIC value of 1113.92). As shown in Figure 3, the correlation between response selection and response inhibition was relatively weak (r = .26).

However, because the coefficient predicting performance on the AB from the response selection factor was relatively small, we performed post-hoc model modifications to see if it was possible to develop a better fitting model. In our second model, we dropped the AB variable and re-estimated the model ($\chi 2$ (4) = 3.33, p = 0.5; SMRI = .06, CFI = 1.00, and an AIC value of 915.68). Both the chi-square and the AIC indicated a slightly better fitting model (see Table 2) after performance, but dropping the AB as an indicator did not significantly improve model fit ($\Delta\chi 2$ (4) = 0.99, p = 0.91. Given the non-significant improvement in overall fit, the full 2-factor model (Model 1) was considered the more parsimonious model.

Next, to test whether response selection and response inhibition processes are reflective of a unitary mechanism, we constructed a general action control one-factor model that collapsed the response selection and response inhibition variables into a single General Action Control latent variable. As shown in Table 2, the fit of the one-factor model (Model 3) was poor ($\chi 2$ (9) = 15.75, p = 0.07; SMRI = 0.106, CFI = 0.77 and an AIC value of 1113.35). Moreover, it provided a significantly worse fit than the full-two factor model (Model 1), $\Delta\chi 2$ (1) = 11.43, $p < 0.001$. Therefore, the full two-factor model, in which tasks were parsed in terms of response selection and inhibition requirements (Model 1), was supported over a single General Action Control factor model.

Table 2. *Fit statistics for the Confirmatory Factor Analysis Models. Chi-squares not significant at the .05 level indicate acceptable fit to the data. Lower standardized root-mean-square residual (SRMR) indicate better fit, with SRMR < .05 indicating a good fit to the data and SRMR < .08 indicating a fair fit to the data. Bentler's comparative fit index (CFI) values >.95 indicate an excellent fit. Lower values of Akaike's information criterion (AIC) indicate a better fitting model. * p < .05.*

Model	χ2	*df*	*p*	SRMR	CFI	AIC
1. Two factors: Response Inhibition and Response Selection (AB incl.)	4.32	8	0.83	0.057	1.00	1103.92
2. Two factors: Response Inhibition and Response Selection (AB excl.)	3.33	4	0.50	0.057	1.00	915.68
3. One factor: General Action Control	15.75	9	0.07	0.106	0.77	1113.35
Single-Task measure replaced by Dual-Task cost						
4. Two factors: Response Inhibition and Response Selection (AB incl.)	5.87	8	0.66	0.071	1.00	1106.99

Discussion

We used an individual differences approach to examine the underlying relationship between two cognitive control functions – the selection of appropriate responses (i.e., response selection) and the inhibition of automatic and inappropriate responses (i.e., response inhibition) – at the latent variable level. A series of models were tested via CFA to assess the relations between six behavioural tasks that have been hypothesized to tap response selection and inhibition processes. The results from the CFA found that the full two-factor model (Model 1), in which tasks were assigned in terms of response selection and response inhibition requirements, provided a significantly better fit to the observed data than the simplest model – a single General Action Control factor. Specifically, we found that variance on the Response Inhibition factor contributes to performance on the Stop-Signal and Go-Nogo tasks, whereas variance on the Response Selection factor plays an important role in the PRP, Stroop and Single-Task paradigms and to a smaller degree in the AB.

The present findings suggest that response selection and response inhibition

processes are separable, non-unitary processes, as these two factors were weakly related (covariance between the two factors = .26). Our findings challenge recent work, which suggests that a common mechanism accounts for both the selection and inhibition of actions (Mostofsky & Simmonds, 2008; Verbruggen et al., 2014). Instead, such dissociation reinforces previous CFA studies that found diversity of other executive functions, as well as some overlap (Fisk & Sharp, 2004; Friedman & Miyake, 2004; Miyake et al., 2000). Moreover, the present work fits well with behavioural evidence from Yamaguchi et al. (2012), who found that the decision to stop an inappropriate response is not dependent on the processing capacity at the central response selection stage. In addition, our results are consistent with neuroimaging and neuro-stimulation findings that posit distinct neural substrates involved in response selection (Dux et al., 2006; Filmer et al., 2013b) and response inhibition processes (for a recent review, see Aron, Robbins, & Poldrack, 2014).

Interestingly, we did not find performance on the Flanker task to correlate significantly with the Stroop task or any of the other performance measures. While there is evidence of commonly observed activations in the anterior cingulate cortex and prefrontal cortex when dealing with response conflict in the Flanker and Stroop tasks (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003), studies adopting an individual differences paradigm frequently show that correlations vary between the two tasks and other cognitive measures such as intelligence (Jensen & Rohwer, 1966; Spilsbury, 1992; Stins, Polderman, Boomsma, & de Geus, 2005). Moreover, factorially combined Stroop and Simon tasks and Flanker and Simon tasks have shown that conflict elicited control mechanisms for the two tasks seem to operate in a conflict-specific (i.e., context specific conflict triggers particular cognitive control processes) rather than a conflict-general manner that acts on any type of task conflict (for a review, see Egner, 2008). These findings therefore suggest that these types of conflict tasks may have different cognitive control functions that are mediated by independent cognitive control loops. Indeed, research indicates that the printed colour and the semantics of a word stimulus in the Stroop task, are processed by separate processing pathways (Chen, Lei, Ding & Chen, 2013; Polk, Drake, Jonides, Smith & Smith, 2008), with word reading showing a significant advantage over colour naming. In contrast, the task-relevant and task-irrelevant stimuli in the Flanker task belong to the same category (e.g., <<><<) and are therefore processed in the same pathway. The Flanker interference effect may therefore be more dependent on perceptual load (Lavie, 1995) due to the dimensional overlap between task-irrelevant and task-relevant information. Thus, although we did not include other tests of perceptual load

in the current study, future work should include such measures to fully understand how individual differences in the Flanker task contribute to action control.

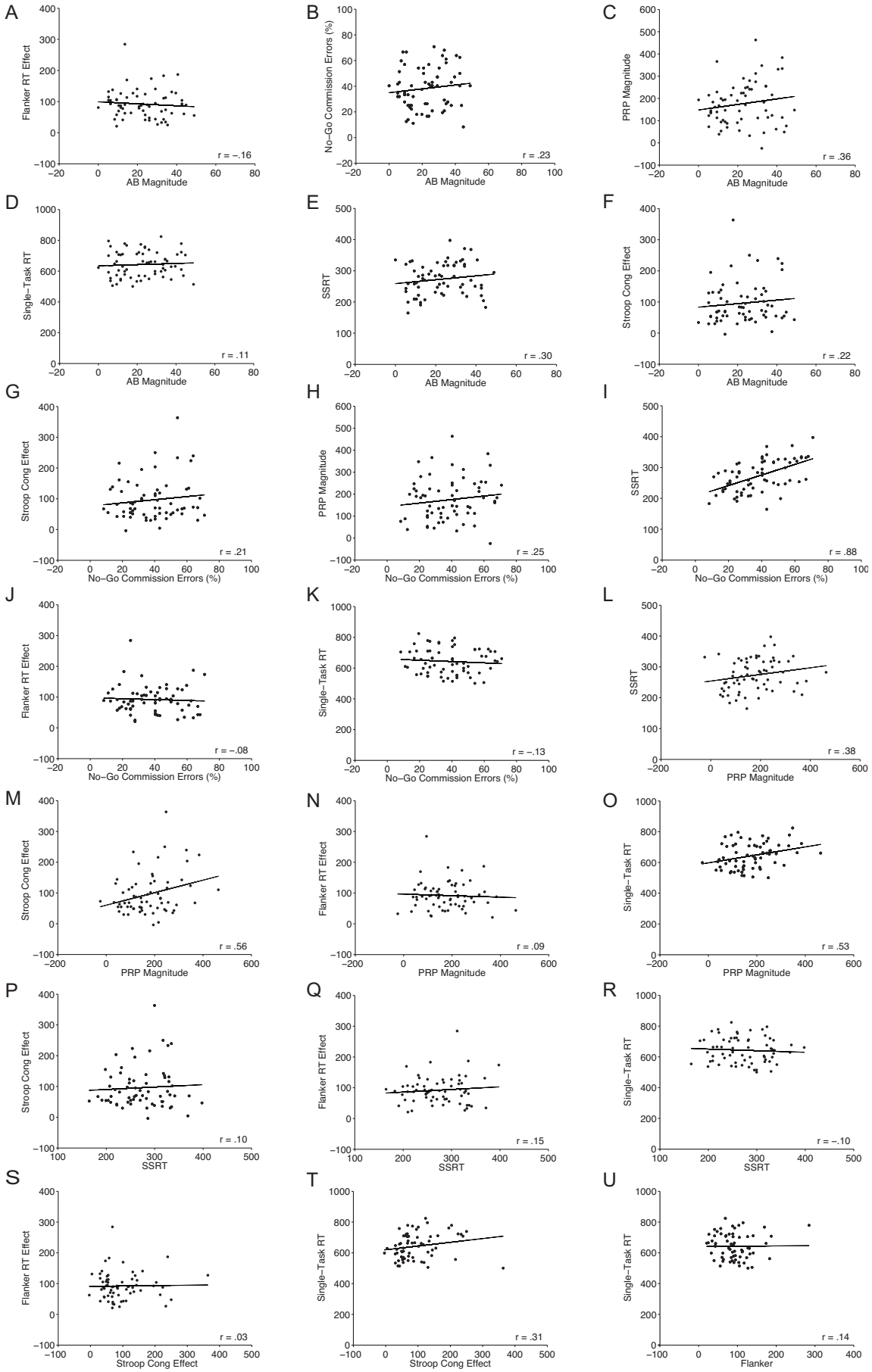
The finding that performance on the Stroop task is more dependent on constraints imposed by response selection, rather than the ability to inhibit distracting automatic responses contrasts with existing studies utilizing CFA methods. In particular, Miyake and colleagues found that the Stroop task significantly loaded on the prepotent response inhibition factor (Friedman & Miyake, 2004; Miyake et al., 2000). Instead, our finding more closely resembles previous research that has found incongruent trials (e.g., the word "blue" in red ink) to create interference at the response selection level (Cohen, Dunbar, & McClelland, 1990; MacLeod, 1991; MacLeod & MacDonald, 2000; Stafford & Gurney, 2007), such that pressing a key associated with a specific colour (e.g., red) competes with the colour word (e.g., the word "blue") as a potential alternative response. Thus, despite the fact that the Stroop task is typically considered to reflect response inhibition, the combination of these prior findings and ours instead imply that the Stroop paradigm actually tapped similar response selection processes to those elicited by PRP and Single-Response Selection Task paradigms.

It must be noted that the AB only weakly loaded on the response selection factor. As this protocol was the only paradigm out of the six tasks submitted to CFA that contained distractor items, it may be possible that this paradigm predominantly measures the suppression of distracting and irrelevant stimuli through controlled attention, which may be separate from the controlled inhibition of prepotent motor responses required in the Stop-Signal and Go-Nogo tasks (Friedman & Miyake, 2004; Nigg, 2000). The weak correlation between the AB, PRP and Single-Response Selection Task also suggests that performance in the AB may predominantly rely on another mechanism dissociated from response selection. A similar finding has been noted in two recent studies by Garner and colleagues (Garner, Matthews, Remington, & Dux, 2015; Garner, Tombu, & Dux, 2014) who investigated whether response selection and sensory consolidation rely on the same capacity-limited central mechanism (Jolicoeur & Dell'Acqua, 1998). For example, in the Garner et al. (2014) study, participants were randomly assigned to a relevant training group (speeded forced-choice sensory motor task matching T1 for an AB or PRP task), an irrelevant training group (i.e., speeded forced-choice sensory motor task not matching T1 for an AB or PRP task), or a control group (no training). The authors showed that while only relevant training attenuated the PRP effect, both relevant and irrelevant training reduced the AB, suggesting that AB performance is at least partly driven by a different underlying mechanism (but see Jolicoeur, 1998; Tombu et al., 2011, for evidence of

overlap).

While we argue for a response selection-inhibition account of the observed two-factor solution, one alternate interpretation is that these components could reflect alternative cognitive processes, such as attentional monitoring or working memory. Specifically, performance in response inhibition tasks is often thought to rely heavily on attentional monitoring when preparing to respond to infrequent stimuli or conflict (Duann, Ide, Luo, & Li, 2009; Erika-Florence, Leech, & Hampshire, 2014; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010), whereas performance in response selection paradigms may be dependent on working memory maintenance processes that support reasoning and rule-processing demands (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Jiang & Kanwisher, 2003; Miller & Cohen, 2001). If our two-factor solution did instead reflect attentional monitoring and working memory processes, then one would predict that the conflict monitoring generated by an incongruent flanker stimuli (the Flanker task), and working memory requirements needed for the sensory consolidation of T1 and T2 (the AB task) should also correlate significantly with one of these two factors. As the Flanker paradigm was omitted from CFA analysis due to its very weak zero-order correlations with the remaining six paradigms and the AB did only weakly load on the response selection factor, our findings instead favour the response selection-inhibition account.

In summary, the present findings support the hypothesis that response selection and response inhibition tap two distinct mechanisms of action control. These results reconcile the previous conflicting empirical work into the nature of response selection and inhibition processes by using an individual differences latent variable approach and a range of cognitive tasks to identify the common sources of variance associated with each process. The results have important implications for how we should conceptualize action control and how one might tailor interventions designed to overcome limitations associated with each domain. In other words, our findings illustrate the value of using multiple response selection and response inhibition paradigms when investigating these two cognitive operations and further suggest that interventions need to be specialized for each aspect of action control.


A
Flanker RT Effect
AB Magnitude
r = −.16
B
No−Go Commission Errors (%)
AB Magnitude
r = .23
C
PRP Magnitude
AB Magnitude
r = .36
D
Single−Task RT
AB Magnitude
r = .11
E
SSRT
AB Magnitude
r = .30
F
Stroop Cong Effect
AB Magnitude
r = .22
G
Stroop Cong Effect
No−Go Commission Errors (%)
r = .21
H
PRP Magnitude
No−Go Commission Errors (%)
r = .25
I
SSRT
No−Go Commission Errors (%)
r = .88
J
Flanker RT Effect
No−Go Commission Errors (%)
r = −.08
K
Single−Task RT
No−Go Commission Errors (%)
r = −.13
L
SSRT
PRP Magnitude
r = .38
M
Stroop Cong Effect
PRP Magnitude
r = .56
N
Flanker RT Effect
PRP Magnitude
r = .09
O
Single−Task RT
PRP Magnitude
r = .53
P
Stroop Cong Effect
SSRT
r = .10
Q
Flanker RT Effect
SSRT
r = .15
R
Single−Task RT
SSRT
r = −.10
S
Flanker RT Effect
Stroop Cong Effect
r = .03
T
Single−Task RT
Stroop Cong Effect
r = .31
U
Single−Task RT
Flanker
r = .14

Supplementary Figure 1. *Scatterplots of the relationship between individuals' performance (collapsed across Session 1 and 2) for each combination of the seven tasks.*

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Study 2: Transcranial Direct Current Stimulation of Superior Medial Frontal Cortex Disrupts Response Selection during Proactive Response Inhibition

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Abstract

Cognitive control is a vital executive process that is involved in selecting, generating, and maintaining appropriate, goal-directed behaviour. One operation that draws heavily on this resource is the mapping of sensory information to appropriate motor responses (i.e., response selection). Recently, a transcranial direct current stimulation (tDCS) study demonstrated that the left posterior lateral prefrontal cortex (pLPFC) is casually involved in response selection and response selection training. Correlational brain imaging evidence has also implicated the superior medial frontal cortex (SMFC) in response selection, and there is causal evidence that this brain region is involved in the proactive modulation of response tendencies when occasional stopping is required (response inhibition). However, to date there is only limited causal evidence that implicates the SMFC in response selection. Here, we investigated the role of SMFC in response selection, response selection training (Experiment 1) and response selection when occasional response inhibition is anticipated (Experiments 2 and 3) by employing anodal, cathodal, and sham tDCS. Cathodal stimulation of the SMFC modulated response selection by increasing reaction times in the context of proactive response inhibition. Our results suggest a context dependent role of the SMFC in response selection and hint that task set can influence the interaction between the brain and behaviour.

Cognitive control enables individuals to flexibly select task-relevant responses (i.e., response selection) and to suppress inappropriate and automatic responses (i.e., response inhibition) according to their goals (Luria, 1970). Extensive research using functional magnetic resonance imaging (fMRI) has shown that a wide range of tasks that engage cognitive control, tap a distributed network of brain regions, including the dorsolateral prefrontal cortex, superior medial frontal cortex (SMFC), anterior cingulate cortex, motor cortex, parietal regions, and the basal ganglia (Duncan, 2010; Miller & Cohen, 2001). However, it is currently unknown whether response selection and response inhibition reflect the same or distinct cognitive operations, and the extent to which they draw on overlapping neural substrates (Mostofsky & Simmonds, 2008; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008).

Response selection – the mapping of sensory information onto motor responses – is an amodal information processing operation that is thought to underlie our inability to multitask efficiently (Pashler, 1984). In the lab, increased reaction time (RT) latency is commonly observed when choosing the correct response from a large subset of response alternatives (single response selection task) relative to a low response selection load, or when individuals attempt to respond to two stimuli in close succession (dual-task). Such multitasking deficits are thought to reflect capacity limitations at the central response selection stage (Dux, Ivanoff, Asplund, & Marois, 2006; Pashler, 1984). Neuroimaging studies suggest that the left hemisphere posterior lateral prefrontal cortex (pLPFC) plays an important role in this bottleneck (Dux et al., 2006; Dux et al., 2009; Jiang & Kanwisher, 2003; Miller & Cohen, 2001). For example, fMRI studies have shown that dual tasks activate this area to a greater extent than single tasks, and that this difference is attenuated as training reduces dual task costs (Dux et al., 2009).

More recently, causal evidence from transcranial direct current stimulation (tDCS) studies implicates the left pLPFC in single- and dual-task response selection, and response selection training effects (Filmer, Mattingley, & Dux, 2013a; Filmer, Mattingley, Marois, & Dux, 2013b). tDCS is a non-invasive brain stimulation method that can be employed to modulate cortical activity and establish a causal role of specific regions or functionally/anatomically connected networks in behaviour (Liang et al., 2014; Yu, Tseng, Hung, Wu, & Juan, 2015). In addition, it can shed light on the systems-level neural mechanisms of specific cognitive operations by influencing performance in a polarity-specific manner (Filmer, Dux, & Mattingley, 2014). Filmer and colleagues (2013b) used a combined behavioural and tDCS paradigm to investigate whether the pLPFC directly contributes to response selection and response selection training gains. Participants

learned the stimulus response mappings for six and two alternative force choice (AFC; high- and low-response selection load respectively) discrimination tasks. Anodal (excitatory), cathodal (inhibitory), or sham stimulation were applied in different sessions with one group receiving stimulation to the left pLPFC and another the right pLPFC. Results demonstrated that under high-load conditions, anodal and cathodal tDCS over the left pLPFC disrupted response selection training benefits relative to sham but this was not observed for the right pLPFC group. These results were also obtained using an alternate reference electrode location and replicated by Filmer et al. (2013a).

Another brain region that has been implicated in response selection operations is the pre-supplementary motor area (pre-SMA; Dux, et al., 2006; Isoda & Hikosaka, 2007; Tombu et al., 2011), a region within the SMFC with extensive pre-frontal connections (Nachev, Kennard, & Husain, 2008). Recent tDCS and transcranial magnetic stimulation (TMS) studies provide causal evidence that this area is involved in response selection processes that occur in contexts with increased task conflict, such as selecting responses when automatic and impulsive response tendencies need to be overridden with an incongruent response (Duque, Olivier, & Rushworth, 2013; Herz et al., 2014; Soutschek, Taylor, Muller, & Schubert, 2013; Spieser, van den Wildenberg, Hasbroucq, Ridderinkhof, & Burle, 2015), or when switching between tasks (Rushworth, Hadland, Paus, & Sipila, 2002). To date, however, the causal role of this area in single-task response selection and training has not been established.

While there is limited causal evidence that the SMFC is a key neural substrate of single-task response selection and training, there is extensive research demonstrating that this area is part of a fronto-subcortical network critical for response inhibition (for a review see Aron, 2011). Indeed, greater pre-SMA Blood-Oxygen-Level-Dependent (BOLD) activity is observed for successful compared to failed stopping (Aron, Behrens, Smith, Frank, & Poldrack, 2007; Boehler, Appelbaum, Krebs, Hopf, & Woldorff, 2010) and TMS and tDCS over the SMFC has been found to disrupt inhibitory control processes (Cai, George, Verbruggen, Chambers, & Aron, 2012; Chen, Muggleton, Tzeng, Hung, & Juan, 2009; Hsu et al., 2011; Obeso, Cho, et al., 2013; Watanabe et al., 2015). In addition, fMRI (Chikazoe et al., 2009; Jahfari, Stinear, Claffey, Verbruggen, & Aron, 2010), EEG (Boulinguez, Ballanger, Granjon, & Benraiss, 2009), TMS (Jahfari et al., 2010; Obeso, Robles, Marron, & Redolar-Ripoll, 2013) and tDCS (Reinhart & Woodman, 2014) studies have further implicated the SMFC in the modulation of response tendencies when participants anticipate that they might have to stop. Such proactive control processes prepare the brain for implementing executive operations. While we refer to this as

'proactive inhibitory response selection control', we note that it could also be described as proactive inhibitory control, favoring accuracy over speed, increased response caution, or preparation for a cognitively demanding event. In contrast to reactive control mechanisms, which are triggered by external events, proactive control is guided by endogenous signals. Consequently, RTs are prolonged when participants anticipate the occurrence of a stop-signal (e.g., maybe stop condition) during a stop-signal task (SST) compared to experimental blocks in which no stop-signals are presented (e.g., never stop; Jahfari, et al., 2010).

Given that the SMFC has been implicated separately in both response selection and response inhibition processes, in tasks using distinct stimuli and methodologies, we examined whether this brain area is causally involved in both operations. Specifically, we ran three tDCS experiments that carefully differed in response selection and response inhibitory requirements while controlling stimulus-processing demands. In Experiment 1, we employed the same paradigm as Filmer et al. (2013b) to investigate the role of SMFC in single-task response selection and training processes. In order to test the role of SMFC in response selection and response inhibition, in Experiment 2 we modified the response selection paradigm to incorporate a stop-signal component. This allowed us to investigate whether the SMFC plays a causal role in modulating inhibitory behaviour. Finally, in Experiment 3 we divided the paradigm into response selection only blocks (i.e., Never Stop condition, no inhibitory context) and blocks where outright stopping was occasionally required (i.e., Maybe Stop condition, inhibitory context present). We did this to examine whether SMFC recruitment in response selection is influenced by the context in which it is performed.

Experiment 1

Method

Participants

Eighteen participants (12 females, mean age = 24, range 21-33 years) from The University of Queensland participated in the experiment and were paid $60 for taking part. All participants were right-handed, reported normal or corrected-to-normal visual acuity, passed a tDCS safety screening questionnaire, and had no history of psychiatric or neurological impairment. Written informed consent was obtained and The University of Queensland Human Research Ethics Committee approved the study protocol. The sample size and subject exclusion criteria were determined before data collection and based on

the same number of participants recruited in the study by Filmer et al. (2013b), that found a significant stimulation-induced effect on response selection processes.

Stimulation protocol

Each participant underwent three tDCS sessions (anodal, cathodal or sham), which were administered a minimum of 48 hours apart. For each session, two 5 x 5 cm saline-soaked surface sponge electrodes were placed on the scalp. The cortical region of interest (MNI: x= 2, y = 12, z = 56), targeting the SMFC (and specifically pre-SMA; see Figure 1A), was based on a recently published meta-analysis into the differential activation effects of two primary response inhibition tasks (Swick, Ashley, & Turken, 2011). The reference electrode was placed over the right mastoid (A2), a region commonly used as a reference electrode site when targeting cognitive control operations with tDCS (Utz, Dimova, Oppenlander, & Kerkhoff, 2010). We specifically chose the right mastoid as a reference electrode location (and with it a bilateral SMFC stimulation slightly biased towards the right hemisphere) because we explicitly did not want to stimulate the left pLPFC – a brain region that has previously been shown to be involved in response selection processes (Filmer et al., 2013a, 2013b). By biasing stimulation towards the right hemisphere, which Filmer et al. (2013b) showed had no effect on response selection, we could be more certain that an observed behavioural effect would be more likely to be due to SMFC stimulation. Given the resolution of tDCS, despite targeting pre-SMA, neighbouring regions (e.g., SMA) may well have been stimulated (all be it to a lesser degree). Thus, as is convention we refer to SMFC (Spieser et al., 2015). In order to increase confidence about the observed tDCS effects in the brain, we computed a forward model of tDCS current flow (implemented in tDCS-Explore, Soterix Medical). Current flow was simulated with a bipolar electrode configuration with the cathode (25 cm^2) centred 1cm posterior from Fz, and the anode (25 cm^2) centred over the right mastoid (A2) and current density corresponding to 0.7 mA total (Figure 1).

tDCS was applied using a battery-driven, constant current NeuroConn stimulator. In line with Filmer, et al. (2013a), stimulation was delivered at 0.7 mA (current density = 0.028 mA/cm^2) for 9 minutes (including 30 second ramp-up/ramp-down periods) for anodal and cathodal tDCS. This intensity of stimulation has been frequently used in other experiments (Nitsche et al., 2008) and is well within accepted safety guidelines (Nitsche et al., 2008). For sham tDCS, the stimulation lasted for 1.15 minutes (including 30 second ramp-up/ramp-down periods). Participants were asked to sit quietly and with their eyes

open during the nine-minute stimulation interval. Debriefing questions confirmed that participants were blind to the nature of the stimulation.

Apparatus

An Apple Mac Mini running MATLAB software (The MathWorks, Natick, MA) and the Psychophysics toolbox extension (Brainard, 1997) were used for stimulus presentation and data collection. Stimuli were presented on a 19" CRT monitor (100 Hz refresh rate) and participants viewed the monitor from a distance of approximately 70 cm.

Design and Stimuli

The stimuli and paradigm were the same as those used by Filmer et al. (2013b). In order to allow for separate training effects to be observed in all three stimulation sessions, and to assess whether response selection is stimulus modality-invariant, participants completed one task per session. Each was an alternative force choice reaction time task requiring a manual response with participants discriminating between symbols (%, #, ~, @, ^, |, +, *), coloured circles, or sounds (eight complex tones; see Filmer, et al., 2013b). The chromaticity coordinates and luminance of the coloured circles were measured with a ColorCal MKII colourimeter (Cambridge Research Systems, Kent, UK). These values were converted to CIE (1976) coordinates. The resulting CIELUV coordinates (u', v', cd/m²) of the coloured circles were: 0.38, 0.51, 30.11 (red); 0.21, 0.55, 93.36 (yellow); 0.16, 0.51, 57.45 (light green); 0.14, 0.51, 26.60 (dark green); 0.16, 0.41, 56.55 (light blue); 0.18, 0.36, 18.44 (dark blue); 0.26, 0.52, 31.44 (brown); 0.27, 0.24, 46.81 (pink). Task order and type of stimulation order were fully counterbalanced across participants.

Each session consisted of blocks of a low response selection load condition (2AFC), in which two out of the eight relevant stimuli were randomly chosen, and a high response selection load (6AFC), to which the remaining six stimuli were allocated. Participants responded manually via a standard Macintosh keyboard. Research by Neath and colleagues (2011) has shown that the use of Macintosh keyboards to collect RT is sensitive to the size of differences we are assessing (>10ms). Half of the participants responded with the index fingers of the left and right hand for the 2AFC task blocks, and the ring, middle, and little fingers of both hands for the 6AFC blocks. The other half of the participants responded with the little fingers of the right and left hand for the 2AFC task blocks, and the ring, middle, and index fingers of both hands for the 6AFC blocks. This was done to avoid any differences between the conditions in terms of dexterity of the fingers used.

Procedure

Participants received oral and written instructions to respond as quickly as possible while minimizing errors. Before the start of the experiment, participants were presented with the images or sounds and the corresponding response keys that would be used in that particular session. The experiment started with a practice phase (three blocks of 30 trials for each response selection load), in which participants had the opportunity to familiarize themselves with the structure of the trials and to learn the relevant stimulus-response mappings for each response selection load. Each trial (see Figure 1B) started with the presentation of a fixation sign in the centre of the screen, which was replaced after 200-600 ms (randomly determined) by the target stimulus. The stimulus remained on the screen for 200 ms and participants had to execute their responses within 1800 ms. During the familiarization phase, participants received immediate feedback on each trial upon making an error. When participants made an error, the word “Wrong” appeared in the centre of the screen. This feedback remained on screen for 300 ms.

Following familiarization, participants completed 18 blocks of 30 trials, divided into the three experimental phases, during which no immediate feedback was given. During each phase, participants were required to complete three blocks each of the high and low response selection load conditions, with the two types of blocks interleaved. The presentation order of the high and low response selection load conditions was counterbalanced across participants. tDCS was applied after the first experimental phase, (pre-tDCS, reflective of session-specific baseline data points), with the second phase commencing immediately after the nine minutes stimulation interval ended (immediate post-tDCS), and the third phase starting 20 minutes after cessation of stimulation (20 mins post-tDCS).

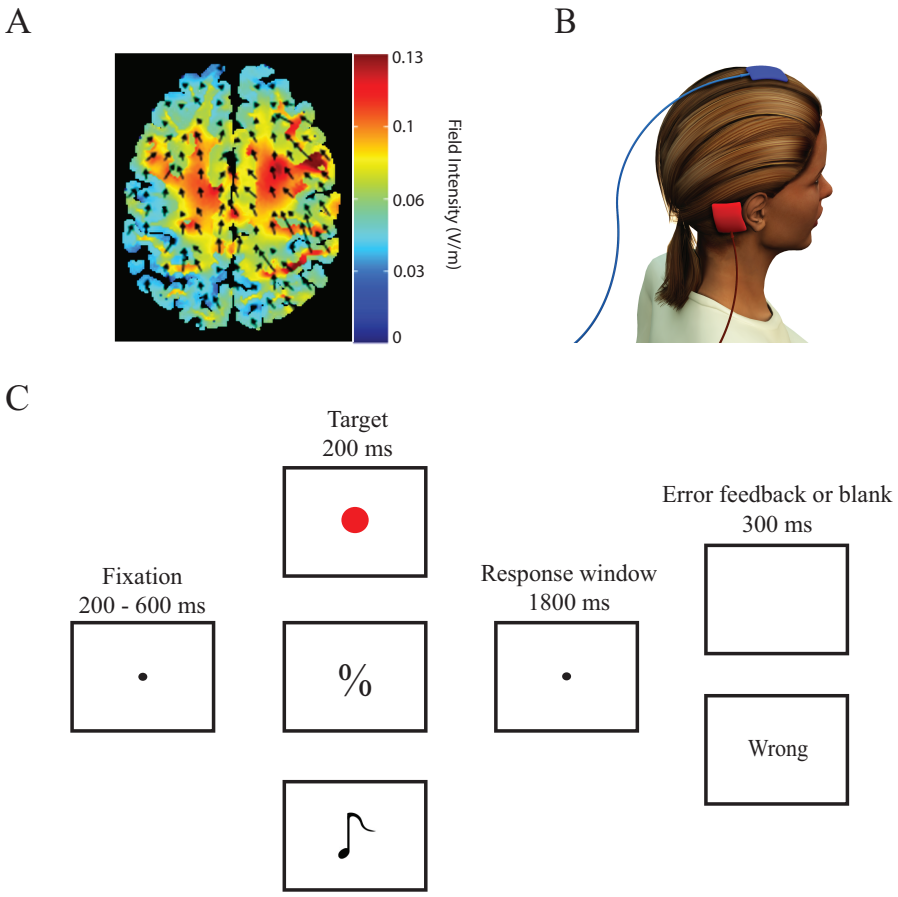

Figure 1. tDCS model and experiment design. (A) A modeled distribution of electric field during active tDCS on an axial view shown projected through a 3D reconstruction of the cortical surface. The forward model is based on pre-SMA cathode and right mastoid anode electrode locations. (B) tDCS electrode montage. The target electrode was placed 1 cm posterior to Fz, located with reference to the 10-20 EEG system (Jasper, 1958). The reference electrode was placed over the right mastoid (A2). (C) Schematic representation of trials for the response selection paradigm (see also Filmer et al., 2013b). All participants completed the response selection paradigm with a different variant of the task (coloured circles, symbols and sounds) used in each session (to control for across session training effects). Participants completed low-load (2 alternative forced choice) and high-load (6 alternative forced choice) blocks.

Results

Analysis plan and power analysis

The effect of tDCS over SMFC on response selection performance (reaction time (RT) and accuracy) was examined using a repeated-measure analyses of variance (ANOVAs) with the factors of stimulation type (anodal, cathodal and sham), phase (pre, immediately-post, and 20 mins post-stimulation) and response selection load (6 vs. 2). A power calculation (Cohen, 1988; Faul, Erdfelder, Lang, & Buchner, 2007) revealed that to achieve 80% power (f = .25) to detect a significant 3 (stimulation type) x 3 (phase) x 2 (response selection load) interaction, a total of 13 participants would be required. We based our sample size on this calculation and the sample size of our previous study (Filmer et al., 2013b).

Reaction times

The RT results are shown in Figure 2. RTs longer than 3 standard deviations above the mean for each response load condition, phase and stimulation type were removed from data analysis (3.6%). The analysis on RTs revealed a significant main effect of phase (F(2,34) = 6.10, p = .01, η^2_P = .26), reflecting an overall training related reduction in RTs as the number of trials increased. A significant main effect of response selection load (F(1,17) = 405.68, p < .001, η^2_P = .96), indicated that overall, participants responded faster under the low response selection load (M = 600 ms) than under the high load (M = 930 ms) condition. Furthermore, the interaction between training phase and response selection load was significant (F(2,34) = 8.72, p = .01, η^2_P = .34), reflecting a stronger training related reduction in RTs (across the three phases) under high response selection load than under low response selection load. No significant main effect of stimulation type (F(2,34) = 0.27, p = .28, η^2_P = .02) was observed, suggesting that there were no overarching differences in RTs between the anodal (M = 766 ms), cathodal (M = 774 ms), and sham (M = 749 ms) stimulation sessions. Of import, the interaction between stimulation type, training phase, and response selection load was not significant (F(4,68) = 2.05, p = .10, η^2_P = .11), nor was the interaction between stimulation type and training phase (F(2,34) = 0.32, p = 0.86, η^2_P = .02), indicating that there was no meaningful difference in training related reductions in RTs across the three phases following anodal and cathodal stimulation relative to sham. Thus, stimulation of SMFC did not disrupt response selection or training-related performance gains.

It should be noted that RT performance during the pre-stimulation phase varied between the three different stimulation conditions for both the high- and low- response selection load condition (see Figure 2). These differences, however, were not statistically significant for the high- (F(2,32) = 0.27, p = .76, η^2_P = .03) or low- (F(2,32) = 1.94, p = .16,

η^2_P = .10) load condition. Thus, the pre-stimulation phase difference did not affect the interpretation of results, as the main point of interest was the pattern of change across the different training phases.

In order to assess whether the pattern of results was different for the three task types employed, we removed the factor of stimulation and separated the RT results into three different discrimination task versions (i.e., one auditory and two visual tasks). A repeated-measures ANOVA on the pre-stimulation baseline RT data with the factor task type revealed a significant main effect of task type for the high-, $F(2,34) = 29.72$, $p < .001$, $\eta^2_P = .73$, and low- response selection load condition, $F(2, 34) = 6.22$, $p = .01$, $\eta^2_P = .05$, such that RTs in the sound discrimination task tended to be significantly higher (M = 1113 ms) than RTs in the circle discrimination task (M = 884 ms) and symbol discrimination task (853 ms) in the high-load condition and low-load condition (sound discrimination task: M = 632 ms; circle task: M = 568 ms; symbol task: M = 601 ms). To further test whether the observed task type RT differences interact with the behavioural pattern of improvement across the different training phases in the high-load condition, we used a mixed ANOVA with task type and phase as within-subject factors and stimulation type/task pairing (e.g., whether the circle discrimination task was paired with anodal, cathodal or sham stimulation) as between-subject factor. Consistent with previous research (Dux et al., 2006; Dux et al., 2009; Filmer et al., 2013b), the same pattern of change across the training phases was present for all three task types and stimulation/task type pairings ($F(8,60) = 0.26$, $p = .98$, $\eta^2_P = .01$).

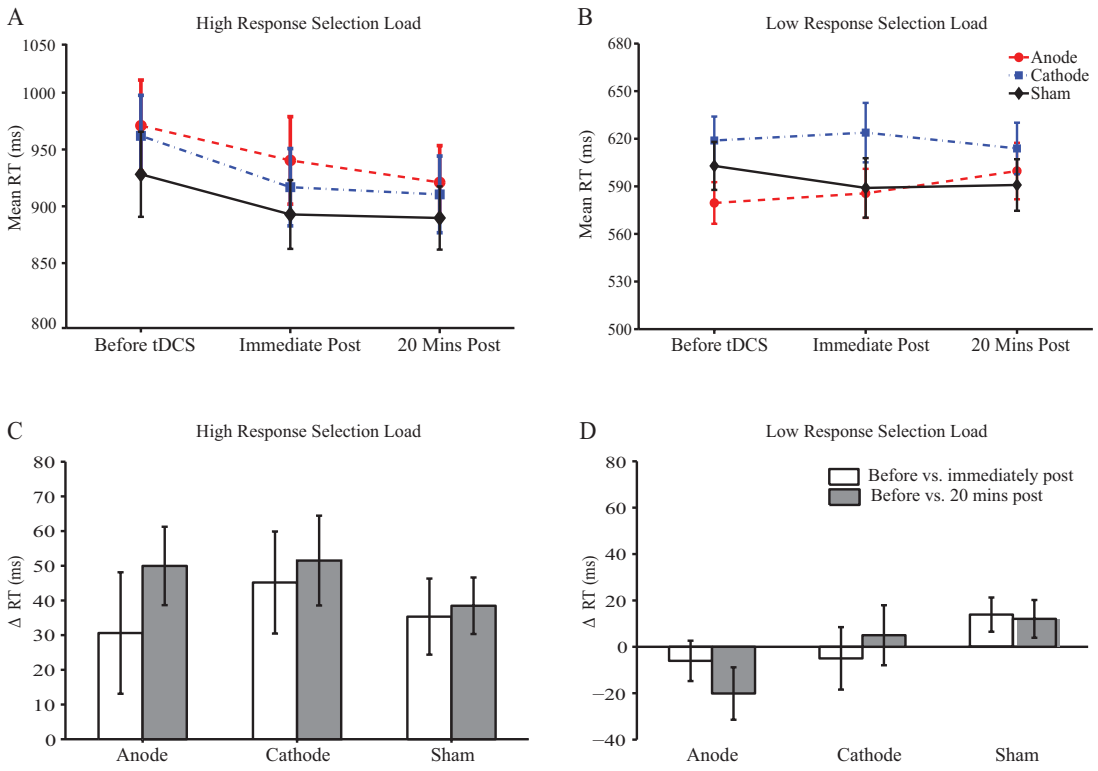

Figure 2. Effect of training and tDCS on the high and low response selection load conditions. (A) and (B) show the mean RT in each stimulation condition across the three phases for the high- (6 alternative forced choice) and low- (2 alternative forced choice) response selection load trials. Error bars represent the standard error of the mean (SEM) for the within subjects variance (Loftus, 1994). (C) and (D) show the change in RT from pre- and immediately post-stimulation, and from pre- to 20 minutes-post stimulation, for the high- (C) and low- (D) response selection load trials. For the high- response selection load, RTs in all conditions reduced with training across the three sessions. The error bars represent the SEM of the change in RT.

Accuracy

The error data are shown in Table 1. A within-subject ANOVA on error rates broadly mirrored the RT data, revealing a significant main effect of phase ($F(2,34) = 11.23$, $p < .001$, $\eta^2_P = .40$) and response selection load ($F(1,17) = 26.89$, $p < .001$, $\eta^2_P = .61$). Furthermore, the interaction between training phase and response selection load was significant ($F(2,34) = 11.17$, $p < .001$, $\eta^2_P = .40$), reflecting a stronger training related increase in accuracy across the three phases under high response selection load than under low response selection load. Importantly, the interaction between stimulation type, training phase and response load was not significant ($F(4,68) = 0.16$, $p = .96$, $\eta^2_P = .01$). Thus, anodal and cathodal tDCS did not modulate response accuracy relative to sham

tDCS and no speed/accuracy trade-off was observed.

Table 1.

Mean error rates and standard deviations (sd) in Experiment 1 based on stimulation type, experimental phase, and response selection load.

	Before tDCS Mean (sd)	Immediate post Mean (sd)	20 mins post Mean (sd)
Anode			
High-load	12.16 (14.25)	8.58 (9.37)	6.73 (9.18)
Low-load	2.72 (3.21)	4.14 (7.29)	2.72 (3.63)
Cathode			
High-load	10.56 (12.01)	5.30 (5.43)	5.19 (6.31)
Low-load	4.69 (8.91)	3.58 (5.34)	2.78 (3.94)
Sham			
High-load	8.52 (10.33)	5.31 (8.17)	5.06 (6.49)
Low-load	2.78 (3.50)	2.84 (5.18)	2.62 (4.38)

Discussion

Research suggests a role of the SMFC in response selection processes (Dux et al., 2006; Isoda & Hikosaka, 2007; Soutschek et al., 2013; Tombu et al., 2011). Our results showed a significant training-related reduction in RTs for the high response selection load task. However, unlike the Filmer et al. (2013b) study that found single-task response selection and training processes disrupted after anodal and cathodal tDCS of the left pLPFC, we found no difference in training magnitude following anodal and cathodal stimulation of SMFC relative to training-related performance gains following sham stimulation. Thus, it appears that the modulation of SMFC activity induced by tDCS does not affect performance on the single-task response selection paradigm.

Experiment 2

Several studies have demonstrated the important role of SMFC, in particular the pre-SMA, during stimulus-driven reactive inhibition processes (Aron et al., 2007; Boehler et al., 2010) that are activated by salient stop-signals, and goal-directed proactive response inhibition processes (Chikazoe et al., 2009; Jahfari et al., 2010) that help restrain prepotent action. In Experiment 2, we therefore investigated whether the SMFC directly exerts modulation of response selection processes within an inhibitory context (i.e., when stopping is occasionally required). To dissociate between the role of the SMFC in response selection and inhibitory control processes we changed the response selection

paradigm (Experiment 1) to a modified version of the standard stop-signal task (Verbruggen, Logan, & Stevens, 2008). Consequently, here we could only use two responses – as is typical in stop-signal research.

Materials and methods

Participants

Eighteen new participants (12 females, mean age = 21, range 18-28 years) from The University of Queensland were recruited and met the same criteria as those employed in Experiment 1. The same statistical approach was also employed.

Apparatus and Stimuli

The same apparatus and stimuli used in Experiment 1 were employed here, with two modifications: on a subset of trials an auditory stop-signal (750 Hz sine wave tone, 200 ms duration) was presented shortly after the primary go (to be responded to) stimulus. As we chose an auditory stop-signal, the tone discrimination task was changed to a task where participants discriminated between abstract shapes (white with a black outline, see Figure 3 for an example).

Design and Procedure

The design and procedure were identical to that of Experiment 1 with the following exceptions (Figure 3): First, participants only performed a high response selection load condition. Second, in order to create a prepotent response tendency and to use an approach more typical of the stop-signal paradigm, the mapping of stimuli onto responses was changed from six to two responses, such that each response key was associated with three stimuli. Third, trials were divided into two different types, stop-signal trials (25% of trials) and go trials (75%).

Stop-Signal Task

In this stop-signal task (see Figure 3), participants were again asked to respond as quickly and as accurately as possible to the relevant stimuli by pressing the corresponding response key on go trials. However, on stop-signal trials, an auditory stop-signal was presented shortly after the onset of the go stimulus. Upon hearing the stop-signal, participants were to withhold their response. The time between the go-signal and stop-signal (i.e., stop-signal delay, SSD) was adjusted online. The SSD was initially set at 250 ms and continuously adjusted with an adaptive staircase procedure to keep response

accuracy to 50% on stop-signal trials. Specifically, each time a participant responded in a stop-signal trial, SSD decreased by 50 ms. In contrast, when inhibition was successful, SSD increased by 50 ms. Individual SSD staircases were used for right and left hand responses.

The experiment started with two practice blocks. The first consisted of go trials only (96 trials) in order to get participants familiarized with the stimulus response mappings. The second practice block consisted of 72 go trials and 24 stop-signal trials. During these familiarization blocks the same immediate feedback was provided as in Experiment 1. In addition, when participants did not respond within the response time window (1800 ms), the words “no response detected” appeared. When participants responded during a stop-signal trial, the words “try very hard to withhold your response” were presented. Each experimental phase (before, immediately-post, and 20 mins post- stimulation) consisted of 2 blocks of 96 trials, including 24 stop-signal trials (432 go trials, 144 stop-trials). Here, feedback was no longer provided.

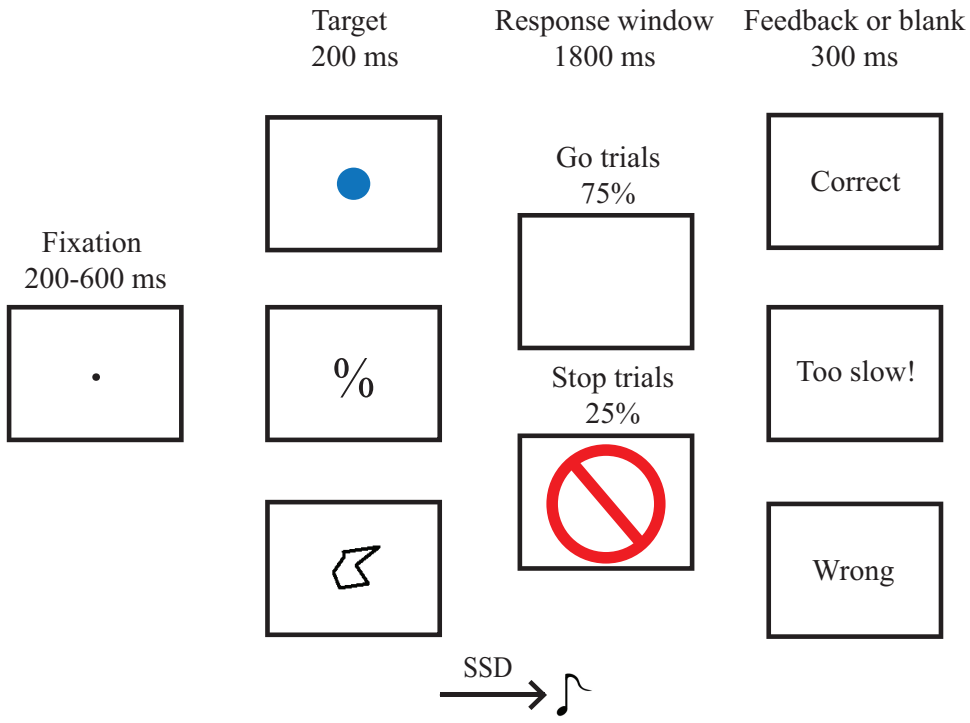

Figure 3. Schematic representation of trials for the stop-signal paradigm. Trials were divided into two different types: stop-signal and go trials. Three quarters of all trials were go-trials. In a stop-signal trial, an auditory stop-signal was played shortly after the onset of the go stimulus at a variable latency known as the stop-signal delay (SSD). The time between the auditory stop-signal and the go stimulus varied and was adjusted after every stop-signal to keep response accuracy at 50% on stop-signal trials.

Stimulation protocol

The same tDCS parameters and site localization approach was used as in Experiment 1.

Results

Analysis plan and power analysis

To investigate the role of SMFC in response selection processes within an inhibitory context, we examined the effect of stimulation on performance measures including the no-signal RTs (correct responses to no-signal trials), stop-signal accuracy (inhibition accuracy), no-signal accuracy, the RTs on failed stop-signal trials (signal-respond RTs) and stop-signal response time (SSRT). Stop-signal reaction time (SSRT), the standard index for response inhibitory control, was calculated using the mean method (Verbruggen & Logan, 2009). Specifically, the mean SSD (computed for each participant from the values of the two staircases) was subtracted from the primary no-signal RTs.

Results for the no-signal RTs, signal-respond RTs, SSRT, SSD, no-signal accuracy, inhibition accuracy for each stimulation type and experimental phase are presented in Table 2. As in Experiment 1, RTs that were longer than 3 standard deviations above the mean for each trial type were removed from data analysis (5.1%). Repeated-measures ANOVAs with the factors of stimulation type (anodal, cathodal and sham), and phase (pre, immediately post-, and 20 mins post-stimulation) were performed on no-signal RTs, signal-respond RTs, SSRTs, no-signal accuracy and inhibition accuracy.

We performed a power calculation (Cohen, 1988; Faul et al., 2007) to estimate the necessary sample size to achieve 80% power (f = .25) to detect a significant 3 (stimulation type) x 3 (phase) interaction and found that a sample size of 15 participants was required. We based our sample size on this calculation, the sample size of Experiment 1 and our previous study (Filmer et al., 2013b).

No-signal reaction times (responses on no-signal trials)

The analysis revealed no significant main effect of phase ($F(2,34) = .77$, $p = 0.47$, $\eta^2_P = .04$). This result reflects generally stable RTs across the three phases, indicating that training-related improvements (i.e., decreased no-signal RTs) did not occur. This was expected, given the relatively easy stimulus-response mappings relative to that in the 6AFC condition of the experiment.

Importantly, there was a marginally significant interaction between the factors stimulation type and training phase ($F(4,68) = 2.36$, $p = .06$, $\eta^2_P = .12$). The differences in

the change in no-signal RTs from pre- versus 20 minutes post-stimulation conditions were significant for cathode vs. anode stimulation ($t(17) = 2.22$, $p = .04$), approached significant for cathode vs. sham stimulation ($t(17) = 2.04$, $p = .06$), and were not significant for anode vs. sham stimulation ($t(17) = 0.26$, $p = .80$). Thus, the results hint at a polarity-specific effect of stimulation on no-signal RT, such that cathodal tDCS of the SMFC prolonged no-signal RTs relative to anodal and sham stimulation. These findings therefore suggest that the SMFC is causally involved in proactive response selection control when participants work under an inhibitory context.

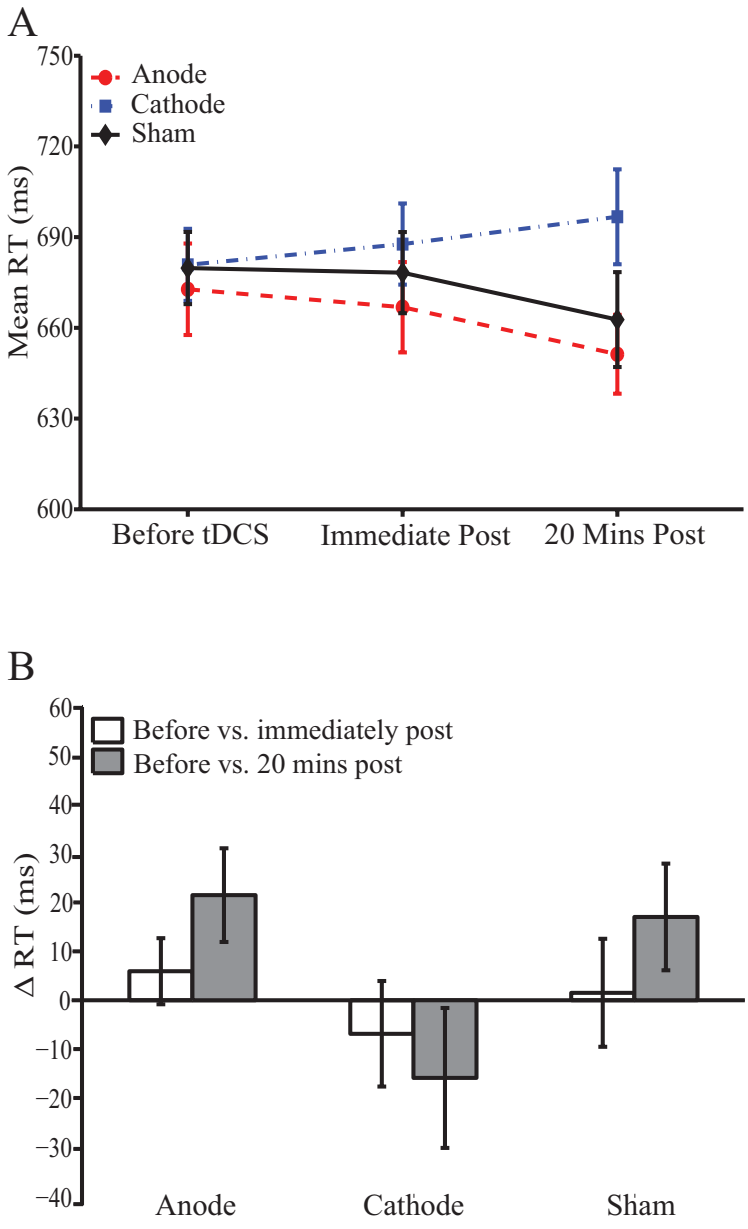

Figure 4. Effect of pre-SMA stimulation on no-signal RTs in the stop-signal task (SST).

(A) Mean RTs in each stimulation condition across the three phases for go trials. Error bars represent the SEM for within subjects variance (Loftus, 1994). (B) shows the difference in no-signal RTs (i.e., non-inhibition trials) between the pre-stimulation and immediately post-stimulation phase and between the pre-stimulation and 20 min post-stimulation phase. The error bars represent the SEM of the change in no-signal RTs. No-signal RTs in the anodal and sham condition slightly decreased across the three phases, whereas no-signal RTs under cathodal stimulation significantly slowed down responding.

To assess whether the pattern of results was different for the three task types employed, we used a mixed ANOVA with stimulation and phase as within-subject factors and stimulation type/task pairing (e.g., whether the circle discrimination task was paired with anodal, cathodal or sham stimulation) as between-subject factor. Consistent with experiment 1, the same pattern of change across the training phases was present for all three task types and stimulation/task type pairings (Training phase x stimulation x stimulation/task type pairings, $F(8,60) = 1.45$, $p = .20$).

Signal-respond reaction times (responses on stop-signal trials)

There was no significant main effect of tDCS on incorrect responses to signal-respond RTs ($F(2,34) = 0.26$ $p = .77$, $\eta^2_P = .02$), but there was a marginally significant main effect of phase ($F(2,34) = 2.72$, $p = .08$, $\eta^2_P = .14$), reflecting generally decreasing signal-respond RTs from pre- to 20 minutes post-stimulation ($F(17,1) = 4.08$, $p = .06$, $\eta^2_P = .19$). Importantly, stimulation did not significantly interact with training phase ($F(4,68) = 1.32$, $p = .27$, $\eta^2_P = .07$), suggesting that overall signal-respond RTs remained relatively stable across the training phases and did not differ between tDCS conditions.

Stop-Signal Reaction Times

For the SSRTs, no significant main effects or interactions with the factor stimulation type were observed (all ps >.3). Hence, anodal and cathodal tDCS of the SMFC did not modulate response inhibition performance relative to sham stimulation.

No-signal accuracy

There were no significant main effects or interactions with the factor stimulation type (all ps > .2). Thus, the effect of cathodal stimulation on no-signal accuracy was limited to no-signal RTs and no speed/accuracy trade-off was observed.

Inhibition accuracy

There were no significant main effects or interactions with the factor stimulation type (all ps > .3).

Table 2.

Behavioural data from Experiment 2. The table shows the mean standard deviation (sd) and mean correct no-signal reaction times (RTs, ms), signal-respond RT (ms), Stop-signal reaction times (SSRT, ms), Stop-signal delay (SSD, ms), inhibition accuracy (%), and mean no-signal RT accuracy (%) for each stimulation type and experimental phase.

	Before tDCS Mean (sd)	Immediate post Mean (sd)	20 mins post Mean (sd)
Anode			
Correct no-signal RT (ms)	673 (152)	667 (161)	651 (138)
Signal-respond RT (ms)	617 (126)	607 (129)	597 (93)
SSRT (ms)	357 (63)	353 (70)	342 (69)
SSD (ms)	316 (158)	314 (192)	309 (167)
Inhibition accuracy (%)	48.50 (4.84)	49.31 (2.95)	50.58 (3.26)
No-signal RT error	7.75 (10.22)	6.75 (8.61)	5.60 (7.53)
Cathode			
Correct no-signal RT	681 (115)	688 (133)	697 (143)
Signal-respond RT	621 (95)	614 (99)	625 (119)
SSRT	346 (65)	332 (59)	345 (75)
SSD	334 (133)	356 (145)	352 (171)
Inhibition accuracy (%)	50.12 (4.87)	50.81 (3.44)	49.42 (3.77)
No-signal RT error	5.83 (5.60)	4.46 (5.24)	4.60 (5.55)
Sham			
Correct no-signal RT	680 (107)	678 (131)	662 (116)
Signal-respond RT	639 (142)	625 (130)	595 (95)
SSRT	346 (66)	337 (63)	354 (57)
SSD	333 (128)	341 (145)	307 (145)
Inhibition accuracy (%)	49.54 (3.82)	49.77 (3.64)	48.84 (2.50)
No-signal RT error	5.40 (5.22)	4.98 (5.74)	4.32 (5.23)

Discussion

In Experiment 2, we observed that cathodal stimulation of the SMFC elongated responding to no-signal trials 20 minutes post-stimulation relative to anodal stimulation. Collectively, the current results suggest that SMFC is involved in response selection. However, this involvement seems to be context dependent, such that SMFC plays a role in

response selection when inhibitory control is occasionally required. We did not however, observe a stimulation-induced effect on SSRTs, inhibition accuracy and signal-respond RTs. While two recent studies found polarity-specific effects on SSRTs after anodal stimulation over pre-SMA (Liang et al., 2014; Yu et al., 2015), the lack of SSRTs and signal-respond RTs are in line with the findings from recent studies by Hsu and colleagues (2011) and Reinhart and Woodman (2014). The authors applied anodal and cathodal tDCS over the SMFC to investigate its functional role in response inhibition operations. While the authors found no effect of tDCS on SSRTs, no-signal RTs and signal-respond RTs, Hsu and colleagues found polarity specific effects of tDCS on the ability to correctly inhibit a response (inhibition accuracy), whereas Reinhart and Woodman found a decrease in no-signal accuracy after cathodal stimulation. While the results differ from the current findings, it must be noted that these studies employed different stimulation protocols, including differences in stimulation intensity, duration parameters, and placement of the reference electrode, which may account for the different outcomes (Filmer et al., 2014). Importantly, the present data are still in line with the SMFC (particularly pre-SMA) playing a central role in response control and response inhibition and given that we used a standard staircase procedure to ensure inhibition accuracy convergence at ~ 50% in Experiment 2, our paradigm was not designed to measure the influence of tDCS on this inhibitory measure.

Experiment 3

Given the marginally significant results in Experiment 2, we conducted a new experiment that was designed to replicate the findings of Experiment 2 with a new sample, and to provide convergent evidence for the role of SMFC in response selection under a stopping/inhibitory context. Participants completed alternating blocks of “Never Stop” (response selection trials in which no stop-signal occurred) and “Maybe Stop” (response selection trials in which occasional stopping was required) trials. As Experiment 2 revealed that only cathodal tDCS over SMFC slowed responding 20 minutes post stimulation relative to anodal stimulation, while anodal stimulation had no effect relative to sham, we compared the effects of cathodal versus sham stimulation here. If the SMFC stimulation-induced RT effects are due to an inhibitory context, then we should find that cathodal stimulation of this area increases no-signal RTs in the Maybe Stop condition.

Materials and methods

Participants

A total of thirty-six new participants (25 females, mean age = 22, range 19-29 years) from The University of Queensland were recruited for this study and were paid $20 for participation. Participants were randomly assigned to one of two groups; one group of 18 participants (13 females, mean age = 22, range 20-29 years) received cathodal tDCS, and the other group of 18 participants (12 females, mean age = 22, range 19-29 years) received sham tDCS. Three individuals from the sham stimulation group were excluded from final analysis due to no-signal RTs that were more than two standard deviations above the mean. All participants met the same criteria as that employed in Experiment 1 and 2 and the same statistical approach was employed.

Apparatus and Stimuli

The same apparatus used in Experiment 1 and 2 was employed here. To assess response selection performance as a function of stopping context, we reverted back to a high response selection load (6AFC) and the same stimuli that were used in Experiment 1. This was done to increase the demands placed on response selection and thus, increase our sensitivity to observe any effects of tDCS on performance (Filmer et al., 2013b). For the colour and symbol discrimination task, the same auditory stop-signal as in Experiment 2 (750Hz sine wave tone, 200 ms duration) was employed. In order to keep modalities separate for go stimuli and the stop-signal, the auditory stop-signal was replaced by a visual stop-signal for the sound discrimination task. For the visual discrimination tasks (circles and symbols), the same auditory stop-signal was employed as in Experiment 2.

Design and Procedure

The design and procedure was similar to Experiment 2 with the following exceptions. As we sought to replicate the key finding of Experiment 2, participants took part in only one experimental session and were randomly assigned to one of two tDCS conditions (i.e., cathodal or sham stimulation group). We further chose a between-groups design to avoid general practice effects. One third of participants in each stimulation condition performed the colour discrimination task, one third performed the symbol discrimination task, and the remaining one third performed the sound discrimination task. In all three tasks participants discriminated between six stimuli. Each experimental phase (pre- immediately post-, and 30 minutes post-stimulation) consisted of four blocks with 96

trials per block (384 trials per phase, 1152 trials in total). The blocks were further sub-divided into Never Stop (192 go trials per phase) and Maybe Stop (144 go trials and 48 stop-signal trials per phase). An instruction screen, showing the specific block condition preceded each block. All participants started with a practice block of the Never Stop condition, which consisted of 96 go trials only. This was followed by a Maybe Stop practice block, which consisted of 72 go trials and 24 stop-signal trials. Immediately after the practice phase, the experimental testing phases started. Half of the participant had the repeating block pattern of Never Stop condition, followed by the Maybe Stop condition, and the other half of the participants had the reverse alternating pattern.

The Never Stop condition was identical to the high response selection load condition in Experiment 1, requiring no proactive inhibitory response selection control. For the Maybe Stop condition the same SST was used as in Experiment 2, with the following modifications: In order to assess response selection processes, the mapping of stimuli onto responses was changed from two to six responses such that each response key was associated with one stimulus (same response mappings as for the NS condition). During a stop-signal trial, the stop-signal was delivered at one of the following stop-signal delays: 450, 550, 650, and 750 ms. The four different SSDs occurred with equal probability in the 25% of stop-signal trials, with ordering pseudo-randomized for each block and each participant. The specific SSDs were chosen as they had resulted in a no-go accuracy of ~50% (Logan, 1997) in our pilot experiments.

Stimulation protocol

The same site localization approach and similar tDCS procedure as in Experiment 1 and 2 were used here with the following exceptions. Total stimulation time was increased to 13 minutes to compensate for the increase in trial numbers. For the cathodal stimulation condition, the current was applied for a total of 13 minutes (including a 30 s ramp up and down period at the start and end of stimulation) at a current intensity of 0.7 mA. To avoid stimulation induced modulations in cortical excitability the parameter and stimulation duration for the sham condition remained the same as in Experiment 1 and 2. However, the duration of time participants believed they were receiving stimulation did not vary from the cathodal stimulation duration (i.e., a total of 13 minutes).

Results

Analysis plan and power analysis

Results for the no-signal RTs, no-signal accuracy, inhibition accuracy for each stimulation type and experimental phase are presented in Table 3. The same data trimming procedure as in Experiment 1 and 2 was employed, which resulted in the removal of 8.6% from data analysis. We particularly focused on no-signal RT performance to investigate context dependent recruitment of SMFC in response selection processes. Based on the findings of our Experiment 2, we had strong a priori predictions and therefore used planned ANOVAs to analyze the no-signal RT data with a similar sample size to that used in Experiment 2.

No-signal reaction times (correct responses to go stimuli)

We conducted separate mixed ANOVAs with the within-subjects factors phase (pre-, immediately post-, and 30 mins post-stimulation) x block (Block 1 and 2) and the between-subjects factor stimulation (cathodal and sham tDCS) for each context condition (Maybe Stop and Never Stop). For the Never Stop condition, the main interaction of interest between phase and type of stimulation was not significant ($F(1,31) = 1.44$, $p = .25$, $\eta^2_P = .04$), indicating that there were no significant differences in no-signal RTs between the sham and cathodal stimulation group across the phases. It must be noted that RTs in the high response selection load condition in Experiment 1 (M = 930 ms) were 180 ms longer than RTs in the Never Stop condition in Experiment 3 (M = 750 ms). While we cannot rule out that differences in response strategies or control adjustments may be responsible for the observed RT variability, it is more likely that intergroup differences can account for the RT differences between the two experiments. Indeed, using the same high response selection load paradigm, Filmer et al. (2013b) reported RTs between 825 ms and 880 ms at baseline in the high load condition, further demonstrating how individual differences in response selection ability varies between different samples.

Critically, for the Maybe Stop condition, phase interacted significantly with the type of stimulation ($F(1,31) = 4.55$, $p = .02$, $\eta^2_P = .13$). This interaction reflected an increase in the no-signal RTs from pre- to 30 mins post- stimulation for the cathodal group but decreased for the sham group (the difference in the change in RT from pre- versus 30 mins post-stimulation compared for the cathodal and sham conditions: $t(1,31) = 2.51$, $p = .02$, two-tailed). This demonstrates that the pre- versus 30 mins post-stimulation no-signal RT difference between the cathodal and sham stimulation group related to the differential RT effects in the Maybe Stop condition. The pattern of results is consistent with our earlier conjecture that SMFC recruitment during response selection operations is dependent on an inhibitory context. Response time performance during the first block

varied between the sham and cathodal group. However, these baseline differences were not statistically significant for the Maybe Stop condition, $t(1.31) = 0.70$, $p = .49$), nor for the Never Stop condition $t(1, 31) = 1.18$, $p = .25$. The results here complement those of Experiment 1 and 2 and demonstrate context dependent SMFC recruitment during response selection processes.

To further illustrate the significance of our findings we employed *Fisher's method* (Fisher, 1932) to combine cathodal vs. sham *p*-values from Experiment 2 ($p = .04$) and Experiment 3 ($p = .02$). This approach works on the logic that it is highly improbable that false positives for the same contrast will occur for two independent sets of data (when only two such contrasts, e.g. Cathode vs. Sham, are conducted). Using this method we achieved a highly significant statistical result (.006) across the two experiments, confirming that tDCS of SMFC influenced performance.

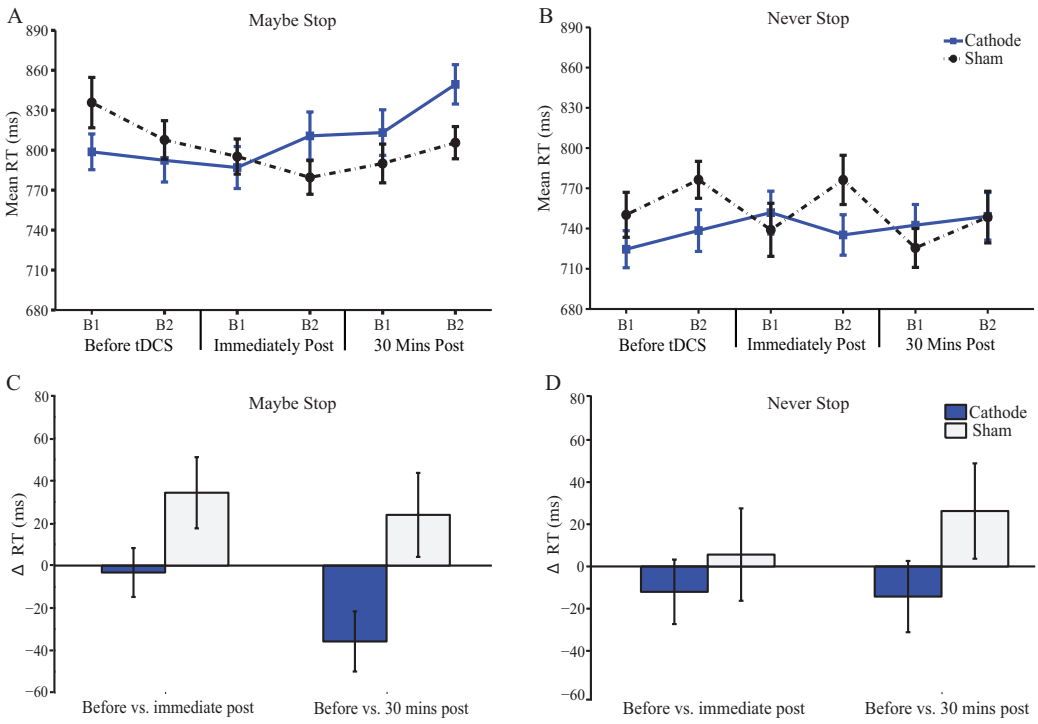

Figure 5. Effect of pre-SMA stimulation on no-signal RTs in the Stop Signal Task (SST). (A) and (B) show the no-signal RTs per stimulation condition across each block (B1 and B2) for each of the three phases for the Maybe Stop context (A) and the Never Stop context (B). Error bars represent the SEM for within subjects variance (Loftus, 1994). (C) and (D) show the difference in no-signal RTs (i.e., non-inhibition trials) between the pre-stimulation and immediately post-stimulation phase and between the pre-stimulation and

20 mins post-stimulation phase for the Maybe Stop context (C) and Never Stop context (D). The error bars represent the SEM of the change in no-signal RT compared with the before stimulation phase. No-signal RTs in the sham condition slightly decreased across the three phases, whereas no-signal RTs under cathodal stimulation slowed down responding.

To assess whether the pattern of results was different for the three task types employed, we used a mixed ANOVA with phase, context and block as within-subject factors and stimulation type (cathodal or anodal tDCS) and task pairing (sounds, circles or symbols) as between-subject factor. There was a significant main effect of task type, such that overall RT in the sound condition was significantly higher (M = 853 ms) compared to overall RTs in the colour (M = 769 ms) and symbols (M = 726 ms) conditions. However, in line with experiment 1 and 2, the same pattern of change across the training phases was present for all three task types and stimulation/task type pairings across the two different contexts (Training phase x context x stimulation x stimulation/task type pairings, $F(4,54) = 1.33$, $p = .27$).

No-signal accuracy

No significant main effects or interactions with the factor stimulation type were found (all ps > .2). Hence, the effect of cathodal tDCS did not affect no-signal response accuracy and no speed/accuracy trade-off was observed.

Inhibition accuracy

There was a significant phase and stimulation type interaction ($F(2,62) = 5.44$, $p = .01$, $\eta^2_P = .15$), such that inhibition accuracy significantly decreased (i.e., poorer inhibition during stop-signal trials) from pre- to 30 mins post-stimulation for the sham stimulation group relative to the cathodal stimulation group, $t(31) = 2.87$, $p = .01$, two-tailed. The results are consistent with the no-signal RT analysis that found stimulation induced slowing 30 mins post-stimulation for the cathodal stimulation group relative to sham and indicate that increased no-signal RTs may have contributed to better proactive inhibitory response selection control and thus, higher inhibition accuracy. This is in line with previous research that found increased preparation before stopping to result in improved response inhibition efficiency during stop-signal trials (Chikazoe et al., 2009; Jahfari et al., 2010).

Table 3.

Behavioural data from Experiment 3. The table shows the mean standard deviation (sd) and the mean correct no-signal reaction times (RTs, ms), signal-respond RT (ms), inhibition accuracy (%), and mean no-signal RT error (%) for the Maybe Stop (MS) and Never Stop (NS) condition for each stimulation type and experimental phase.

	Before tDCS		Immediate post		30 mins post	
	MS Mean (sd)	NS Mean (sd)	MS Mean (sd)	NS Mean (sd)	MS Mean (sd)	NS Mean (sd)
Cathode						
Correct no-sig RT (ms)	796 (90)	732 (113)	799 (94)	744 (127)	831 (97)	746 (129)
Inhibition accuracy (%)	46.76 (21.42)	-	48.40 (22.52)	-	50.35 (23.32)	-
No-signal RT error	8.68 (8.46)	8.74 (5.32)	6.83 (6.77)	7.81 (6.71)	6.91 (6.50)	8.80 (6.64)
Sham						
Correct no-sig RT (ms)	822 (82)	763 (98)	787 (87)	757 (145)	797 (93)	737 (139)
Inhibition accuracy (%)	49.72 (20.24)	-	46.66 (22.34)	-	43.33 (20.40)	-
No-signal RT error	6.71 (5.63)	8.09 (9.07)	4.58 (4.09)	4.93 (3.97)	4.77 (4.46)	7.40 (9.05)

Discussion

In Experiment 3, we replicated our key Experiment 2 finding and showed that cathodal stimulation prolonged no-signal RTs in the inhibitory context but not in the non-inhibitory context. In contrast, for the sham stimulation group, no-signal RTs decreased in the inhibitory and non-inhibitory context across the different training phases. This pattern of results suggests a context dependent recruitment of SMFC in response selection processes.

General Discussion

Here we examined whether the SMFC is causally involved in both response selection and response inhibition operations. In Experiment 1, using the same paradigm as Filmer et al. (2013b), which previously provided causal evidence for the involvement of pLPFC in response selection and training processes, we found no change in performance when participants received anodal or cathodal tDCS relative to sham. Thus, we found nothing to suggest that SMFC is directly involved in single-task response selection processes. In Experiment 2, we again investigated whether this region is directly involved in response selection when participants operate under a context where they have to inhibit behaviour on a subset of trials. We found that cathodal stimulation slowed responding on no-signal trials (i.e., trials with no stop-signal presentation) relative to responses following anodal stimulation. This finding suggests that the SMFC is causally involved in response

selection processes when participants operate proactively under an inhibitory context. To test the reliability of our Experiment 2 finding, we designed a third Experiment that tested this hypothesis by including alternating Maybe Stop blocks where stopping was occasionally required and Never Stop blocks where stopping was never required. Consistent with this context hypothesis, we demonstrated that cathodal stimulation to SMFC again prolonged responding on no-signal trials relative to responses following sham stimulation. Importantly, planned ANOVAs revealed that this stimulation-induced slowing occurred only during Maybe Stop blocks when participants operated under an inhibitory context, and not during the Never Stop context where stopping was not required.

Collectively, our results suggest that the SMFC plays a key role in inhibitory response selection control. This observation is broadly consistent with the proposed role of SMFC as a modulatory structure of response tendencies when occasional stopping of a response is required (Forstmann et al., 2008). In addition, it is consistent with recent evidence, which found that TMS over the SMFC resulted in slower responses for no-signal trials in a stop switching (Neubert, Mars, Buch, Olivier, & Rushworth, 2010) and a conditional stopping paradigm (Lee et al., 2016) relative to trials with sham TMS.

It may be argued that the employed stimulation intensity of 0.7 mA was relatively weak. However, while it is possible that stronger stimulation intensity may have increased the effect of the stimulation on the SMFC, it has previously been shown that increases in tDCS intensity can also change the direction of cortical excitability (Batsikadze, Moliadze, Paulus, Kuo, & Nitsche, 2013). As such, stronger stimulation intensity may not have necessarily increased efficacy of stimulation. Importantly, the current experimental procedure was based on a previously published response selection study (Filmer et al., 2013b) that found a disruption of response selection and training effects after anodal and cathodal tDCS (stimulation intensity 0.7 mA, 9 minutes duration) over the left pLPFC. While we did not find any significant effect of stimulation in Experiment 1 on single-task response selection, the same stimulation parameters resulted in increased no-signal RTs after cathodal tDCS when participants operated under an inhibitory context. Thus, the results suggest that our stimulation paradigm was strong enough to elicit a behavioural change in response selection performance.

Regarding specificity of our stimulation, while previous research by Uy and Ridding (2003) has reported relatively focal effects of tDCS using 5 x 5 cm electrodes, a recent tDCS, EEG and multiscale entropy study by Liang and colleagues (2014) found that tDCS stimulation over pre-SMA produced not only modulatory changes within the brain region of stimulation but also resulted in tDCS induced changes in the networks that overlapped

with the site of stimulation. The results of Liang et al. (2014) are in line with our current-flow model, which found that stimulation extended to other neighbouring areas, including the SMA proper. TMS studies have shown that the SMA is involved in complex finger movement sequences (Serrien, Strens, Oliviero, & Brown, 2002). However, it is unlikely that tDCS would have prolonged the simple button responses required, especially given the lack of a stimulation-induced effect on response selection processes in Experiment 1, or the Never Stop blocks in Experiment 3. As Maybe Stop and Never Stop blocks were alternated throughout the experiment and no break was given between the two conditions, these results perhaps indicate that the stimulation-induced proactive slowing effect from the Maybe Stop condition partly carried across to the non-inhibitory context condition. Having said this, performance in the Never Stop condition did not statistically differ between the sham and cathodal stimulation groups. Future work will be needed to further test this hypothesis. It must also be noted that we found no effect of anodal stimulation on response selection processes, showing that our results reflect a polarity-specific influence of tDCS and are not due to a more general effect of arousal from stimulation. Thus, while we can't rule out that stimulation of neighboring areas also contributed to the current findings, the reported effects and current-flow modeling suggest that our cathodal stimulation protocol affected the SMFC to a large extent.

An alternative explanation for our results must also be considered. Previous response inhibition studies have reported dorso-lateral prefrontal cortex (DLPFC) activation with increased working memory load (Chikazoe et al., 2009; Jahfari et al., 2010). Given the anatomical and functional connections between the SMFC and the DLPFC, our findings could be interpreted as representing interference with response maintenance in working memory when stopping was anticipated. Proactive inhibitory control is guided by endogenous signals that require working memory to maintain activation and exert a potential behavioural change in a goal-directed fashion. Moreover, it is possible that the choice of the right mastoid as the reference electrode location may have stimulated medial-temporal lobe and its surrounding long-term memory-related structures. Both interpretations cannot be ruled out, but disruption to working memory processes or long-term memory would likely result in an increase of erroneous responses to the primary go-stimuli, which we did not find in all three experiments.

As response selection processes were only modulated by cathodal (inhibitory) stimulation when participants operated under an inhibitory context, our data imply that this reduced excitability in the SMFC may have enhanced the proactive role of this area in inhibitory response selection control. These findings may sound contradictory at first, but it

is important to note that a decrease in neuronal excitability in a given brain region does not necessarily correlate with increased behavioural and functional inhibition. Indeed, Obeso and colleagues (2013) showed that repetitive transcranial magnetic stimulation (rTMS) over the pre-SMA increased inhibitory control in the stop-signal task by reducing pre-SMA excitability. Similarly, a study by Herz et al. (2014) reported performance improvements over impulsive response tendencies on the Simon task after impairing pre-SMA function with rTMS. While the neurophysiological mechanisms of tDCS are still to be definitely determined, it has been suggested that cathodal stimulation may improve behavioural performance by reducing sensitivity to neural noise (Antal et al., 2004). Here, perhaps cathodal stimulation of the SMFC modulated the level of inhibition in the motor system by increasing the signal-to-noise ratio. It has been shown that M1 receives input from the pre-SMA (Deiber, Honda, Ibanez, Sadato, & Hallett, 1999) and that decreased pre-SMA activity exerts an inhibitory influence on the motor cortex (Neubert et al., 2010). Given that M1 is associated with the initiation and execution of movement, decreasing pre-SMA excitability may have modulated M1 activity, which in turn results in increased proactive slowing across the entire response selection process.

The present findings are in line with the idea that the inhibitory control network in the brain can be triggered endogenously when a task confers an executive setting. Specifically, in a series of experiments, van Gaal and colleagues (van Gaal, Ridderinkhof, Scholte, & Lamme, 2010; van Gaal, Ridderinkhof, van den Wildenberg, & Lamme, 2009) have demonstrated that the inhibitory control network could be activated unconsciously by sub-threshold no-go primes. These no-go primes induced RT slowing and activated the pre-SMA and rIFG. A recent study by Chiu and Aron (Chiu & Aron, 2014) further extended this finding by showing that an overt inhibitory executive setting (i.e., inhibitory context that requires an inhibitory control setting) is necessary to observed this unconscious inhibition (but see Lin & Murray, 2015). To wit, RT slowing for strongly masked no-go prime trials did not occur when participants operated under a non-inhibitory context (i.e., outright stopping was not required). Our results are thus broadly consistent with this literature by showing that the SMFC is recruited for response selection operations when the inhibitory control network is activated by internally generated goal states.

In summary, we provided causal evidence for a role of SMFC in response selection, but only found evidence of this under conditions when occasional stopping is also required. Specifically, we found that stimulation of the SMFC did not modulate training effects when participants performed a single-task response selection task. However, when adding an inhibitory context to the response selection paradigm, we observed a polarity-

specific effect of stimulation, such that cathodal stimulation prolonged no-signal RTs relative to anodal and sham stimulation when no external stop-signal was presented. This context dependent stimulation effect on response selection processes confirms that response selection and response inhibition processes overlap at least partially in the SMFC. The findings further suggest that this inhibitory response selection control function is not just dependent on external stimuli but is also proactively driven by internal goal-states.

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Study 3: Dynamic, Continuous Multitasking Training Leads to Task-Specific Improvements but does not Transfer across Action Selection Tasks

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Abstract

The ability to perform multiple tasks concurrently is an ever-increasing requirement in our information-rich world. Despite this, multitasking typically compromises performance due to the processing limitations associated with cognitive control and decision-making. While intensive dual-task training is known to improve multitasking performance, only limited evidence suggests that training-related performance benefits can transfer to untrained tasks that share overlapping processes. In the real world, however, coordinating and selecting several responses within close temporal proximity will often occur in high interference environments. Over the last decade, there have been notable reports that training on video action games, that require dynamic multitasking in a demanding environment, can lead to transfer effects on aspects of cognition such as attention and working memory. Here we asked whether continuous and dynamic multitasking training extends benefits to tasks that are theoretically related to the trained tasks. To examine this issue, we asked a group of participants to train on a combined continuous visuomotor tracking task and a perceptual discrimination task for six sessions, while an active control group practiced the component tasks in isolation. A battery of tests measuring response selection, response inhibition, and spatial attention was administered before and immediately after training to investigate transfer. Multitasking training resulted in substantial, task-specific gains in dual-task ability, but there was no evidence that these benefits generalized to other action control tasks. The findings suggest that training on a combined visuomotor tracking and discrimination task results in task-specific benefits but provides no additional value for untrained action selection tasks.

The modern, information rich world demands that we often have to undertake multiple tasks concurrently. Despite this, the effective selection of task-relevant responses (i.e., decision-making/response selection) and the suppression of task-irrelevant information/responses (i.e., response inhibition) are often significantly compromised when humans attempt to execute multiple cognitive operations simultaneously. Multitasking ability can be assessed in a wide range of action selection paradigms that place strong demands on central information processing resources. For instance, in a classic dual-task paradigm (Dux, Ivanoff, Asplund, & Marois, 2006; Dux et al., 2009; Schumacher et al., 2001; Sigman & Dehaene, 2008) individuals perform two simple tasks simultaneously, relative to by themselves, whereas in the commonly used psychological refractory period (PRP) method (Pashler, 1994; Welford, 1952), participants perform speeded responses to two tasks/stimuli that occur in relatively close or far temporal proximity. While conditions differ across paradigms, a consistent finding is the observed dual-task cost – performance impairments in one or both tasks, as indexed by a decrease in accuracy and/or increase in reaction time (RT) when two tasks need to be performed simultaneously or close in time, relative to when the two tasks are performed far apart or in isolation.

Fortunately, evidence suggests that dual-task costs can be reduced with practice/training, with participants consistently displaying experience-related improvements on the task itself (Garner, Tombu, & Dux, 2014; Hazeltine, Teague, & Ivry, 2002; Liepelt, Strobach, Frensch, & Schubert, 2011; Schumacher et al., 2001; Strobach, Frensch, Soutschek, & Schubert, 2012; Van Selst, Ruthruff, & Johnston, 1999). Neuroimaging studies investigating the neural underpinnings associated with reduced multitasking costs have found that dual-task training decreases cortical activity in sub-regions of the dorsolateral prefrontal cortex, posterior lateral prefrontal cortex, basal ganglia and parietal cortex after training (Dux et al., 2009; Erickson et al., 2007; Garner & Dux, 2015), a network of areas that is frequently recruited in a wide range of tasks that require the executive control of action (Aron et al., 2007; Aron & Poldrack, 2006; Duncan, 2010; Miller & Cohen, 2001). Currently, the exact mechanisms that contribute to training-related behavioural and neural adaptation effects are not fully understood. However, a recent large-scale neuroimaging study by Garner and Dux (2015) suggests that training increases the separation of the neural representations of the constituent tasks, suggesting that more fine-tuned task representations contribute to a reduction in dual-task interference, which in turn may facilitate the coordination of two practiced tasks.

While dual-task interference can be reduced with training, the extent to which dual-task training generalizes to other non-trained multitasking measures, or secondary

measures of cognitive processes that are closely linked to multitasking ability, is still hotly debated. It has been hypothesized, generally, that the probability of transfer from one measure to another is increased when tasks draw on the same cognitive processes and overlapping neural substrates as the trained task (Kuwajima & Sawaguchi, 2010; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009; Thorell, Lindqvist, Bergman Nutley, Bohlin, & Klingberg, 2009). However, so far, the majority of dual-task studies show little evidence for significant transfer after dual-task practice (Garner, Matthews, Remington, & Dux, 2015; Liepelt et al., 2011; Owen et al., 2010; Ruthruff, Van Selst, Johnston, & Remington, 2006; Strobach, Liepelt, Pashler, Frensch, & Schubert, 2013), with only a few dual-task training laboratory based studies reporting positive training transfer gains (Liepelt et al., 2011; Lussier, Gagnon, & Bherer, 2012). Collectively, training-related enhancements to other tasks seem to predominantly occur if the untrained tasks share strong similarity with the trained task in terms of response modality (e.g., responding via keyboard press) or input modality (e.g., both tasks employ visual stimuli), timings with the trained task (Lussier et al., 2012), or overlap in terms of common or abstract rules (Garner, Lynch, & Dux, 2016). In contrast, training gains are disrupted when the practiced stimuli are presented in another modality (e.g., visual to auditory; Garner, Lynch, & Dux, 2016). These findings indicate that trained responses are not fully automatic and that the observed modality transfer effects may be due to an improved capacity-limited central response selection mechanism that integrates modality-specific information to a response.

While the observations described above suggest that training transfer effects are possible but rather limited, larger transfer gains have been shown when assessing the impact of video action game training on executive control. Action gaming typically requires the performance of several actions simultaneously, such as the continuous tracking of a moving target while monitoring and responding to game-related stimuli to achieve the required goals and sub-goals (Boot, Kramer, Simons, Fabiani, & Gratton, 2008). The continuous requirement in action games to constantly monitor and coordinate several tasks within close temporal proximity, heavily tax perception, attention and capacity-limited response selection processes. Indeed, such interventions have been shown in a number of studies to not only lead to training-related performance improvements on the trained task but have also generalized to other aspects of central executive control such as multitasking, attention, and working memory (but see Gaspar et al., 2014; Oei & Patterson, 2013). For example, in a highly prominent recent study, Anguera et al. (2013) observed task-specific multitasking enhancements but also gains across working memory and sustained attention after twelve x 1 hour sessions (over the course of four weeks) of dual-

task action video game training in a sample of older participants. Specifically, in this study, participants had to keep a moving car in the center of a winding road while simultaneously responding to a speeded shape discrimination task as quickly and accurately as possible (multitasking condition) or perform the component tasks in isolation (single task condition). As mentioned above, the results showed that multitasking ability improved after the two tasks had been trained in combination (multitasking group) relative to when the two tasks had been trained in isolation (single task group) or not at all (no contact control group). Crucially, the study found significant post-training gains on measures of working memory and sustained attention – two cognitive operations that are thought to reflect central executive control capabilities (Engle, Tuholski, Laughlin, & Conway, 1999).

So far, an overview of the action control training literature indicates that the engagement in tasks that require online, dynamic decision-making within a demanding environment leads to the best chance of positive transfer to other tasks that recruit similar neural networks and are theoretically related to the trained tasks. However, there are a number of key factors worth considering, before one can definitively conclude that training transfer is possible following such training. As several recent reviews of cognitive training discuss (e.g., Melby-Lervåg & Hulme, 2013; Mishra, Anguera, & Gazzaley, 2016; Noack, Lovden, & Schmiedek, 2014; Shipstead, Redick, & Engle, 2012), a gold standard cognitive intervention should 1) employ outcome measures with a clear targeted theoretical construct; 2) minimize potential placebo effects and potential treatment confounds by including an active control group that ensures equal task engagement and enjoyment; 3) randomly allocate participants to treatment or control to validate trained and transfer gains; and 4) transfer tasks should be restricted to tasks that are related to the trained construct.

Motivated by the inconsistent findings from the dual-task/action gaming and transfer literature and guided by the latest cognitive training principles, our study had two aims. We asked whether task-specific dual-task costs can be attenuated with training when participants are required to engage in rapid decision-making in a high interference environment, and if so, whether these benefits extend to tasks that are theoretically related to the trained tasks. To address these questions, we created a dynamic paradigm, which employs a continuous, dynamic visuomotor tracking task in conjunction with a perceptual discrimination task to tax action selection processes in a context that is often found in real world situations. Second, to determine whether training-induced benefits extend to other action control tasks, participants completed a battery of psychological tasks at pre- and post-training. In a previous factor-analytic study (Bender, Filmer, Garner, Naughtin, & Dux, 2016), we showed that the construct of response selection could be measured via tasks

such as the PRP, single- and dual response selection, the Stroop and to a lesser degree the Attentional Blink (AB). Hence, to examine the transferability of any training-induced multitasking benefits to other response selection measures, participants completed the PRP, a six alternative forced choice (AFC) single response selection task, the Stroop task and the AB. Secondary processes of cognitive operations linked with response selection, including tests of response inhibition (Go-Nogo task) and measures of selective attention (Flanker task) were also included.

Methods

Participants attended ten sessions, one per day with two rest days included. The first, second, ninth, and tenth sessions were the pre- and post-training sessions, while the remaining six sessions were training session. Performance was compared pre- and post-training between a multitasking training group who had trained on a perceptual discrimination task while performing a simultaneous visuomotor tracking task, and an active control group (single-task training group) who had completed the component tasks in isolation.

Participants

Minimum sample sizes were calculated to achieve 80% power (f = .30) to detect a significant 2 (training group) x 2 (session) interaction if a true effect was present. Power calculations revealed that a minimum sample size of 14 participants per group would be required. We based our combined sample size on this calculation and the sample size of our previous training studies (Garner et al., 2016; Garner et al., 2014).

Forty-seven adults aged between 18 and 40 years (40 females, mean age = 22) provided written informed consent to take part in this study, which was approved by The University of Queensland's Research Ethics Committee. All participants were right-handed, had normal or corrected to normal vision, with no history of neurological, vascular or psychiatric disorder and were not taking any hypertension or psychotropic medications. All participants were recruited through The University of Queensland's paid research participation pool and received AUD10 per hour for participation and were further able to earn bonus dollars for performance. The analyses reported here stem from 39 participants as one participant was excluded for not completing all three stages of the study and an additional seven participants were excluded for poor performance (more than three standard deviations above the RT or below the accuracy mean) in one or more of the six cognitive tasks during pre-training. These exclusion procedures were determined a priori.

Materials and Apparatus

The experiment was run on an Apple Mac Mini running Matlab (The MathWorks, Natvick, MA) and the Psychophysics toolbox extension (Brainard, 1997) was employed to control the displayed of stimuli on a 21" CRT monitor (100 Hz refresh rate) and for data collection. For all the tasks, responses were registered through a standard Apple USB keyboard (Neath, Earle, Hallett, & Surprenant, 2011) and participants viewed the monitor from an approximate distance of 57 cm.

Procedure

Pre-training sessions. The paradigm was divided into three phases as illustrated in Figure 1. Participants were randomized to either the multitasking training group that trained on a continuous visuomotor tracking and an intermittent shape discrimination task simultaneously (N = 19) or an active control group (single-task training group) that trained on both component tasks in isolation (N = 20). A no-contact control group was not included, as these groups often differ significantly in terms of motivation and expectancy effects (Shipstead et al., 2012). Importantly, age ($t(37) = .35$, $p = .73$) and gender break down ($t(37) = .41$, $p = .67$) did not differ between the groups. In order to avoid expectancy differences across the groups, we told each participant that the training paradigm was created to investigate the effects that training has on cognitive control functions.

In phase 1, participants completed two pre-training sessions, administered one day apart from each other, lasting approximately 1.5 - 2 hours each. On day 1, participants were administered a battery of seven tasks (Bender et al., 2016) in order to test the cognitive impact of training to other closely related action control processes. An index of multitasking was provided by the PRP, whereas other response selection, inhibitory control and selective attention measures were provided by the Stroop task, six AFC single response selection task, AB task, Go-Nogo and Flanker task[4] (please refer to the below Transfer Task section for a more comprehensive description of each task). All tasks were completed in randomized order.

In the second pre-training session, participants first took part in an adaptive staircase procedure to determine the individual difficulty levels in the visuomotor tracking (nine 60 second trials) and shape discrimination task (nine 120 second trials), so that each participant performed the two tasks at ~ 80% accuracy (Anguera et al., 2013). These difficulty levels were then continuously applied during the training sessions and were further utilized to establish the parameters of the two tasks in the multitasking condition, so

[4] Participants also completed a stop-signal task. However, this data was discarded due to a technical issue.

that each participant performed the multitask condition at their own individual difficulty level. Following baseline thresholding evaluation, participants ran through five 3-mins trials of each condition (i.e., single shape discrimination task condition, single visuomotor tracking task condition, and a concurrent shape discrimination and visuomotor tracking multitask condition) to assess multitasking costs at baseline. At the end of each trial, the overall percentage of time spent within the moving target disc (single visuomotor tracking task and dual-task condition) and the mean RT and proportion of correct responses to all shapes (single detection and dual-task condition) were displayed.

Training sessions. In phase 2, participants trained for three consecutive days, followed by two days of rest and another three consecutive days of training. Each session included twelve 3-minute trials (72 trials in total across the six sessions), in which participants in the multitasking group exclusively performed the visuomotor tracking and shape discrimination task concurrently, while participants in the single-task training group divided their time equally between the single shape discrimination task (six x 3-minute trials) and the single viusomotor tracking task (six x 3-minute trials), with task order randomized across participants. After each trial, participants in both training groups received performance feedback. The performance feedback in the multitasking group consisted of the participants' mean visuomotor tracking accuracy and shape discrimination accuracy, whereas performance feedback in the single-task group was trial-type dependent. To maximize motivation and in line with previous training paradigms (Dux et al., 2009; Garner et al., 2014), participants in both groups were awarded bonus points. To encourage equal task engagement of each component task, participants in the multitasking training group received one bonus point if performance on both component tasks was over 70%, while participants in the single-task training group received one bonus point if performance was over 85% in the single visuomotor tracking- or single shape discrimination accuracy. In contrast, if accuracy was below the designated values, participants in both groups lost a bonus point.

Post-training phase. The third phase started one day after completion of training. On day 1, participants ran through both single- and multitasking trials (same procedure as the testing phase in phase 1, session 2) to assess the impact of single- or multitask training on multitasking performance. On the final day, participants completed the same seven cognitive tasks as on day 1 (phase 1) in order to measure transfer to other action control

tasks. All ten sessions took place at approximately the same time of day for each participant.

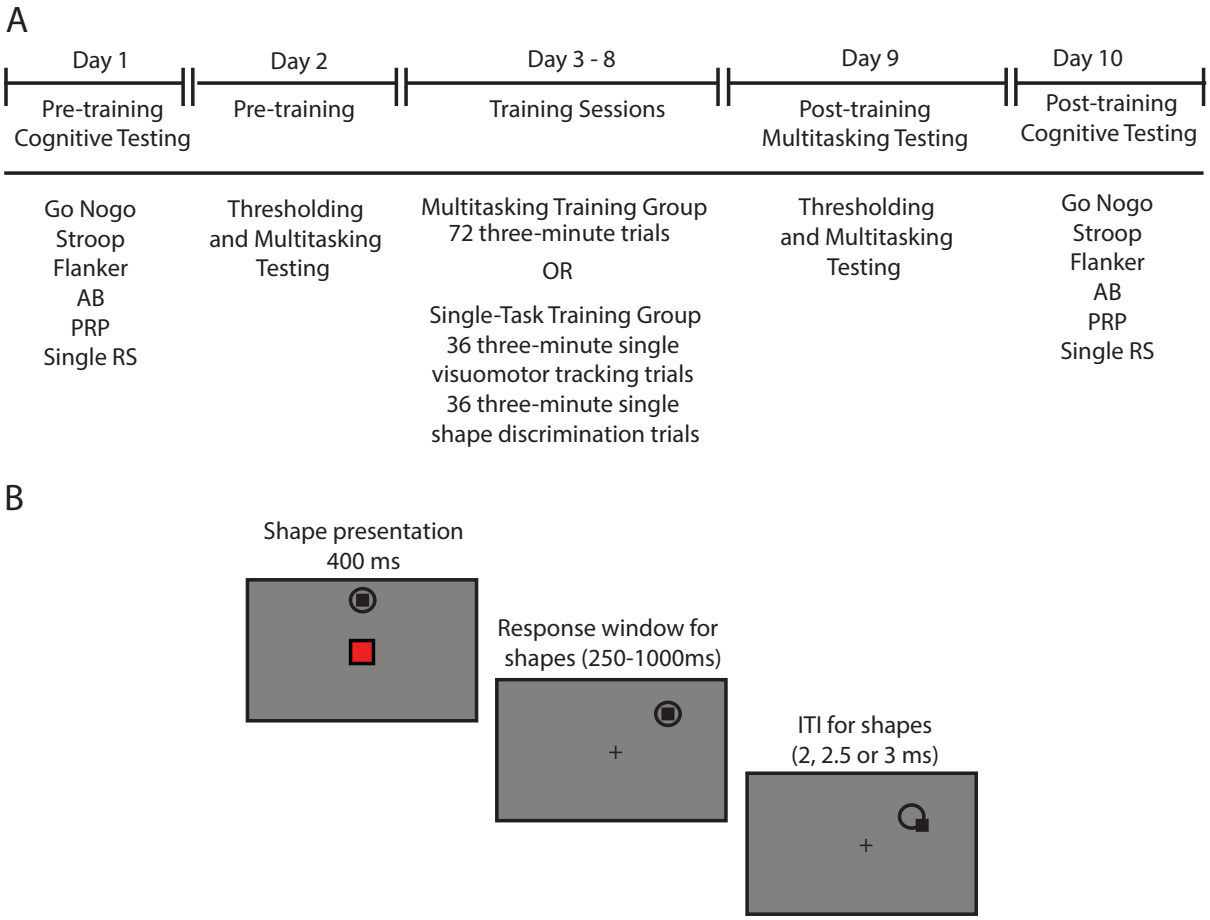

Figure 1. Experiment design overview. (A) Outline of the experimental paradigm. Participants first took part in a pre-training phase in which they completed a battery of cognitive tasks (Day 1), thresholding and multitasking testing (Day 2). Participants then trained on either a combined visuomotor tracking and shape discrimination task (multitasking group) or on both component tasks in isolation (single task group) over six days. Two post-training sessions were conducted, in which participants again undertook the multitasking tasks (Day 9) and the battery of cognitive tasks (Day 10). (B) Trial outline for the visuospatial tracking and shape discrimination task.

Tasks and Stimuli

Trained Tasks. We followed the general techniques of Anguera and colleagues (Anguera et al., 2013) to assess multitasking performance in a dual visuomotor tracking and shape discrimination task. To ensure equal visual stimulation between the multitasking and

single-task conditions, shapes were presented in the centre of the screen in the single visuomotor tracking task but participants were instructed to ignore these discrimination stimuli. Similarly, a moving target disc was presented during the shape discrimination task, with participants asked to ignore the moving disc.

Visuomotor tracking task. During each tracking epoch, participants had to continuously pursue a visually presented moving black target disk (0.50°) with the mouse so that the black cursor (0.10°) remained as close as possible to the centre of the moving target, while ignoring the presentation of shapes in the centre of the screen (see Figure 1). At trial onset the cursor was positioned within the centre of the target disc, which was located at the top centre of the screen. The participants' right hand held the mouse through which they could control the motions of the cursor and the left hand was used to initiate the start of each trial by pressing the spacebar on the keyboard. The trajectory of the target was generated by the visible target bouncing off the edge of the display or off two invisible discs in a Newtonian direction. Movements in the x- and y-axis were calculated independently at a screen resolution of 1024 by 768 pixels. A one centimetre protective radius ensured that the tracking target did not overlap with the centrally presented shapes.

Visual shape discrimination task. Each trial began with an instruction screen that displayed the coloured target shape for the upcoming trial and further reminded participants to respond as quickly as possible by pressing the space bar on a keyboard when the target stimulus matched the one presented on the screen, while ignoring the appearance of distractor shapes. For each trial, a new target was randomly drawn from twelve possible coloured (red, green, blue, or yellow) shapes (square, hexagon, or star), with the remaining non-target shapes serving as distractors. Target presentation occurred at 50% probability with shapes randomly presented for 400 ms in the centre of the screen every 2, 2.5 or 3 seconds.

Dual task. In the dual-task condition, participants were required to perform the shape discrimination task and visuomotor tracking task simultaneously.

Thresholding procedure

To ascertain that multitasking deficits are not due to individual differences in task skills, participants first underwent an adaptive thresholding procedure (pre-training phase, session 2) to determine an individual difficulty level that would result in ~80 accuracy in each single-task condition. To determine the best RT window and tracking speed to keep

accuracy at ~80%, a standard regression technique[5] over the visuomotor tracking and discrimination thresholding trials was calculated separately at the end of the thresholding blocks and the resultant levels were then utilized for the remainder of the experiment.

During both visuomotor tracking and shape discrimination thresholding, the difficulty of the task changed if accuracy was above 82.5% or below 77.5% at the end of the trial. In order to achieve ~ 80% accuracy, an adaptive algorithm calculated proportional level changes that were dependent on how close participants performed above or below the 80% criterion, with each 1.75% increment away from the criterion resulting in a level change. Both staircases comprised of 49 levels.

All participants started with nine x 60 seconds visuomotor tracking trials. For the visuomotor tracking task the different levels represented the minimum (.0100 dps, level 1) and maximum (.0112, level 49) speeds at which the target was moving across the screen. Changes in target speed levels corresponded to 0.0040 increments if the target speed was between 0.0100 (level 1) and 0.0820 (level 19), whereas 0.0010 increments were employed for target speeds between 0.0820 (level 19) and 0.1110 (level 49), with all participants starting with an initial tracking speed of 0.920 (level 29). Thus, if a tracking speed of 0.920 resulted in a visuomotor tracking accuracy of 86%, then tracking speed would increase by .002 dps (86 % - 80%)/1.75) in the subsequent trial, whereas a 74% performance would result in a .003 decrease in target speed. Continuous performance feedback was provided in the thresholding phase only and consisted of the cursor turning red as soon as the cursor moved outside the radius of the moving target disk.

The visuomotor tracking threshold procedure was followed by nine x 120 seconds trials of the visual shape discrimination task. For the shape discrimination task, the same staircase algorithm was employed to determine the RT window in which the proportion of correct responses to all shapes (i.e., correctly responding to the target shape and correctly inhibiting a response to all distractor shapes) converged to the ~ 80% criterion. Each level signified the total amount of time that a participant had to respond to the presented target shape. The RT windows ranged from 1000 ms (level 1) to 250 ms (level 49) and was initially set at 450 ms RT window (level 29). If performance on a given trial was greater than the criterion, a shorter RT window (shortest window = 250 ms, level 49) was calculated, whereas performance below the criterion led to a longer RT window (longest

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[5] We employed standard regression techniques (ordinary least squares) to determine the slope and intercept between the thresholding step level and accuracy [slope,intercept]= regression(trial_accuracy,thresholding_step).
Once the linear function was identified, the thresholding step that corresponds to the desired 80% accuracy was calculated [test_threshold_step] = round (slope*median_accuracy_score+intercept).

window = 1000 ms) for the subsequent trial. Specifically, RT window changes between 1000 – 550 ms resulted in 25 ms level changes, whereas changes in RT windows between 550 – 250 ms corresponded to 10 ms level changes. These parameters were chosen following extensive pilot testing.

A centrally presented fixation square provided performance feedback during the thresholding session. The fixation square turned green for 50 ms if participants responded correctly to the target shape within the allocated response-window or when a response to a non-target distractor shape was successfully suppressed (see thresholding procedure). In contrast, if participants failed to respond to the target shape within the allocated response-window or responded incorrectly to a non-target shape, the fixation square would turn red for 50 ms.

Transfer tasks

Psychological refractory period. In this task (see Figure 2), participants first learned the stimulus-response mappings of two different sensorimotor tasks (20 trials per block). In the first training block, participants learned the stimulus response mappings of a visual discrimination task (Task 1), which required participants to respond to one of four different symbols (%, @, &, or #) via key press. In the second training block, participants followed the same task structure as in Task 1, except that the visual discrimination task changed to an auditory discrimination task (Task 2). Here, participants responded via key press to one of four different complex tones. The final practice block was identical to the trials in the experimental phase. Each trial began with the presentation of a Task 1 (T1) symbol at the center of the screen and after either a short (200 ms) or long (1000 ms) stimulus onset asynchrony (SOA) the second task (T2) auditory target was presented. Stimuli remained on-screen for 200 ms and participants were asked to respond as fast as they could to the two tasks while maintaining accuracy and without grouping their responses. Next, participants started the experimental phase, which consisted of four testing blocks, each containing 40 trials equally divided between the two SOA conditions. The dependent measure was the PRP effect. The effect was computed by subtracting the obtained RT of the second task in the 1000 ms condition from the RT in the 200 ms condition. Better performance was indicated by lower differences scores.

Single response selection task. In this task participants were required to discriminate between six different coloured fractals via key press. Each stimulus was mapped to a specific response key and hand (A, S or D for left hand responses and J, K or L for right hand responses), with the mapping of hand to task counterbalanced across

participants. In each trial, the central fixation cross was followed by one of the fractal stimuli for 200 ms. Participants were instructed to respond as quickly and as accurately as possible via key press to the stimulus. Prior to the experimental phase, participants first completed 36 practice trials and then moved on to the experimental phase (four blocks of 36 trials). The key dependent variable was the reaction time, with lower RTs indicating better performance.

Stroop task. In this classic Stroop task, participants were instructed to report the corresponding ink colour of four coloured ("blue", "red", "yellow", "green") and four non-coloured ("saucer", "fork", "cup", "spoon",) words via key press. Each trial began with the presentation of the fixation cross, which was replaced by the presentation of a word target (500 ms). Three different types of trials were conducted: 1) in congruent trials the printed colour word matched the ink colour (e.g., "red" printed in red); 2) in incongruent trials the printed colour word and ink colour mismatched (e.g., "red" printed in blue ink colour); and 3) in neutral trials a non-colour word was printed in any of the four colours (e.g., "cup" printed in yellow ink colour). The word target was equally likely to either be congruent, incongruent, or neutral, with the order of trial types randomised. Prior to the experimental phase (four blocks of 36 trials), participants completed 24 response-mapping practice trials. The key dependent measure was the "Stroop congruency effect". This effect was calculated by computing the mean RT difference between congruent and incongruent trials. Lower difference scores represent better performance.

Attentional blink. Each trial consisted of a rapid serial visual presentation (RSVP) stream comprising of two targets (letters of the alphabet, excluding I, L, O, Q, U, V, X) and eight digits (ranging from 2-9) serving as distractors. Participants were instructed to report the identity of the two target letters at the conclusion of the RSVP stream. There was no speeded response pressure and participants were told to guess if unsure. Each stimulus was presented for 100 ms. Target 1 (T1) was presented at serial position 3 with Target 2 (T2) following T1 after either 200 ms (lag 2), 300 ms (lag 3), 500 ms (lag 5), or 700 ms (lag 7). After 24 initial practice trials, participants performed four test blocks (24 trials per block). To calculate the AB magnitude (dependent measure), we subtracted the mean of lags 2 and 3 T2|T1 accuracy from the mean of lags 5 and 7. A smaller magnitude of the AB deficit represents better performance.

Go-nogo task. In the go-nogo task, participants were instructed to discriminate between two white, abstract 3D shapes. One shape represented the go stimulus and the other shape represented the no-go stimulus. The participants' task was to press the "G" key on a computer keyboard as soon as the go stimulus appeared in the center of the

screen, but to withhold the response if the no-go stimulus appeared (25% of trials). Go and no-go stimuli were counterbalanced across participants with speed and accuracy equally emphasized. Each trial began with a fixation cross (200 ms), followed by one of the two stimuli (200 ms) and an 1800 ms response window. After completing 24 familiarization trials, participants completed four test blocks (36 trials per block). The key dependent measure of interest was the proportion of commission errors on no-go trials (i.e., failure to stop a response). Fewer commission errors indicated better response inhibition.

Flanker task. The participants' task was to indicate in which direction a central arrow target (> or <), flanked on both sides by two arrows, was pointing. Participants made their responses by pressing the ">" key and the "<" key for rightward-pointing arrows targets and leftward-pointing arrows, respectively. On congruent trials, the flankers were two arrows pointing in the same direction as the target arrow on each side (e.g., >>>>>). On incongruent trials, the flankers were arrows pointing in the opposite direction as the target arrow (e.g., >><>>). Finally, on neutral trials the target arrow was flanked by horizontal lines (e.g., --<--). After the presentation of a fixation cross, the five-arrow array appeared and remained on screen for 200 ms. Participants received 24 practice trials, followed by four experimental blocks (36 trials per block). There were an equal number of trials per condition and the order of trial types was randomly intermixed. The dependent measure was the "flanker congruency effect". This effect was computed by calculating the mean RT difference between the congruent and incongruent trials. Lower RT difference scores indicated better performance.

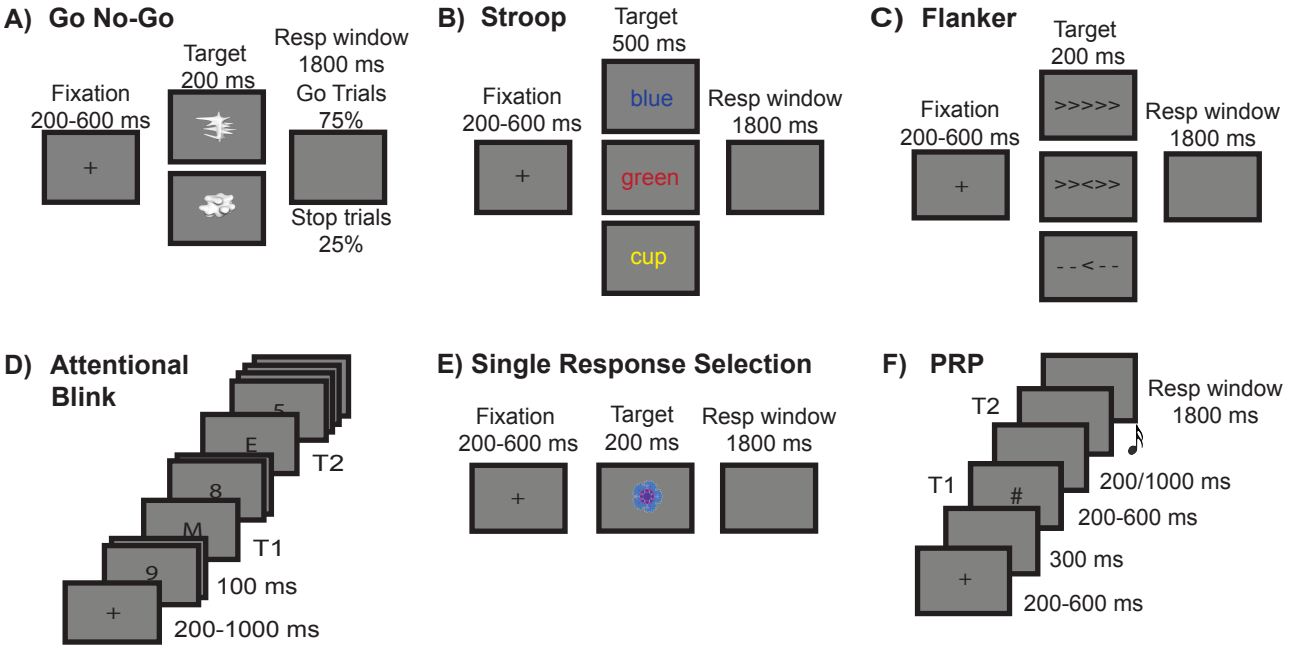

Figure 2. Schematic representation of the transfer tasks.

Data Analysis

In order to evaluate the strength to which the evidence points towards or against the null hypothesis, we employed Bayesian methods in addition to traditional null hypothesis significance testing (Rouder, Morey, Verhagen, Swagman, & Wagenmakers, 2016). This was important for the present study since it was likely that at least some of the tasks would show no effect of training. Thus, we needed to be able to assess evidence favoring the null.

Cognitive tasks

To establish whether the observed performance during the pre-training session showed the standard effects for the Go-Nogo (Go RTs, Nogo commission errors), Stroop (Stroop Congruency Effect), Flanker (Flanker Congruency Effect), Single response selection (RS), PRP (PRP effect), and AB (AB magnitude) tasks, we first evaluated performance (accuracy and/or RTs) using mixed ANOVAs with the relevant key measures of interest at baseline (Session 1) as a within-subject factor and group (single, multitasking) as between-subject factor. Training-related transfer effects were quantified as a reduction in the standard effects between pre- and post-training sessions.

In order to quantify the degree to which the evidence supports the null hypothesis (i.e., training-related improvements transfer to other action control tasks) or the alternative (training-related improvements do not transfer to other action control tasks), Bayesian mixed-measures ANOVAs were conducted in JASP (Love, Selker, Marsman, Jamil, Dropmann, Verhagen et al., 2015) for each transfer task. Bayes Factors (BFs) express the probability that the null or the alternative hypotheses are true, given some data. Inverse Bayes Factors (BF_{10}) were used to denote that prior odds should be updated by a factor of 10 in favour of the alternative hypothesis (multitasking training has an effect) compared to the null (multitasking training has no effect). To compare the posterior probability of a null model (a model without a session by group interaction) against a model including the interaction, we used the fact that Bayes factors are transitive. Thus, by transitivity we divided the model with main effects (BF_{10}) by the model that adds the group interaction (BF_{20}), with the resultant BF_{12} indicating the evidence in favour of the main effects model. Overall, BF of 1-3 signifies weak evidence, BF 3-10 indicates substantial support, and BF > 10 correspond to strong evidence (Kass & Raftery, 1995).

Multitasking performance

Multitasking cost was estimated as the difference between the dual task trials and single-task trials ([dual task detection trials – single task detection trials) + (dual task tracking trials – single task tracking trials)], with smaller scores indicating better multitasking performance (i.e., less interference when engaging in the two tasks simultaneously). To examine differences at baseline, performance (multitasking cost, perceptual discrimination performance, and tracking performance) across the two groups (multitasking, single) was examined using independent t-tests. Multitasking cost differences between groups were evaluated with a mixed design ANOVA (NHST and Bayesian) with session (pre, post) as within-subject factor and group (single, dual) as between-subject factor.

Training data

Mixed-measures 6 (session) x 2 group (single, multitasking) ANOVAs (traditional NHST and Bayesian) were conducted for each training task (perceptual discrimination accuracy and visuomotor tracking accuracy) to investigate whether there were any group differences in overall performance gains.

Results

Multitasking cost

To investigate the effects of training on multitasking performance, we first explored performance before training on the sample as a whole (Table 1). The overall mean accuracy for the single discrimination task and single tracking task was in 83% and 80% respectively, demonstrating that the adaptive thresholding procedure successfully determined a detection and tracking level of ~80% accuracy on each component task, with no significant baseline differences between the two training groups on either discrimination accuracy ($t(37) = -1.86$, $p = .07$) or tracking accuracy ($t(37) = 0.84$, $p = .40$). At pre-training, simultaneous performance of the shape discrimination task and the visuospatial tracking task resulted in large multitasking costs (main effect of single-task vs. multitask: mean multitasking cost = 15.58%; $F(1,37) = 202.77$, $p = <.001$, $\eta^2_P = .846$). Importantly, as seen in Table 2, there were no multitasking cost baseline differences between the two training groups ($t(37) = -0.11$, $p = .91$).

To determine the effect of multitask and single-task training on multitasking performance, a mixed-design session (pre-training, post-training) x group (multitasking, single) ANOVA revealed a main effect of session ($F(1,37) = 4.46$, $p = .042$, $\eta^2_P = .108$),

indicating that multitasking performance improved significantly from pre-training to post-training. Critically, as seen in Figure 3, the improved multitasking performance was specific to the multitasking training group, as reflected in the significant session x group interaction ($F(1,37) = 8.42$, $p = .006$, $\eta^2_P = .185$), even though both groups showed significant pre- to post-training improvements in their respective training-related tasks (Table 2). Bayesian ANOVAs revealed that a model in which the group interaction was added to the model explained the data better ($BF_{12} = 0.88$ in favour of the main effects model) than a main effects model (i.e., session and group entered separately).

These results replicate previous findings (Anguera et al., 2013; Dux et al., 2009; Garner et al., 2014; Hazeltine et al., 2002; Schumacher et al., 2001; Strobach, Frensch, Soutschek, et al., 2012; Van Selst et al., 1999), and demonstrate that multitasking training resulted in a significant decrease in multitasking cost relative to the control group, who trained on the two tasks in isolation.

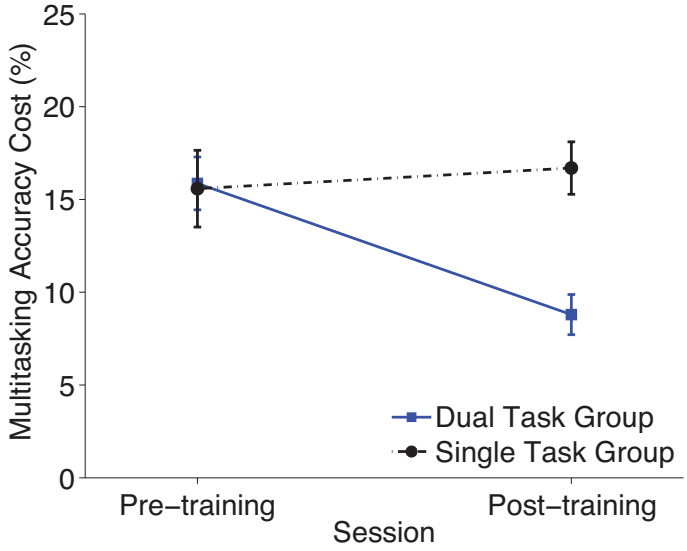

Figure 3. Multitasking costs ([dual task detection trials – single task detection trials) + (dual task tracking trials – single task tracking trials)], pre- and post-training as a function of group (Dual Task, Single Task) showed a session x group interaction ($F(1,37) = 8.42$, $p = .01$, $\eta^2_P = .185$), indicating that gaining trains were specific to the multitasking training group. Multitasking cost error bars represent SEM.

Table 1. Summary data for the training tasks collapsed across groups. The table shows the mean standard deviation (SD) and mean, and training-related changes for the overall multitasking cost (%), dual tracking cost (%), dual discrimination cost (%), dual discrimination reaction time (RT) cost (ms), single tracking accuracy (%), dual tracking accuracy (%), single discrimination accuracy (%), dual discrimination accuracy (%), single discrimination RT (ms), and dual discrimination RT (ms).

Bold text indicates significant effect at $p < .05$ level.

	Pre-training	Post-training	Pre-to Post		
	M (SD)	*M (SD)*	*F*	*p*	*Bayesian ANOVA* BF_{10}
Overall multitasking cost	15.58 (7.81)	12.84 (6.83)	4.46	**.04**	1.25
Dual tracking cost	-0.46 (4.57)	-0.10 (2.07)	0.24	.63	0.26
Dual discrimination accuracy cost	16.18 (7.10)	12.95 (6.44)	7.26	**.01**	2.58
Dual discrimination RT cost	12.83 (20.11)	16.45 (10.78)	1.23	.27	0.43
Single tracking accuracy (%)	80.20 (3.62)	85.76 (3.16)	67.61	**<.001**	1.54
Dual tracking accuracy (%)	80.65 (5.29)	85.86 (2.66)	37.63	**<.001**	448345.66
Single discrimination accuracy (%)	83.25 (6.36)	87.79 (6.60)	13.45	**.01**	57.86
Dual discrimination accuracy (%)	67.07 (8.29)	74.84 (8.38)	45.21	**<.001**	65672.91
Single discrimination RT (ms)	326.29 (32.12)	320.88 (28.02)	7.87	**.01**	5.63
Dual discrimination RT (ms)	339.13 (40.76)	337.34 (34.42)	0.28	.60	0.26

Table 2. Summary data for the training tasks by group. The table shows the mean standard deviation (SD) and mean overall multitasking cost (%), dual tracking cost (%), dual discrimination cost (dual disrim cost, %), dual discrimination reaction time cost (dual discrim RT cost, ms), single tracking accuracy (%), dual tracking accuracy (%), single discrimination accuracy (single discrim accuracy, %), dual discrimination accuracy (dual discrim accuracy, %), single discrimination RT (single discrim RT, ms), and dual discrimination RT (dual discrim RT, ms). **Bold** text indicates significant effect at $p < .05$ level.

	Multitasking Group		**Single Task Group**		Group by Session					
	Pre-Training	Post-Training	Pre-Training	Post-Training	Baseline Group Comparisons					
	M (SD)	*M (SD)*	*M (SD)*	*M (SD)*	*t*	*p*	*F*	*p*	$\eta 2P$	*Bayesian ANOVA* BF_{10}
Overall multitasking cost	15.86 (6.21)	8.79 (4.72)	15.58 (9.25)	16.69 (6.33)	-0.11	.91	8.42	**.01**	.185	0.88
Dual tracking cost	-1.48 (1.74)	-0.45 (1.65)	0.51 (6.08)	0.22 (2.41)	1.40	.18	0.77	.39	.020	23.55
Dual discrim cost	17.34 (6.23)	9.24 (4.49)	15.07 (7.84)	16.47 (6.09)	-1.00	.32	14.62	**<.001**	.283	0.09
Dual discrim RT cost	15.81 (21.2)	16.04 (9.68)	10.00 (19.09)	16.84 (11.9)	-0.90	.38	1.08	.31	.028	22.92

Single tracking accuracy (%)	80.70 (4.39)	85.93 (2.77)	79.72 (2.73)	85.60 (3.56)	-0.83	.41	2.35	.63	.006	33.67
Dual tracking accuracy (%)	82.18 (3.89)	86.37 (2.93)	79.21 (6.09)	85.38 (2.34)	-1.82	.08	1.36	.25	.036	17.97
Single discrim accuracy (%)	85.13 (6.51)	87.53 (6.54)	81.46 (5.82)	88.04 (6.82)	-1.86	.07	2.92	.10	.073	9.81
Dual discrim accuracy (%)	67.79 (9.50)	78.29 (7.74)	66.39 (7.13)	71.57 (7.79)	-0.52	.61	5.20	**.03**	.123	4.58
Single discrim RT (ms)	323.71 (29.4)	318.66 (26.88)	328.75 (35.05)	322.99 (29.6)	0.49	.63	0.03	.85	.001	32.06
Dual discrim RT (ms)	339.52 (39.30)	334.71 (31.80)	338.75 (44.05)	339.83 (37.4)	-0.06	.95	0.71	.41	.019	24.17

Training data

During the training phase, participants in the multitasking group performed the shape discrimination task and visuomotor tracking task concurrently (72 three-minute trials over six sessions), while the single task training group spent their time equally on the single visuomotor tracking task (36 three-minute trials over six sessions) and shape discrimination task (36 three-minute trials over six sessions).

In order to assess if training was equally enjoyable for the multitasking and single-task group, participants rated their training experience on a scale from 1 (minimally) to 10 (maximally) at the end of the final session. Crucially, there was no significant difference between the multitasking group (M = 8.26) and the single-task group (M = 7.45; $t(37)$ = 1.70, p = .10; BF_{10} = 0.96).

To investigate whether there were any group differences in overall performance gains across the six training sessions, we conducted a series of mixed-design ANOVAs. A 6 (session) x 2 group (single vs. multitasking training) ANOVA for discrimination accuracy revealed a significant main effect of session ($F(5,185)$ = 3.64, p = .004, , η^2_P = .090), indicating that overall, performance improved across successive training sessions. Given the relatively easy nature of the task, the single-task training group reached asymptote after the first training session and performed the shape discrimination task at ceiling across the remaining sessions (Figure 4). The resultant significant interaction between session x group revealed that the increase in accuracy was significantly higher for the multitasking training group (mean change = 5.56%) than for the single-task training group (mean change = 0.02%, $F(5,185)$ = 3.24, p = .008, η^2_P = .081). Bayesian ANOVAs confirmed this pattern of results and weakly favoured the model that included a session by group interaction (BF_{12} = 2.25 in favour of the main effects model).

Analyses of tracking accuracy revealed a main effect of session ($F(5,185) = 2,59$, $p = .027$, $\eta^2_P = .065$), such that overall tracking accuracy significantly increased from Session 1 ($M = 85\%$) to Session 6 ($M = 87\%$), and did not differ between groups ($F(5,185) = .98$, $p = .434$, $\eta^2_P = .026$). Bayesian ANOVAs revealed no evidence for group differences ($BF_{12} = 89.58$ in favour of the main effects model).

As seen in Figure 4B, there was an observed drop in mean accuracy and increase in SEM for Session 4 (Single Task Group). Further inspection of the data revealed an outlier (one participant's mean tracking accuracy dropped to 58%). However, re-running the analysis without this participant did not change the pattern of results, again revealing a significant main effect of session ($F(5,185) = 3.34$, $p = .01$, $\eta^2_P = .081$) that did not differ between groups ($F(5,185) = 1.79$, $p = .12$, $\eta^2_P = .043$). The results therefore indicate similar visuomotor tracking performance across the six sessions for both training groups.

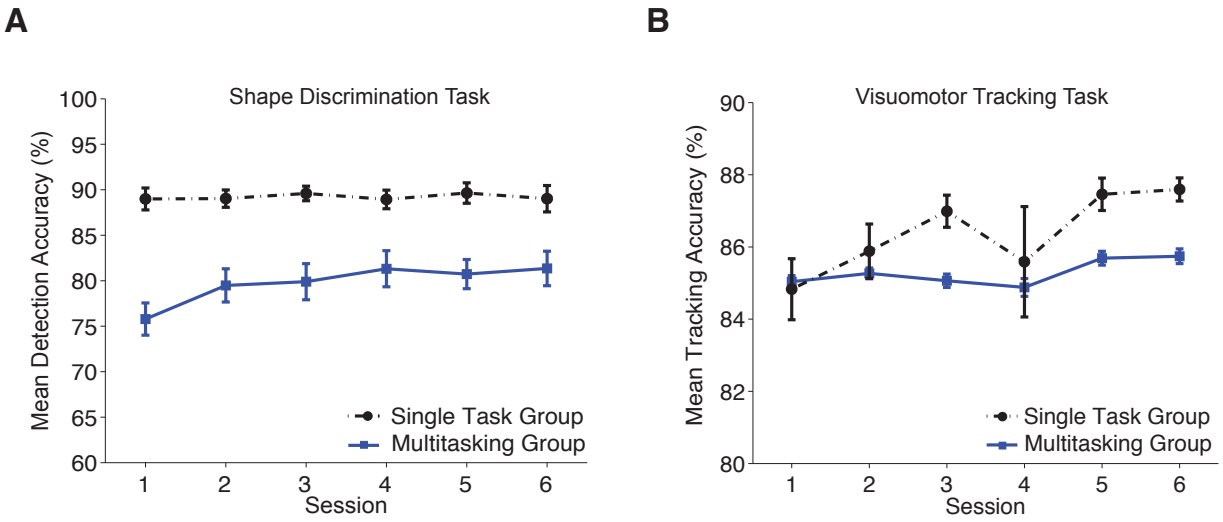

Figure 4. Training data by group (Multitasking, Single Task) across the six training sessions. (A) shows the mean visuomotor tracking accuracy and (B) shows the mean shape discrimination accuracy (%). Error bars represent SEM.

Cognitive tasks

As shown in Table 3, standard effects were observed in all six tasks, with no significant baseline differences between the two training groups (all *p*s > .21). To explore the benefits of multitask and single-task training on other action control measures, the sample was first assessed as a whole (Table 4). Significant main effects of training on response selection and response inhibition tasks were only observed for the single response selection task and the Go-Nogo task (all ps < .01).

To investigate the effect of group membership on transfer (Table 3), mixed-measure ANOVAs examining session (pre-training, post-training) x group (single vs. multitasking training) showed no significant training-related differences between groups on all outcome measures ($p > .15$). Bayesian ANOVAs confirmed this pattern of effects for all outcome measures, such that main effects models, in which session and group were entered separately, were preferred to session x group models (BF_{12} ranging from 13.76 – 31.83 in favour of the main effects model). In summary, these analyses provide strong evidence that the training-related benefits generated from our protocol do not transfer to any of the other action control measures employed.

Table 3. Summary data for the transfer tasks by group. The table shows the mean standard deviation (SD) and mean single response selection reaction times (RTs, ms), baseline group comparisons and changes in task performance for each transfer task as a function of group (Multitasking Group and Single Task Group): Attentional Blink magnitude (AB mag), Psychological Refractory Period magnitude (PRP mag), Stroop effect (ms), Flanker effect (ms), Go Nogo Commission (Nogo com.) error (%) and Go RTs (ms).

	Multitasking Group		Single Task Group							
	Pre-training	Post-training	Pre-training	Post-training	Baseline Group Comparisons		Group by Session			
	M(SD)	*M (SD)*	*M (SD)*	*M (SD)*	*t*	*p*	*F*	*p*	*η2P*	*Bayesian ANOVA BF_{12}*
Action Selection Tasks										
Single RS Task (RT)	643.39 (88.28)	586.74 (72.57)	619.73 (90.71)	582.41 (90.21)	-0.83	.41	1.62	.21	.042	16.99
AB mag	22.59 (15.03)	17.87 (14.95)	21.46 (13.25)	22.50 (13.71)	-0.25	.81	1.18	.29	.031	20.0
PRP mag	213.18 (97.87)	216.76 (127.47)	243.96 (213.40)	200.09 (209.52)	0.58	.56	2.15	.15	.055	13.76
Stroop effect	126.71 (93.35)	102.57 (76.02)	116.85 (76.95)	93.86 (91.03)	-0.36	.72	0.01	.97	.000	31.83
Flanker effect	86.29 (42.99)	81.13 (23.11)	96.75 (38.93)	94.12 (52.65)	0.80	.43	0.07	.80	.002	31.19
Nogo com. error (%)	23.25 (15.47)	26.02 (15.69)	17.22 (13.95)	25.41 (12.40)	-1.27	.21	1.73	.20	.045	16.59
Go Nogo RT (ms)	312.14 (26.73)	298.66 (36.97)	322.69 (43.64)	298.82 (32.92)	0.92	.37	1.30	.26	.034	18.76

Table 4. Summary data for the transfer tasks collapsed across groups. The table shows the mean standard deviation (SD), mean, and training-related changes for all transfer tasks: single response selection (RS) reaction times (RTs, ms), Attentional Blink (AB) magnitude, Psychological Refractory Period (PRP) magnitude, Stroop effect (ms), Flanker effect (ms), Go-Nogo Commission error (%) and Go RTs (ms). **Bold** text indicates significant effect at $p < .05$ level.

	Pre-training	Post-training	Pre-to Post		
	M (SD)	*M (SD)*	*F*	*p*	*Bayesian ANOVA* BF_{10}
Action Selection Tasks					
Single RS Task (RT)	631.26 (89.16)	584.52 (81.05)	38.18	**<.001**	23888.00
AB magnitude	22.01 (13.97)	20.25 (14.33)	0.48	.49	0.28
PRP magnitude	228.96 (165.98)	208.21 (172.39)	1.55	.22	0.46
Stroop effect	121.66 (84.34)	98.10 (83.07)	1.71	.10	0.78
Flanker effect	91.65 (40.76)	87.79 (41.02)	0.63	.43	0.30
Go-Nogo Go RT (ms)	317.55 (36.32)	298.74 (34.48)	16.78	**<.001**	107.76
Go-Nogo com. errors (%)	20.16 (14.83)	25.71 (13.91)	-7.09	**.01**	4.15

Discussion

In this study, we investigated the effects of a dynamic dual-task training regime on multitasking performance and further assessed whether training-related benefits generalize to other untrained action control tasks that have previously been shown to share underlying or related mechanisms with the trained tasks (Bender et al., 2016). We had participants train on a concurrent perceptual discrimination and visuomotor tracking task (multitasking group), while the single-task group performed these two component tasks in isolation. We had two main goals in conducting this study. First, in line with previous dual-task findings (Anguera et al., 2013; Dux et al., 2009; Garner et al., 2014; Hazeltine et al., 2002; Schumacher et al., 2001; Strobach, Frensch, Soutschek, et al., 2012; Van Selst et al., 1999), we aimed to examine whether extensive multitasking training leads to training-related benefits. Multitasking performance before and after training was examined by quantifying the difference between the multitasking trials and single-task trials. Consistent with previous studies, our findings showed that multitasking performance selectively improved for participants that trained exclusively on the combined visuomotor tracking and perceptual discrimination task (multitasking group) and not for the active control group that trained on the two component tasks in isolation. Importantly, this training-related benefit was not due to initial performance differences between the two groups at baseline, as both groups showed similar costs when performing both tasks

simultaneously. In addition, we also found training gains on the trained tasks irrespective of group condition. The results therefore provide further support to the idea that dual-task training induces the learning of task-specific skills.

Second, by employing a wide array of cognitive tasks pre- and post-training, we were able to show that the observed dual-task training effects from this combined dynamic visuomotor tracking and perceptual discrimination task did not generalize to other action control tasks. Specifically, while standard effects for each measure were observed pre- and post-training, we did not find any evidence of transfer for dual-task training effects on the PRP or any other response selection measures. Given that all response selection transfer tasks included new visual stimuli and, as in the case of the PRP, a different input modality (auditory stimuli for the second task), the results suggest that training leads to learning how to coordinate stimulus and modality-specific information more efficiently. The results are in line with previous dual-task (Garner et al., 2016; Liepelt et al., 2011) and action game studies (Anguera et al., 2013; Gaspar et al., 2014) that showed no significant evidence of transfer to other dual-task conditions. Our finding also fits well with early research by Thorndike and colleagues (e.g., Thorndike & Woodworth, 1901a, 1901b), which found that the success of training-related transfer to other tasks was dependent on the degree of similarity between the trained task and transfer task. There was also no evidence of training-related enhancements to tests of response inhibition (Go-nogo) and spatial attention (Flanker). An overall small decrease in commission errors on the Go-nogo task was observed for both groups post-training, but the accompanying overall increase in Go RTs indicates that this reduction was likely driven by a speed/accuracy trade-off.

Overall, the pattern of results is largely consistent with the dual-task training (Garner et al., 2015; Liepelt et al., 2011; Owen et al., 2010; Ruthruff et al., 2006; Strobach et al., 2013) and brain training literature (for a review see Simons et al., 2016), which finds little evidence that multitasking training generalizes beyond task-specific skills and further contradicts previous findings in the action video game training literature that found training-related enhancements of executive control skills (e.g., Anguera et al., 2013; Green & Bavelier, 2003; Strobach, Frensch, & Schubert, 2012). The absence of transfer on learning seems inconsistent with the neuronal overlap theory, which postulates that transfer may occur if the trained tasks and transfer tasks draw on common neural substrates (Kuwajima & Sawaguchi, 2010; Lustig et al., 2009; Thorell et al., 2009). When considering executive control of actions, a reasonable prediction of this theory is that if two different action control tasks draw on the same frontoparietal and subcortical system, then improving the process of the trained tasks that taps this brain region should also result in improved

effects for other action control processes subserved by that system. In contrast, we found that training on two tasks simultaneously reduced the dual-task costs on the exact trained tasks but this training benefit did not generalize to other action control tasks. Thus, the absence of a training-induced effect on any transfer task and the presence of a task-specific multitasking training effect is in keeping with the idea that repeated exposure to particular tasks or stimuli may facilitate more efficient resource allocation and in turn, more optimal dual-task performance in the practiced situation.

As multitasking costs only improved when the two tasks were practiced in combination, our data imply that the critical aspect of decreased dual-task cost may lie in allowing the brain to learn how two specific tasks can be coordinated efficiently (Schubert & Szameitat, 2003). However, future research is needed to develop a greater understanding of the underlying mechanisms that drive training-related neural plasticity.

To date, relatively little is known about the underlying mechanisms that give rise to positive transfer effects. While our current intervention employed a dynamic dual task to tax action selection processes in a context that is often found in real world situations, it differs significantly from interactive video action games that require participants to intentionally vary their task priorities amongst many dimensions in order to achieve the required goals and sub-goals. To successfully perform these games, participants are inherently forced to form judgments about the underlying rules and relationships that exist between the different tasks, which has recently been shown to lead to transfer to new stimulus sets (Garner et al., 2016). This suggests that the brain may use the abstract association between tasks to transfer learning at the response selection/decision-making stage. Further work is needed to clarify whether training regimes that require the formations of abstract rules leads to positive transfer in other executive domains.

Although the current work employed an adaptive thresholding procedure so that participants performed each task at ~80% accuracy prior to the start of training, we did not adaptively modify difficulty levels in response to participant improvement during training. While participants rated their training experience as positive, it is nevertheless possible that titration of difficulty during training could have led to higher motivation levels, which has recently been shown to have a positive effect on transfer after task-switching training (Doerrenbaecher, Mueller, Troeger, & Kray, 2014). Thus, future work should include an adaptive training paradigm to understand whether titration enhances motivation that aids participants in reaching greater cognitive training effects.

In sum, by using a rigorous intervention design and dynamic, continuous multitasking paradigm, we were able to demonstrate that repeated exposure to two

combined tasks induces the learning of task-specific strategies that do not generalize to a wide range of action control tasks.

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General Discussion

Summary of Research Findings

The overarching aim of this thesis was to examine the cognitive and neural substrates involved in selecting appropriate actions and inhibiting inappropriate responses. Specifically, I examined the behavioural and neural overlap of these key cognitive operations by 1) determining the latent structure that underlies performance in a wide range of action control tasks that differ in response selection and response inhibition requirements; 2) investigating how response selection operations interact with response inhibition processes in the superior medial frontal cortex (SMFC); and 3) exploring the effects of a dynamic dual-task training regime on multitasking performance and whether training benefits extend to other response selection and inhibitory control tasks. I addressed these research questions by using a range of behavioural approaches (Study 1 and 3) and a combined behavioural and non-invasive brain stimulation technique (Study 2).

The aim of Study 1 (Bender, Filmer, Garner, Naughtin, & Dux, 2016) was to examine the underlying relationship between response selection and response inhibition. More specifically, the goal of this investigation was to test whether performance on a diverse battery of response selection and response inhibition tasks is underpinned by two distinct action control mechanisms or one general action control function. In two sessions, administered seven days apart from each other, response selection performance was assessed using the Psychological Refractory Period (PRP) task (Pashler, 1994; Telford, 1931), a Single versus Dual Response Selection paradigm (Dux, Ivanoff, Asplund, & Marois, 2006), and the Attentional Blink (AB) task (Raymond, Shapiro, & Arnell, 1992), whereas inhibitory control ability was assessed using the Stop-Signal Task (SST; Lappin, 1966; Verbruggen & Logan, 2008), a Go-Nogo paradigm (Donders, 1969; Robertson, Manly, Andrade, Baddeley, & Yiend, 1997), the Eriksen Flanker task (Eriksen & Schultz, 1979) and the Stroop task (Stroop, 1935). To examine how these two cognitive operations are related, I performed a series of confirmatory factor analyses (CFA) and then compared the models via the appropriate fit statistics. I found that a full two-factor model, in which tasks were parsed in terms of response selection and response inhibition demands, was supported over the simplest model – a single General Action Control factor. Specifically, in the full two-factor model, variance on the Response Selection factor contributes to the PRP, Stroop and Single-Task paradigms and to a smaller degree in the AB, whereas variance on the Response Inhibition factor plays an important role on the Stop-Signal and Go-Nogo tasks.

The results are in line with existing models of response selection (Pashler, 1994) and response inhibition (Logan & Cowan, Boucher, Palmeri, Logan, & Schall, 2007; 1984; Verbruggen & Logan, 2009) that argue for independent go and stop processes and further fit well with neuro-stimulation findings and neuroimaging research that have implicated distinct neural substrates in response inhibition (e.g., Aron, Robbins, & Poldrack, 2014) and response selection (e.g., Dux et al., 2006; Filmer, Mattingley, Marois, & Dux, 2013) processes. The CFA findings therefore suggest that response selection and inhibition functions are best described as two distinct, although weakly related mechanisms, rather than a unitary general action control process.

While the latent variable approach in Study 1 provides support for the non-unitary nature of response selection and inhibition, extensive neuroimaging and brain stimulation evidence indicates that the neural substrates for these two cognitive operations overlap in the superior medial frontal cortex (SMFC). The aim of the second study (Bender, Filmer, & Dux, 2016) was to determine the causal role of this region in response selection, response inhibition and the proactive modulation of response tendencies when stopping is occasionally required. This study was motivated by previous work that had implicated the posterior lateral prefrontal cortex in response selection and training processes by using transcranial direct current stimulation (tDCS; Filmer et al., 2013). To test the role of the SMFC in response selection, inhibition and training I applied tDCS over the SMFC immediately after the first phase of sensorimotor training.

Using the same pre- versus post stimulation performance comparisons as Filmer et al. (2013), I found no change in response selection performance when participants received anodal (excitatory) or cathodal (inhibitory) tDCS relative to sham stimulation (Experiment 1). Thus, I found no evidence to suggest that SMFC is directly involved in single-task response selection processes. However, when participants anticipated that the inhibition of a motor response was occasionally required (inhibitory context), cathodal tDCS over the SMFC modulated response selection performance by increasing reaction times (Experiment 2). To ensure the reliability of my Experiment 2 finding, I designed a third Experiment that alternated Never Stop blocks where stopping was never required (as per Experiment 1) and Maybe Stop blocks where stopping was occasionally required (as per Experiment 2). In line with my Experiment 2 findings, cathodal tDCS over SMFC again prolonged response times when response selection was performed under an inhibitory context. Collectively, these findings provide causal evidence that response selection and response inhibition processes overlap in the SMFC. The findings are in line with the notion that an inhibitory task set can endogenously activate the inhibitory control network in the

brain (Chiu & Aron, 2014; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010; van Gaal, Ridderinkhof, van den Wildenberg, & Lamme, 2009). Collectively, the results indicate that the SMFC is recruited for response selection operations when proactive inhibitory control is required.

The final study aimed to investigate whether intensive dual-task training can extend to other response selection and response inhibition tasks. More specifically, the study tested whether training-induced multitasking benefits from a fast paced and visually demanding visuomotor tracking and perceptual discrimination task can transfer to other response selection and response inhibition tasks, given that these two operations have been suggested to share common cognitive and neural underpinnings (Mostofsky & Simmonds, 2008). Two types of training regimes were employed. The single-task training group divided their time equally between the visuomotor tracking task, which required participants to continuously pursue a visually presented moving black target disk with a mouse, and a perceptual discrimination task, in which participants were asked to perform a button press as soon as the target shape appeared on the centre of the screen. The multitasking training group practiced the visuomotor tracking and perceptual discrimination task concurrently. To assess whether dual-task training benefits extend to other untrained action control tasks, participants completed a battery of tasks measuring response selection (PRP, Single Response Selection Task, and AB), inhibition (SST, Go Nogo task, and Stroop) and spatial attention (Flanker) pre- and post-training. Pre- versus post-training performance comparisons revealed that only the multitasking training group showed task-specific multitasking benefits on the combined visuomotor tracking and perceptual discrimination task. These results suggest that training on a fast paced visuomotor tracking and discrimination task results in task-specific benefits and further suggest that repeated exposure to particular tasks or stimuli may enable more efficient resource allocation and in turn, more optimal dual-task performance in the practiced situation, but this is yet to be directly tested.

Importantly, I found that this training-related multitasking improvement did not transfer to other theoretically related untrained tasks. The absence of a transfer effect challenges the neuronal overlap theory, which assumes that transfer may occur if the trained tasks and transfer tasks draw on common neural substrates (Kuwajima & Sawaguchi, 2010; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009; Thorell, Lindqvist, Bergman Nutley, Bohlin, & Klingberg, 2009). Overall, the observed results in this study suggest that training on a fast paced visuomotor tracking and discrimination task results in

task-specific benefits but these benefits do not extend to theoretically related untrained tasks.

Implications of Research Findings

The findings reported in Study 1, 2 and 3 have important implications for our understanding of how response selection and response inhibition processes should be conceptualized and how interactions between the two processes can stimulate new theory-driven behavioural treatments to target executive control impairments. Based on the current results, this thesis can contribute answers to questions in the field of action control: (1) Is response selection and response inhibition underpinned by a unitary action control mechanism? (2) How do response selection and inhibition processes interact to mediate behavioural change? (3) Do dual-task training benefits extend to other new tasks that are theoretically related, and what steps can be undertaken to maximize transfer to other tasks/domains?

Is response selection and response inhibition underpinned by a unitary action control mechanism?

The current findings cast doubt on the notion that response selection and response inhibition operations are governed by the same action control process (Mostofsky & Simmonds, 2008; Verbruggen, McLaren, & Chambers, 2014). If these two cognitive operations would draw on a unitary underlying response selection stage, then it would be expected that action control paradigms that differ in response selection and response inhibition requirements would load highly on a single action control factor. In addition, if response selection and inhibition processes draw on a unitary processing stage, then it would be expected that response selection and response inhibition demands recruit overlapping neural substrates. Moreover, given that response selection processes have been shown to improve with training, training-related benefits should possibly transfer to other response selection and inhibitory control tasks. The current findings speak against these predictions, as performance on a wide range of commonly employed response selection and inhibition tasks load on two distinct but weakly related, latent factors (Study 1). Moreover, a single response selection task does not recruit the superior medial frontal cortex (SMFC), whereas performing response selection under an inhibitory context does (Study 2). Furthermore, training on a dynamic dual-task results in task-specific benefits that do not extend to other response selection and response inhibition tasks (Study 3), suggesting that training only strengthens associations between specific stimulus response

mappings and the coordination of two tasks (Schubert & Szameitat, 2003). Taken together, the present findings therefore indicate that action control is made up of at least two distinct, but weakly related processes that share some overlapping neural substrates to mediate behavioural change and thus provide evidence against the notion that response selection and inhibition processes are governed by a unitary action selection mechanism (Mostofsky & Simmonds, 2008; Verbruggen et al., 2014). Rather, the current results are in accordance with theoretical accounts that propose independent response selection and inhibition processes that interact briefly to implement behavioural change. Specifically, the interactive race model (Boucher et al., 2007) posits that the race between the stop and go process is independent for most of the duration, with the two cognitive operations only interacting briefly at the interactive stage where inhibitory control prevents the go process from reaching threshold. Further support for the diversity and unity between response selection and response inhibition comes from neuroscientific findings that posit common and distinct neural substrates involved in response selection and response inhibition processes (Aron et al., 2014). The findings therefore illustrate the importance of using response selection and response inhibition paradigms when investigating these two distinct cognitive operations.

In addition, previous observations of Stroop interference effects have motivated the suggestion that performance on this measure is attributable to the ability to inhibit distracting automatic responses (Friedman, 2004; Miyake et al., 2000). However, the findings of Study 1 show that performance on the Stroop task is more dependent on response selection capacity limitations and closely resembles previous research that found incongruent trials to create interference at the response selection level. Thus, despite the fact that the Stroop task is typically considered to reflect response inhibition, the combination of these prior findings and ours instead indicate that the Stroop paradigm may tap similar response selection processes to those elicited by other response selection paradigms that tax capacity-limited central resources. Future research should assess this hypothesis further by manipulating response selection demands and inhibitory control demands in the Stroop paradigm.

How do response selection and inhibition processes interact to mediate behavioural change?

While Study 1 provides correlational evidence that response selection and response inhibition processes are distinct but weakly related mechanisms, the findings of Study 2 provide causal evidence for an interaction between the two operations. The

current observations of a context-dependent involvement of the SMFC in proactive inhibitory response selection control indicates that specific contexts and rule representations can trigger the inhibitory control network to proactively bias response selection in a goal-directed fashion (van Gaal et al., 2010; van Gaal et al., 2009). Specifically, the context-dependent interplay between response selection and response inhibition (Study 2) demonstrates how response selection processes are constantly adjusted via learning mechanisms that underlie stimulus-response associative and rule-based behaviour. Future research could investigate whether differences in motivation, emotional factors or reward sensitivity also recruit the inhibitory control network to mediate response selection in a goal-directed fashion.

The Study 2 findings have important implications for the development of new behavioural treatments, as proactive control has been shown to be impaired in older adults, individuals with antisocial, delinquent or addictive behaviour (Iselin & Decoster, 2009; Paxton, Barch, Racine, & Braver, 2008), and neuropsychiatric disorders such as attention deficit hyperactivity disorder (ADHD), schizophrenia and bipolar disorder (for a review, see Braver, 2012). Importantly, training older participants on a proactive control task has been shown to result in a shift from a reactive control strategy to a proactive strategy (Braver, Paxton, Locke, & Barch, 2009), indicating that control strategies can be modified with training. Thus, context-dependent proactive response selection control processes may open the avenue for new behavioural training paradigms designed to moderate motor responses toward drug- or food related stimuli. Indeed, several studies have found that intensive pairing of food-related stimuli to stopping in a stop-signal or go-nogo paradigm decreased food consumption (Houben, 2011; Veling, Aarts, & Stroebe, 2013). Similarly, stimulus-specific stop training resulted in decreased alcohol consumption (Jones & Field, 2013) and a similar training paradigm influenced behavioural treatment outcomes in alcohol dependent participants one year post-training (Wiers, Eberl, Rinck, Becker, & Lindenmeyer, 2011). Future research could combine a cognitive training regime with brain stimulation to modulate proactive slowing in children and adults with proactive control deficits as observed in ADHD or drug, food and alcohol addiction.

Do dual-task training benefits extend to other new tasks that are theoretically related and what steps can be undertaken to maximize transfer to other tasks/domains?

The dual-task training data in Study 3 demonstrate that training induced only task-specific benefits but no observable transfer to new, theoretically related tasks. The finding contrasts with the neuronal overlap theory, which postulates that transfer may occur if the

trained and transfer tasks draw on common neural substrates (Kuwajima & Sawaguchi, 2010; Lustig et al., 2009; Thorell et al., 2009). Instead, the data indicate that decreased dual-task interference after training may be due to learning concrete stimulus-response associations so that specific tasks can be coordinated efficiently based on current-task rules (Schubert & Szameitat, 2003), thus allowing response selection to become more automatized and less susceptible to the negative effects of concurrent load (Logan, 1978).

However, a key objective of a cognitive training regime is that training-induced improvements generalize to other tasks and cognitive domains but to date, there is little evidence that cognitive training generalizes beyond task-specific skills (Owen et al., 2010; Redick et al., 2013; Shipstead, Harrison, & Engle, 2012; Simons, 2016). The findings from Study 2 demonstrate that activation of the inhibitory control network is heavily dependent on an individual's internal representation of task rules. Thus, a key to behavioural flexibility may be the employment of rule representations and implementation intentions (Gollwitzer, 1999; Gollwitzer & Sheeran, 2006) to guide appropriate response selection in novel situations. Implementation intentions refer to if-then plans that link critical cues or contexts to specific actions (e.g., whenever I see a red traffic sign, I will slow down and stop the car). However, in real world situations humans are often required to make temporal abstractions in complex environments by grouping together a set of interrelated response options (Botvinick, 2012; Botvinick, Niv, & Barto, 2009). Work from our group has recently shown that abstract rule-like representations lead to transfer to new stimulus sets (Garner, Lynch, & Dux, 2016). Given these findings, it may be that the use of abstract rules reduces the negative effects of concurrent load, thus freeing attention at the capacity-limited response selection stage. It is therefore important to get a better understanding of how rules are developed and how rule learning leads to generalization and the ability to form abstract rules. Future research could employ an individual differences approach to investigate how the ability to form abstract rules relates to executive training and transfer effects.

Conclusions

The executive control of action is critical in daily life as it allows people to select task-relevant actions or to suppress task-irrelevant responses when required. This thesis investigated the relationship between response selection and response inhibition - two key action control processes that contribute to flexible goal-related behaviour. To date, it is not known whether response selection and response inhibition rely on the same or distinct underlying mechanisms, and the extent to which both processes share common cognitive

and neural underpinnings. Using an individual differences approach, I found that performance on a wide range of commonly employed response selection and response inhibition tasks tapped two distinct mechanisms of action control that are weakly related. I also found that response selection and response inhibition processes interact in the superior medial frontal cortex to mediate response selection under an inhibitory context. Furthermore, a large-scale dual-task training study showed that training-induced benefits are task-specific and do not transfer to other action control tasks. Taken together, the findings presented in this thesis extend our knowledge about the relationship between response selection and response inhibition and imply that action control is subserved by distinct response selection and response inhibition processes that interact at the neural level to mediate behavioural change. Together, the findings have significant theoretical and practical implications as they highlight the importance of using separate response selection and response inhibition paradigms when investigating these two key action control processes and further suggest that cognitive control training interventions need to be specialized.

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