Autonomic and Electrophysiological Correlates of Cognitive Control in Aging

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Submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

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To my Dreama-Reama …
I’m finally done sitting at that dining room table in my pink puffy coat.
PS – Love you most.

General Abstract

This thesis tested a model of neurovisceral integration (Thayer & Lane, 2001) wherein parasympathetic autonomic regulation is considered to play a central role in cognitive control. We asked whether respiratory sinus arrhythmia (RSA), a parasympathetic index, and cardiac workload (rate pressure product, RPP) would influence cognition and whether this would change with age. Cognitive control was measured behaviourally and electrophysiologically through the error-related negativity (ERN) and error positivity (Pe). The ERN and Pe are thought to be generated by the anterior cingulate cortex (ACC), a region involved in regulating cognitive and autonomic control and susceptible to age-related change.

In Study 1, older and younger adults completed a working memory Go/NoGo task. Although RSA did not relate to performance, higher pre-task RPP was associated with poorer NoGo performance among older adults. Relations between ERN/Pe and accuracy were indirect and more evident in younger adults. Thus, Study 1 supported the link between cognition and autonomic activity, specifically, cardiac workload in older adults.

In Study 2, we included younger adults and manipulated a Stroop task to clarify conditions under which associations between RSA and performance will likely emerge. We varied task parameters to allow for proactive versus reactive strategies, and motivation was increased via financial incentive. Pre-task RSA predicted accuracy when response contingencies required maintenance of a specific item in memory. Thus, RSA was most relevant when performance required proactive control, a metabolically costly strategy that would presumably be more reliant on autonomic flexibility.

In Study 3, we included older adults and examined RSA and proactive control in an additive factors framework. We maintained the incentive and measured fitness. Higher pre-task RSA among older adults was associated with greater accuracy when proactive control was needed most. Conversely, performance of young women was consistently associated with fitness. Relations between ERN/Pe and accuracy were modest; however, isolating ACC activity via independent component analysis allowed for more associations with accuracy to emerge in younger adults. Thus, performance in both groups appeared to be differentially dependent on RSA and ACC activation. Altogether, these data are consistent with a neurovisceral integration model in the context of cognitive control.

Acknowledgements

I thought that writing my dissertation was difficult – Then I sat down to write these acknowledgements. You see, to me, these acknowledgements are the most important part of this entire thesis. Yes, I can hear some of my fellow colleagues gasping right now, but it's the truth. They are my chance to formally recognize and officially thank all of those special people in my life that made this journey possible. But, as usual, I have a terrible case of writer's block, mainly because I know there is no way I can possibly thank each of these individuals enough for what they have done for me. I've been working on these acknowledgments for days now, trying to find the right words, trying to get the proper flow, trying to make them *perfect*. I can just hear my advisor, Jane, right now, "Lesley, don't worry about making it perfect. Just write *something*." So, even though these words are not perfect and they will never be enough, here they are.

First, I would like to thank my advisor, Jane Dywan. I can honestly say that I never would have made it through this degree without her constant encouragement, guidance, and support. Jane was not only there for me as an academic advisor but also as a mentor, constantly pushing me forward while reassuring me that she was always right there behind me. At times she supported me in small ways, like when she drilled the different uses for "less" versus "fewer" into my head. However, at other times she supported me in major ways, like when she continued to advise me even after retiring, a sacrifice which I will never be able to thank her for enough.

Next, I would like to thank my committee members, Dr. Sid Segalowitz and Dr. Karen Arnell, for all that they have done for me. They both gave generously of their time, and their insightful suggestions and thoughtful questions pushed me to examine my data more critically and helped me to develop further as a scientist and a researcher.

A very special thank you goes to James Desjardins. His technological expertise and ability to troubleshoot virtually any equipment problem made this work possible, and his kindness and sense of humor kept me sane even on some of my most challenging days. I would also like to thank Allison Flynn-Bowman who always seemed to be there, ready and willing to help me with whatever I needed (BioSemi assistance, an ear, a piece of chocolate). Her generosity and friendship provided a source of comfort and reassurance during my time as a graduate student that cannot be overstated.

A great deal of thanks also goes to all of those BUCANL members, past and present, who helped me set up participants, run experimental sessions, and process data, including Rae Gibson, Sara Tisi, Allan Campopiano, Stefon Van Noordt, Jamie Elmers, Christine Michael, and Lui Lui. I would also like to thank Karen Mathewson and Bill Tays, former BUCANL colleagues who provided me with important data analysis training and support.

I would also like to thank all of my friends who have shared with me in this journey, including Angela Dzyundzyak, Meghan Weissflog, and Jackie Sievert. I would also like to thank Katie Helfer for being the most understanding and patient best friend a person could ever ask for.

Next, I would like to thank each one of my family members who made this journey possible. I would like to thank my older brother, Michael, for believing in me and for encouraging me to take the graduate school leap 8 years ago. I would like to thank my younger brother, James, for always supporting me and reminding me to relax and have fun every once in a while. A huge thank you also goes to my sister-in-law, Kristen, for always being there for me, for listening compassionately, for encouraging me, and for being the sister I never had. A very special thank also goes to my Sophia and my Mikey for making me put down my work to play with them every now and then, providing what my yoga teacher refers to as the all important "pause that refreshes."

An enormous deal of gratitude also goes to my aunt and God Mother (a.k.a., my Fairy God Mother), Josie. She not only provided a great deal of financial support that I desperately needed during my last few years as a graduate student, but she was always there for me, reminding me that I "was in control" and that I could finish this degree.

My parents … What can I say? I want to thank them for everything – for letting me live at home, for feeding me, for putting up with my messy room, for trying to understand my research even when it was impossible for them to do so, for letting me take over every room of their house with my millions of papers. I want to thank my Dad for his Wednesday night dinners, for all of the gas and car repair money, for bringing me all of those hot chocolates and blizzards when I was overwhelmed with work, and for making me stop and take a walk with him and Freckles when he knew I needed one. I want to thank my Mom for always being there to listen to me talk/vent/freak out about my research, for encouraging me to take time off from work to relax and have fun, for bringing me cheese and crackers (and wine!) on Friday nights, for making me dance and sing in the living room with her, for helping me keep things in perspective, and for making me laugh.

And my Joe … Again, what can I say? I want to thank him for everything – for loving me and supporting me, for listening to me talk/vent/freak out about my research, for encouraging me to stop and relax every once in a while, for making me feel beautiful even when I was in my dissertation-writing uniform (i.e., sweatpants, sweatshirt, no make-up, glasses, a frizzy ponytail), for cooking me victory meals after successful FARS presentations, for making me take time off from school to do totally spontaneous things like travel to NYC to see Weezer, and for making me feel like the most special neuroscientist on Earth.

And lastly, a special thank you to Freckles, my love dog, for keeping me company every day of this dissertation writing journey.

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Chapter 1: General Introduction

The Role of Autonomic Regulatory Control in Cognitive Aging

> Claude Bernard also repeatedly insists, and this deserves especial notice, that when the heart is affected it reacts on the brain; and the state of the brain again reacts through the pneumo-gastric (vagus) nerve on the heart; so that under any excitement there will be much mutual action and reaction between these, the two most important organs of the body (Darwin, 1872/1999, pp. 71-72; as cited in Thayer & Lane, 2009).

Recognition of the intimate relationship between the heart and the brain has a long history. As the above quote by Charles Darwin indicates, the famous French physiologist, Claude Bernard, acknowledged the physiological connection between these two organs almost 150 years ago, during a lecture he delivered in 1865 at the Sorbonne (Thayer & Lane, 2009). Although physiologists have been aware of this heart-brain connection for well over a century, an understanding of how specifically the heart and brain interact has been slow to emerge. Early work was focussed on the relations between heart rate (HR) and/or HR variability (HRV, the variability in beat to beat interval) and performance on cognitive tasks. Researchers found that although any type of task would increase electrodermal activation, when it came to HR or HRV, attention to external stimuli slowed the heart (and increased HRV) whereas attention to internal stimuli (i.e., cognitive work) contributed to acceleration of HR (and a decrease in variability; e.g., Lacy, Kagan, Lacy, & Moss, 1963; Lacy & Lacy, 1970). Further work demonstrated that HRV proved to be even more sensitive to task parameters than HR itself, and much of the subsequent work focussed on factors that contributed to this variability and how it increased or decreased in response to different tasks, all of which required some aspect of active attention (Mulder & Mulder, 1981).

There was also a growing appreciation that HRV was influenced by the parasympathetic branch of the autonomic nervous system (e.g., Katona & Joh, 1975) and that this control was modulated through cell activity in the anterior cingulate cortex (ACC), suggesting a complex and indirect link between central and peripheral aspects of cardiac and respiratory control (e.g., Frysinger & Harper, 1986). Theoretical accounts, although stressing different roles for central and peripheral systems, nonetheless reflected a view that the pattern of psychophysiological changes that occur during various tasks reflected physiological adjustments that promoted an adaptive response to environmental demands (Öhman, Hamm, & Hugdahl, 2000). Richard Jennings, in his Presidential Address to the *Society for Psychophysiological Research*, asked his colleagues to remember that the mind is in the body and asked them to seriously consider "…..how the processing of information – the function of our brain – is constrained by the location of the brain in the human body" (Jennings, 1992, p. 269).

Interest in this issue has begun to broaden considerably. Rather than use HRV as an outcome measure, such as to determine the physiological effects of cognitive load (e.g., Backs & Seljos, 1994), there is a growing interest in trying to determine whether a well-modulated autonomic system could be seen as supporting physical or mental health (e.g., Guinjoan et al., 2004) or whether it has implications for emotion regulation (e.g., Friedman & Thayer, 1998). The interest in the relationship between autonomic regulatory cardiac control and the control of attentional resources also continues (e.g., Somsen, Jennings, & van der Molen, 2004), and there are questions as to whether these relations change with development (Beauchaine, Gatzke-Kopp, & Mead, 2007; Beauchaine, 2001). It is within this context that I have chosen to examine the general model of neurovisceral integration (Porges, 1995, 2007; Thayer & Lane, 2000, 2009) as it relates to normative age-related changes in higher-level cognitive control.

Autonomic Control of Cardiovascular Function

An understanding of the heart-brain connection has continued to evolve and encompasses neurophysiological, biochemical, and behavioural domains. We now know that the autonomic nervous system is comprised of two major divisions, the sympathetic and parasympathetic branches (Porges, 1995). These two branches innervate most of the body's major organs where they exert antagonistic control. Such control allows for the dynamic regulation of major organ systems throughout the body, including the cardiovascular system (Berntson, Cacioppo, & Quigley, 1993). For instance, when external demands are present, the sympathetic branch accelerates cardiovascular activity in an effort to mobilize the resources necessary to meet the environmental challenge. Conversely, when external demands are absent, the parasympathetic branch inhibits cardiovascular activity in order to conserve energy and resources.

Cardiac autonomic regulation is mediated by the tenth cranial nerve, i.e., the vagus, which originates in the medulla and projects, independently of the spinal cord, to the heart. The vagus involves a bidirectional system containing both afferent and efferent fibers through which neural information flows. According to Porges (1995), this bidirectional system permits dynamic, continuous communication between brain control centres and the heart that work together to regulate homeostasis. Vagal afferent fibers are responsible for providing feedback to the brain through their connection from the heart to the nucleus tractus solitarius. This continuous feedback allows the brain to effectively regulate cardiac activity. Vagal efferent fibres, on the other hand, originate in the brainstem and innervate the upper portion of the right atrium of the heart, the sinoatrial node. The sinoatrial node acts as the heart's pacemaker, firing regularly and allowing the heart to beat steadily. Impulses from the sinoatrial node trigger a sequence of electrical events in the heart that cause muscle contractions which pump blood out of the heart for circulation throughout the body. Importantly, vagal efferent fibres exert an inhibitory influence on the sinoatrial node, decreasing sinoatrial node firing, and consequently, slowing heart rate.

Although both the sympathetic and parasympathetic branches of the autonomic nervous system are integral to the health and adaptability of an organism, resting cardiovascular regulation favors parasympathetic predominance, which not only slows HR but also increases the variability between heart beats (Jose & Collison, 1970). The differential effects of these two branches on beat-to-beat heart rate result from differences in the time courses of their respective neurotransmitters (Task Force of The European Society of Cardiology and The North American Society of Pacing and Electrophysiology, 1996). The sympathetic branch's influence is mediated by the release of norepinephrine, the effects of which are relatively slow, requiring about 4 seconds to peak. The parasympathetic branch's influence is mediated by the release of acetylcholine, the effects of which are fast, requiring less than a second to peak. Thus, the beat-to-beat variability that characterizes healthy human heart rate, i.e., HRV, is predominantly mediated by the fast-acting parasympathetic nervous system.

Parasympathetic cardiac control can be assessed by estimating respiratory sinus arrhythmia (RSA), the high frequency variation in the beat-to-beat interval of heart rate that accompanies normal respiration (Berntson, Bigger Jr., J. T.Eckberg, et al., 1997; Berntson, Cacioppo, & Grossman, 2007). During inspiration, respiratory mechanisms in the brainstem attenuate vagal efference to the heart which increases heart rate and decrease the variation between heart beats. During expiration, vagal efference to the heart is restored which reduces heart rate and increases the variation between heart beats. By measuring the interval between successive heart beats (R-R intervals) on an electrocardiogram (ECG), the magnitude of RSA can be quantified, and thus, an index of phasic autonomic cardiac control can be produced.

Psychophysiological Theories of Cardiac Autonomic Regulation

Psychophysiological models have been developed to describe the relationship between cardiac autonomic regulation and psychological processes. One of the most influential of these is Porges' polyvagal theory, which posits that the behavioural adaptability of mammals is rooted in the phylogenetic development of the autonomic nervous system (Porges, 1995, 2007). According to Porges, there are two distinct branches of vagal efference to the heart, each programmed to produce different response strategies. The first branch, the unmyelinated or *vegetative* vagus, originates in the dorsal motor nucleus. A phylogenetic relic of primitive vertebrates like reptiles and amphibians, the unmyelinated vagus suppresses metabolic demands during threatening situations by promoting immobilization behaviours (e.g., freezing). The second branch, the myelinated or *smart* vagus, originates in the nucleus ambiguus and is considered, in this model, to be distinctly mammalian (but see, Taylor, Al-Ghamdi, Ihmied, Wang, & Abe, 2001). According to the Porges' model (1995, 2007), the myelinated vagus acts as a brake that can rapidly regulate cardiac output according to the metabolic requirements associated with various environmental demands. For instance, if a mammal is faced with a threat or challenge, the vagal brake is temporarily reduced, leading to an increase in cardiac output (i.e., increased heart rate). This inhibition of the vagal brake allows for the mobilization of the metabolic resources necessary to support fight or flight behaviour. Conversely, in the absence of threat, vagal inhibition will be maintained (or even increased), lowering cardiac output, and supporting social engagement behaviours. Thus, according to polyvagal theory, the phylogenetic development of the myelinated vagal brake is responsible for supporting the complex social, emotional, and attentional processes that are uniquely characteristic of mammals. Although various aspects of this theory have been subject to critique and revision (see Grossman & Taylor, 2007), the general principle of RSA playing a role in the regulation of energy exchange during metabolic and behavioural change endures (Berntson et al., 2007).

In addition to polyvagal theory, a model of neurovisceral integration has been developed by Julian Thayer and colleagues (Thayer & Lane, 2000, 2009). Although not dramatically different from the polyvagal theory (Porges, 1995, 2007) in highlighting the importance of the heart-brain connection, the emphasis of the neurovisceral integration model is on how cognitive, emotional, and physiological processes are regulated in an integrated fashion in the service of adaptive, goal-directed behaviour (Thayer & Lane, 2000, 2009). According to Thayer and Lane, this integration is achieved by a flexible network of neural structures, including the medial prefrontal cortex (mPFC), that operate as a “super-system,” coordinating signals from the central and peripheral nervous systems. This central-peripheral integration is critical for goal-directed behaviour because it promotes flexible adaptation, allowing an organism to respond appropriately to changing environmental demands. Based on this model, Thayer and Lane have proposed that baseline HRV, as a measure, may provide an index of the efficiency of central-peripheral nervous system integration, and hence, an organism’s capacity for self-regulation. More specifically, the presence of higher baseline HRV will be associated with enhanced self-regulation, and thus, the capacity for greater behavioural flexibility and adaptability in the context of a dynamically changing environment.

Although Thayer and Lane (2000, 2009) have stressed the importance of the mPFC in their model of neurovisceral integration, their model further emphasizes the role of the central autonomic network (CAN). The CAN refers to a set of midbrain and higher cortical structures that include the insular cortex, ACC, the ventromedial PFC, the central nucleus of the amygdala, and the hypothalamic nuclei (Benarroch, 1993, 1997; Critchley, Corfield, Chandler, Mathias, & Dolan, 2000; Critchley, 2005; Matthews, Paulus, Simmons, Nelesen, & Dimsdale, 2004; Ter Horst & Postema, 1997). As part of the CAN, these structures are responsible for modulating autonomic influences on the heart.

Both polyvagal theory (Porges, 1995, 2007) and the neurovisceral integration model (Thayer & Lane, 2000, 2009) emphasize the importance of flexible autonomic regulation for adaptive functioning and goal-directed behaviour. From the perspective of both models, we would expect that greater centrally-based modulatory control over cardiac function, and hence arousal, would facilitate an individual’s ability to regulate their behaviour in a way that is maximally adaptive with regard to environmental challenges and demands.

Physiological and Behavioural Correlates of Cardiac Autonomic Regulation

The measurement of cardiac autonomic regulation, via RSA, has proven useful in a range of contexts. For instance, lower baseline RSA has been shown to be a serious risk factor for infants (Porges, 1992), increasing the likelihood of apnea and bradycardia (Sostek, Glass, Molina, & Porges, 1984). In adults too, low RSA is associated with a number of negative health outcomes (Thayer & Lane, 2007), including the presence of hypertension (Maver, Strucl, & Accetto, 2004), congestive heart failure (Saul et al., 1988), diabetes (Liao et al., 1995), and obesity (Petretta et al., 1995). Reduced RSA is also associated with all-cause mortality, even after controlling for other risk factors (Dekker et al., 1997, 2000). Finally, lower RSA is associated with a number of negative health and lifestyle choices including tobacco use (Nabors-Oberg, Sollers, Niaura, & Thayer, 2002), alcohol consumption (Ingjaldsson, Laberg, & Thayer, 2003), and sedentary lifestyle (Rossy & Thayer, 1998), although the basis of the association is unclear (e.g., Kleiger, Stein, & Bigger, 2005)

In addition to physical health, cardiac autonomic regulation has been associated with various forms of psychopathology including anxiety disorders and depression. For instance, lower baseline RSA is particularly evident in those with panic disorder (Friedman, 2007), and to some degree, generalized anxiety (Thayer, Friedman, & Borkovec, 1996; Thayer & Lane, 2000) and social anxiety disorders (Grossman, Wilhelm, Kawachi, & Sparrow, 2001). Recent work also suggests that individuals with comorbid anxiety disorders (i.e., the presence of more than one anxiety disorder) have lower baseline RSA levels compared to non-anxious controls, an important finding given that anxiety disorders often co-occur (Pittig, Arch, Lam, & Craske, 2013). There is also a considerable body of work documenting the links between RSA and depression (Rottenberg, Clift, Bolden, & Salomon, 2007; Rottenberg, Salomon, Gross, & Gotlib, 2005; Rottenberg, 2007). A recent meta-analysis demonstrated that baseline RSA was lower in depressed compared to non-depressed participants, and furthermore, that baseline RSA was negatively correlated with depression severity (Kemp et al., 2010).

Cardiac autonomic regulation has also been shown to relate to emotion regulation more generally. For instance, lower baseline RSA is associated with prolonged potentiated startle responses during threat of shock, a reflection of ongoing, anticipatory worry in individuals with reduced cardiac autonomic regulation (Melzig, Weike, Hamm, & Thayer, 2009). Baseline RSA is inversely related to aggression and trait hostility (Mezzacappa et al., 1997; Sloan et al., 1994) and to the intensity of sadness (Dywan, Mathewson, Choma, Rosenfeld, & Segalowitz, 2008), whereas more recently, Oveis et al. (2009) reported that baseline RSA was positively associated with tonic positive emotionality, as reflected in personality traits (i.e., increased extroversion and agreeableness), enduring positive mood, and trait optimism. Furthermore, baseline RSA was shown to be positively related to positive hedonic tone (i.e., increased cheerfulness), positive tense arousal (i.e., increased calmness), and satisfaction with life (Geisler, Vennewald, Kubiak, & Weber, 2010).

Thus, there is a growing body of evidence that supports the basic tenets of the neurovisceral integration model and confirms that the ability to modulate arousal through phasic autonomic cardiac control plays a role in a broad range of human experience, taking in physical and mental health, emotion regulation, and personality characteristics. With respect to the early interest in whether phasic vagal cardiac control has a place in predicting cognitive function and attentional control (e.g., Jennings, 1992; Lacy & Lacy, 1970; Mulder & Mulder, 1981; Öhman et al., 2000), the story is still unclear prompting the questions to be addressed in the present thesis.

The Relationship between Cardiac Autonomic Regulation and Cognitive Performance

Early psychophysiologists who explored the relationship between RSA and cognitive performance tended to use RSA as a dependent measure. For instance, Mulder and Mulder

(1981) examined RSA as participants completed a sentence comprehension task and a working memory task, both of which included processing demand manipulations. In both cases, they found that RSA decreased as the processing demands of the tasks increased. Similarly, Vincent, Craik, and Furedy (1996) examined RSA as participants retrieved words that they had previously encoded either semantically (deeply) or visually (in a more shallow manner). They found that RSA suppression was greatest when participants recalled words that they had encoded deeply. Thus, in both of these cases, RSA suppression was greatest when the cognitive demands of the task were greatest. These sorts of studies led some cognitive researchers to adopt RSA as a psychophysiological index of mental workload, something that, prior to this point, had mainly been measured in terms of self report.

These early studies (Mulder & Mulder, 1981; Vincent et al., 1996) certainly revealed important information about the effects of cognitive effort on cardiac autonomic arousal but, importantly, they examined RSA purely from a reactive perspective, utilizing it as an outcome measure. However, as researchers gained a better understanding of the role that higher cortical regions played in the modulation of cardiac autonomic arousal, and as theoretical accounts of central-peripheral integration continued to be refined, researchers became increasingly interested in utilizing RSA as a predictor variable. In other words, they wanted to determine whether individual differences in resting RSA, considered an index of general vagal modulatory control, were associated with performance differences on cognitive tasks.

Some of the earliest research in this area came from work with infants. Besides the early evidence that low RSA was associated with health risk in infants (e.g., Porges, 1992), RSA was also found to relate to their attentional control. Richards (1985) noted that infants with higher RSA were less susceptible to distraction than were infants with lower RSA. In addition, Linnemeyer and Porges (1986) reported that infants with higher baseline RSA looked at unfamiliar stimuli for longer periods and familiar stimuli for shorter periods, than did infants with lower baseline RSA. Marcovitch et al. (2010) demonstrated that 3.5 year old children with higher baseline RSA did significantly better on tasks requiring cognitive regulation, performance monitoring, and response control than did children with medium to low baseline RSA.

Some evidence for a relationship between higher RSA and enhanced cognitive performance has been reported in adult samples as well. For instance, Hansen, Johnson, and Thayer (2003) examined the degree to which baseline RSA related to performance on various cognitive tasks in a group of young men. They asked participants to complete an n-back working memory task and a continuous performance battery, thus tapping both executive and non-executive functions. Their data indicated that participants with higher baseline RSA made fewer errors on the working memory task, and they also made faster correct responses and fewer false positive responses on those aspects of the continuous performance battery that required executive control, including a serial pattern matching task. Importantly, Hansen et al. found no evidence indicating a relationship between RSA and performance on those aspects of the continuous performance battery that involved non-executive components, such as the simple reaction time task. Thus, Hansen et al.’s findings not only provide support for the link between autonomic regulatory control and cognitive performance in a sample of younger adults, but they also highlight the potential importance of this relationship for performance on tasks that specifically tap executive functions.

The fact that cardiac autonomic regulation may be relevant to executive functions, specifically, is noteworthy because these are the very abilities that appear to be most vulnerable to the aging process (Park & Reuter-Lorenz, 2009). For instance, age-related performance decrements tend to be most apparent on tasks that require the use of attention, inhibition, and working memory -- executive functions that rely on a high degree of cognitive control. We note, however, that significant variability exists across older adults in terms of cognitive control, leading researchers to question what specific mechanism(s) might underlie the presence of such variability. Given the evidence linking RSA and cognitive performance, we propose that one potential candidate may be individual differences in cardiac autonomic regulation.

The relationship between cardiac autonomic regulation and cognition has often been overlooked in older adults despite clear evidence that warrants such research. For instance, aging is known to lead to structural and functional declines in the ACC and the mPFC (Kochunov et al., 2009), regions involved in the support of both cognitive and autonomic regulatory functions (Critchley, 2005; Critchley et al., 2003, 2000). Furthermore, research has consistently shown that cardiac autonomic regulation declines with age, but importantly, the rate and level of this decline vary from person to person (De Meersman & Stein, 2007). A remaining issue, therefore, is whether cognitive performance in older adults may differ as a function of the level of cardiac autonomic regulation that one has managed to maintain with age.

Although few studies have addressed this issue, those that have seem to provide support for this possibility. For instance, recent work from Kim et al. (2006) demonstrated that the presence of lower RSA among older disabled women was associated with an increased risk of future cognitive impairment. Furthermore, several studies have demonstrated that the presence of hypertension, a state of autonomic imbalance that tends to increase with age and is characterized by reduced parasympathetic control, is associated with diminished cognitive function (Breteler, 2000; Robbins, Elias, Elias, & Budge, 2005; Saxby, Harrington, McKeith, Wesnes, & Ford, 2003; Waldstein, Brown, Maier, & Katzel, 2005; Waldstein, 2003). Thus, we were interested in examining whether cardiac autonomic regulation was associated with the behavioural performance of older or younger adults on executive function tasks that required a high degree of cognitive control.

The Electrophysiological Approach to ACC Function

We were also interested in examining neural indices of cognitive control. Although many neural regions are involved in the modulation of cognitive control, the ACC is among the most important (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Some of the earliest research on ACC function was based on lesion studies in humans and animals, and the results of this work demonstrated the importance of this structure for emotion and affect regulation (Bush, Luu, & Posner, 2000). However, with the development of sophisticated neuroimaging and electrophysiological techniques came an increased appreciation for the role of the ACC in higher-level cognition. One of the most important discoveries came from electrophysiological work which demonstrated the occurrence of a reliable scalp negativity following the commission of an error response (Falkenstein, Hohnsbein, Hoorman, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). Research indicated that this negativity, known as the error-related negativity (ERN), occurred approximately 50 to 100 ms after the execution of an erroneous response, and importantly, that it was generated by the ACC (e.g., Dehaene, Posner, & Tucker, 1994; Miltner et al., 2003).

Following the discovery of the ERN, great debate ensued regarding the exact functional significance of this ACC-generated response. Originally, the ERN was thought to occur only following error responses, hence its name, the *error-related negativity* (Falkenstein et al., 1990; Gehring et al., 1993). However, further investigation revealed that the ERN can occur on both correct and error trials, though the negativity is usually larger in response to errors (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). This led investigators to extend the role of ERN beyond error detection to include a more general response evaluation or performance monitoring process. Further work from Holroyd and Coles (2002) linked the occurrence of the ERN to activity in the mesencephalic dopamine system. Research indicates that fluctuations in dopaminergic activity accompany the unexpected occurrence of rewards and punishments. Thus, Holroyd and Coles claimed that the commission of an error leads to a drop in dopamine that acts as a negative reinforcement signal to the frontal cortex. This negative reinforcement signal disinhibits pyramidal neurons in the ACC, which in turn, generate the ERN response. Thus, according to Holroyd and Coles, the ERN may act as an ACC-generated alarm that sounds when outcomes are worse than expected, signalling the rest of the cortex that there is a need for increased cognitive control.

Thus, it is clear that the ACC plays a key role in modulating cognitive control in the service of goal-directed behaviour (Ridderinkhof et al., 2004). However, as we have already mentioned, the ACC is also involved in the regulation of cardiovascular autonomic arousal (Critchley, 2005; Critchley et al., 2003, 2000). More specifically, increasing research suggests that the ACC plays a critical role in generating autonomic states of arousal that are adaptive for successful performance on cognitive tasks. Thus, in order to provide a more thorough test of the hypothesized link between central (i.e., cognitive) and peripheral (i.e., RSA) nervous system integration, we were interested in exploring ACC function more directly. Specifically, we wanted to determine whether pre-task RSA, our index of baseline cardiac autonomic regulation, could reliably predict ACC-electrocortical activity. Documenting such associations would provide support for the growing consensus that ACC function must be considered within a broader context that integrates both the cognitive and autonomic regulatory functions of this structure. Thus, all of the tasks included in the current thesis were designed as ERP paradigms, so that we could examine potential relations with ACC-generated electrocortical components, including both the ERN and corresponding error positivity (Pe).

The Present Studies

The studies that make up this thesis were designed to gain a better understanding of the role of phasic vagal cardiac regulation for performance in contexts that require higher levels of cognitive control. Specifically, we were interested in whether pre-task RSA, our index of baseline cardiac autonomic regulation, would relate to behavioural performance and/or electrophysiological indices of cognitive control among older and/or younger adults. The studies presented in the following three chapters were each based on different datasets collected over the course of 5 years. Although each study utilized a different cognitive task, in each case, the task included more than one level of difficulty. This allowed us to determine whether relations with pre-task RSA varied according to the level of cognitive control required by the task. If centrally mediated autonomic regulation contributes in a meaningful way to cognitive control, one might expect this relationship to become increasingly evident as the control demands of a task increase.

Study 1 (Chapter 2) represented our initial exploration of relations between behavioural, electrophysiological, and autonomic indices of cognitive control. We examined these associations in both older and younger adults in the context of a complex Go/NoGo task that varied working memory load requirements. Given this task's reliance on both working memory and inhibitory control, it represented an ideal starting point for our investigation into the hypothesized link between RSA and executive function performance. Our goal for Study 2 was to more strategically manipulate the parameters of a Stroop paradigm in order to help clarify the conditions under which associations between RSA and behavioural performance are likely to emerge. We were specifically interested in whether RSA might be more or less likely to relate to behavioural performance based on the *type* of cognitive control strategy that the task encouraged an individual to adopt (i.e., *proactive* versus *reactive*). Because Study 2 served as pilot work for Study 3 (Chapter 4), we only included younger adults, and we focused specifically on the relationship between RSA and behavioural performance. Study 3 (Chapter 4) represented an extension of Study 2 (Chapter 3), and therefore, included both older and younger adults. Multiple measures, including behavioural performance, RSA, and indices of ACC function (ERPs and ACC global field amplitude), were collected and analyzed. We also included a fitness component to this study. Research indicates that increased aerobic fitness is associated with better cognitive performance (Chang, Huang, Chen, & Hung, 2013; Hillman et al., 2006) as well as increased cardiac autonomic regulation (Billman, 2002; Goldsmith, Bigger, Bloomfield, & Steinman, 1997; Goldsmith, Bigger, Steinman, & Fleiss, 1992). Thus, we expected fitness to be another important factor to consider when examining relations between cardiac autonomic regulation and cognitive control.

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Chapter 2: Cardiac workload and inhibitory control in younger and older adults[1]

1. Introduction

Phasic vagal cardiac control can be assessed by estimating respiratory sinus arrhythmia (RSA), which refers to the slight ebb and flow of HR that accompanies the normal respiratory cycle (Berntson, Cacioppo, & Grossman, 2007). Specifically, RSA is an index of parasympathetic modulation of cardiac function and, importantly, it is considered a marker of autonomic flexibility and behavioural adaptability (Beauchaine, 2001; Porges, 1995; Thayer, Hansen, Saus-Rose, & Johnsen, 2009). Thus, higher RSA is considered reflective of a neurophysiological system that can readily adapt to environmental changes and /or demands. Of interest is the fact that the parasympathetic, compared to the sympathetic system, seems to be particularly susceptible to age-related decline (De Meersman & Stein, 2007; Korkushko, Shatilo, Plachinda, & Shatilo, 1991; Umetani, Singer, McCraty, & Atkinson, 1998). Consequently, normal aging typically involves a disruption of autonomic regulatory balance that results in a state of sympathetic predominance in older adults. The purpose of the present study is to examine the degree to which autonomic regulatory control affects performance (behavioural and electrocortical) on a challenging Go/NoGo task at three levels of working memory (WM) load.

Those interested in centrally mediated autonomic regulation have typically focused on its association with emotion regulation and reactivity (Beauchaine, Gatzke-Kopp, & Mead, 2007; Hagemann, Waldstein, & Thayer, 2003; Thayer & Lane, 2000). However, interest has also been slowly developing in the relationship between RSA and cognitive performance. Some of the first studies demonstrated a link between higher RSA and better

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[1] A version of this chapter has been published. Capuana et al. (2012). *Biological Psychology, 90*, 60-70.

attentional control in infants and children (Linnemeyer & Porges, 1986; Richards, 1985; Staton, El-sheikh, & Buckhalt, 2008). More recently, higher baseline (or resting) RSA, measured prior to initiation of a task, has been shown to relate to enhanced working memory and attentional control among adolescents and younger adults. Resting RSA was also associated with enhanced performance on a subset of continuous performance tasks that involved sustained attention (Hansen, Johnsen, & Thayer, 2009) as well as an n-back working memory task known to depend on executive control (Hansen, Johnsen, & Thayer, 2003). Mathewson, Dywan, Snyder, Tays, and Segalowitz (2011) also found that higher resting RSA was associated with enhanced performance on those aspects of a touch-screen spatial maze task that required executive control. These findings suggest that higher resting RSA, a marker of increased autonomic flexibility, is associated with enhanced performance in the context of cognitive tasks that tap executive control. They also provide support for theoretical models that link higher resting RSA with enhanced cognitive performance, including Porges' Polyvagal Theory (1995) and Thayer and Lane's Neurovisceral Integration Hypothesis (2000; 2009).

We note, however, that although Hansen et al. (2003) reported an association between resting RSA and executive control, the same association did not occur in the context of a simple response time task. Other researchers have found that cognitive performance was not associated with resting RSA but rather with other measures of RSA, including on-task RSA and RSA reactivity (Chapman, Woltering, Lamm, & Lewis, 2010; Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009; Mathewson et al., 2010). Thus, the complex nature of relations between various measures of phasic vagal cardiac control (resting, on-task, reactive RSA) and cognitive performance does not yet permit definitive conclusions to be drawn regarding the role that autonomic regulatory function plays in the allocation and control of attention.

Nonetheless, if autonomic regulation contributes in an essential way to attentional control, this relationship should become more evident as attentional demands increase (unless demands greatly exceed an individual's capacity, which may affect motivation in a negative way). To test this hypothesis, we used a modified version of Hester, Murphy, and Garavan's (2004) Working Memory Inhibitory Control (WMIC) task. The WMIC task taps two major executive functions, inhibitory control and working memory, across three levels of task difficulty. The WMIC has been shown to elicit activation in the ACC and dorsolateral prefrontal cortex (DLPFC; Hester et al., 2004). These regions, along with other midbrain and higher cortical regions, e.g., insular cortex, ventromedial prefrontal cortex, the central nucleus of the amygdala, and the hypothalamic nuclei, are considered part of a central autonomic network (CAN) that is also responsible for modulating autonomic influences on heart rate (Benarroch, 1993; Critchley, Corfield, Chandler, Mathias, & Dolan, 2000; Napadow et al., 2008; Ter Horst & Postema, 1997). Because both the ACC and DLPFC are recognized CAN regions and because Hester et al. (2004) noted the centrality of these two structures for performance on the WMIC, we thought it represented an appropriate task with which to explore potential relations between RSA and cognitive performance.

Whereas RSA reflects phasic vagal cardiac control, rate pressure product (RPP, systolic blood pressure x heart rate/100) represents the heart's overall workload (Kitamura, Jorgensen, Gobel, Taylor, & Wang, 1972). Research indicates that RPP correlates highly with myocardial oxygen consumption, or the amount of oxygen the heart consumes to meet current metabolic demands associated with mental or physical challenge (Gobel, Norstrom, Nelson, Jorgensen, & Wang, 1978; Nelson, Gobel, Jorgensen, Wang, & Taylor, 1974). Thus, a higher resting level of RPP would indicate that the heart is experiencing a relatively greater workload than it should even in the absence of physical or mental challenge (Fredericks, Choi, Hart, Butt, & Mital, 2005). We assume that inadequate modulation through the parasympathetic system (lower RSA) could result in higher cardiac workload and hence higher levels of RPP. Specifically, we would expect this to be the case for older adults for whom autonomic regulatory function is reduced (De Meersman & Stein, 2007). However, there is a possibility that these relations could hold for younger adults as well given that higher blood pressure is associated with poorer cognitive performance across age groups (Robbins, Elias, Elias, & Budge, 2005). Despite its potential relevance for cognitive task performance, RPP has not received much attention in the cognitive aging literature to date. Therefore, the second goal of the present study was to investigate whether pre-task RPP, or resting cardiac workload, would also be associated with task performance among older and/or younger adults.

The third goal of this study was to determine whether our measures of cardiac regulation (RSA/RPP) were associated with event-related potentials (ERPs) generated in the ACC and closely aligned structures. Chapman and colleagues (2010) found a relationship between on-task RSA and N2 amplitude during an emotionally-arousing Go/NoGo task. Because the NoGo N2 is commonly localized to the ACC, Chapman et al. claimed that this association highlighted the importance of the ACC as an integration zone for cognitive control and bodily arousal. As well, we have reported a relationship between resting RSA and the size of the error-related negativity (ERN) and the error positivity (Pe), two response-locked components associated with the commission of an error (Dywan, Mathewson, Choma, Rosenfeld, & Segalowitz, 2008). Although there is continuing debate surrounding the exact functional significance of these ERP components, it is generally agreed that the ERN reflects critical aspects of error detection and performance monitoring (Taylor, Stern, & Gehring, 2007). What is important for the current study is that evidence points to a generator site in the ACC for both components: the ERN, usually observed in dorsal regions and related supplementary motor areas, and the Pe in rostral regions (van Boxtel, van der Molen, & Jennings, 2005; Van Veen & Carter, 2002). As stated previously, the ACC is a key structure within CAN that modulates autonomic arousal (Critchley et al., 2003). Thus, by examining the ERN and Pe in the present study, we will not only be able to determine whether our measures of autonomic regulation (RSA/RPP) relate to cognitive control processes supported by the ACC, but also whether RSA/RPP relate to the size of ACC-generated electrophysiological components elicited in response to error commission.

Our fourth and final goal was to examine the above questions from an aging perspective. It is well established that aging is associated with declines in attentional control (Prakash et al., 2009). Effective attentional control is at least partly dependent on the ACC (Crottaz-Herbetter & Menon, 2006) and involves two processes, the enhancement of task-relevant information and the suppression, or inhibition, of information that is not relevant (Bar et al., 2006). Importantly, there is evidence that older adults have particular difficulties with the inhibition aspect of attentional control (Gazzaley, Cooney, Rissman, & D'Esposito, 2005). Moreover, there is general agreement that reduced attentional control is usually attributed to age-related decline in the structural integrity of the DLPFC (Milham et al., 2002) and medial PFC (mPFC), including the ACC (Kochunov et al., 2009), and that a decline in dopaminergic enervation of frontal brain regions plays a role (Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006). However, as stated previously, both the DLPFC (Napadow et al., 2008) and ACC (Critchley et al., 2003; Matthews, Paulus, Simmons, Nelesen, & Dimsdale, 2004; Ter Horst & Postema, 1997) are also involved in modulating autonomic arousal, and this centrally mediated regulation is also vulnerable to the aging process (Korkushko et al., 1991). Thus, a remaining question is whether the mild autonomic dysregulation that is associated with aging also contributes to reduced attentional control among older adults, over and above the general decline associated with age. This would be evident if those older adults who demonstrate greater autonomic dysregulation (lower resting RSA; higher RPP) are less able meet the behavioural demands of a complex, attention-demanding task.

1.1 The current study

Electrophysiological and cardiac responses were recorded while older and younger adults completed a modified version of the WMIC task (Hester et al., 2004), a primary inhibitory control task with an embedded working memory (WM) component. Participants were instructed to hold a set of letters in mind and then make Go and NoGo responses to serially presented probes. Participants were instructed to hit a response key for probe letters that *did not match* those from the WM set (Go trials) and to withhold responding to probe letters that *did match* those currently held in WM (NoGo trials).

Our modified version of Hester et al.’s (2004) WMIC task offered a unique context in which to explore potential relations between autonomic, electrocortical and behavioural indices of regulatory functions associated with the CAN system. First, the WMIC task was expected to present a strong challenge to response control because the letters that participants are maintaining in WM are the same letters that require the withholding of a response when they appear as probes. Second, the WMIC paradigm represents a unique dual task context. The majority of dual tasks include a secondary task with participants switching their focus between primary and secondary task objectives as needed. However, because task switching efficiency has been shown to decline with age (Kray & Lindenberger, 2000), these types of dual task paradigms can offer younger adults a distinct advantage. The WMIC task, however, requires individuals to utilize the contents of WM (the secondary task) in order to execute appropriate Go/NoGo responses (the primary task). Consequently, the design of the WMIC task does not involve participants switching between primary and secondary objectives, and as such, it allows for the examination of dual task performance among older and younger adults without potential contamination from younger adults' greater task switching efficiency.

In addition to its unique inhibitory control and dual task nature, the WMIC task utilizes three levels of WM load to constrain attentional capacity. Thus, we can assess the relationships in question from an additive factors perspective. That is, as the need for control processes increase, the relevance of ACC function, as indexed by the amplitude of the ERN/Pe, and autonomic regulation, as indexed by RSA and RPP, should become more evident with respect to performance, i.e., accuracy and response times (RTs). Additionally, based on current functional magnetic resonance imaging (fMRI) findings, Hester et al. (2004) confirmed the presence of enhanced ACC and DLPFC activation associated with WMIC performance. Because these structures are part of the CAN (Benarroch, 1993) and have also been shown to modulate autonomic arousal (Critchley et al., 2003; Matthews et al., 2004; Ter Horst & Postema, 1997), we propose that those executive function tasks that are particularly dependent on ACC and DLPFC support might also be particularly sensitive to indices of autonomic regulatory control (RSA/RPP).

1.2 Hypotheses

In general, we expected older adults to make more NoGo errors across all three WM loads of the modified WMIC compared to their younger counterparts. We also expected older adults to produce smaller ERN/Pe components in response to the commission of NoGo errors, a finding which has been reported in other aging studies (Band & Kok, 2000; Falkenstein, Hoormann, & Hohnsbein, 2001; Mathewson, Dywan, & Segalowitz, 2005; Nieuwenhuis et al., 2002; West, 2004), and is likely due to an age-related reduction in available dopamine in striate and extrastriate prefrontal systems (e.g., Cruz-Muros et al., 2007), particularly since it is thought to be a dopamine signal that marks the experience of making a response that does not conform to intended goal relevant behaviour (Holroyd & Coles, 2002). We further hypothesized that within each age group, centrally-mediated autonomic regulation (RSA) and cardiac workload (RPP) would be associated with behavioural performance, with the strongest relations occurring in the most demanding condition. Moreover, we were interested in exploring whether pre-task RSA and/or RPP would relate to the size of ACC-generated electrocortical components, including the ERN and Pe. Finally, we expected that the size of these relationships would be most evident when autonomic regulation would presumably be most beneficial, i.e., at higher levels of WM load.

2. Methods

2.1. Participants

Participants included 25 Brock University students, and 19 healthy older adults from the local community. Three younger adults were excluded from the analysis because their error rates exceeded 50%, and one older adult was excluded due to poor EEG quality. Therefore, the final sample included 22 younger adults (17 women, 18-27 years, *M* = 20.5) and 18 older adults (11 women, 65-83 years, *M* = 72.3). Participants had normal or corrected to normal vision, were fluent English speakers, and were free from self-reported cardiac, neurological, or psychiatric conditions, and from use of psychoactive medications or beta-adrenergic blockers.

Older adults were administered the Mini-Mental Status Examination (MMSE), a brief screening device used to detect the presence of cognitive impairment in aging populations. All scored within the normal range on this measure (26-30, *M* = 28.6, *SD* = 1.1). Education level did not differ between the two groups ($p > .31$), but as expected, older adults scored higher on the SCOLP “Spot the Word” vocabulary task (*M* = 85% correct) than younger adults (*M* = 77% correct), $t(38) = 2.69$, $p < .02$. There was no difference in the years of education for older (14.1) and younger adults (14.4). The project received clearance from Brock University’s Research Ethics Board, participants gave informed consent, and all individuals received a small honorarium for participating.

2.2. Working Memory Load Inhibitory Task (WMIC)

The modified WMIC task (see Figure 2-1) required participants to hold a set of letters in mind and then respond to single letter probes presented on a computer screen. Instructions were to hit a key when the probe did not correspond to any items currently in WM and withhold responding whenever a match occurred. We modified the task to include 18 runs, each of which included 101 probes to ensure a sufficiently large sample of errors on which to base stable error-related ERPs.

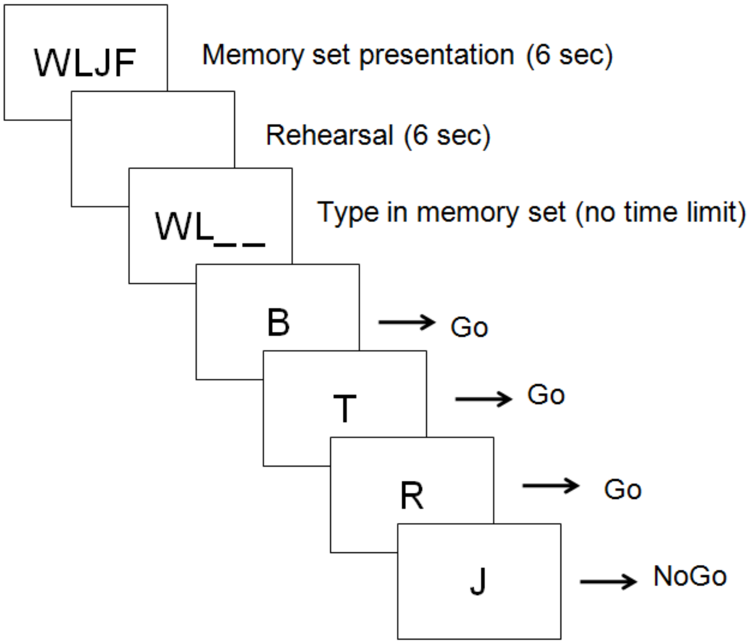

Figure 2-1. A depiction of the Working Memory Inhibitory Control Task (WMIC) in which participants are required to inhibit responding to any letter that is part of the set being kept in mind across a set of Go/NoGo trials. Four items represent a medium WM load.

At the start of each run, participants were shown a string of 2, 4, or 6 uppercase letters for 6 seconds. Memory set letter presentation was followed by a 6-second blank screen that constituted a rehearsal period. After this rehearsal period, a window appeared that instructed participants to type in the letters they were holding in mind. No time limit was imposed for this recall period. If participants did not enter the memory set correctly, a computerized signal alerted them and the letters were presented again for 6 seconds, followed by another 6-second rehearsal period. Most participants required no more than one presentation, and no more than one repetition was ever required. Once the memory set was entered correctly, a series of decision trials then ensued. Each decision trial consisted of a single uppercase letter presented for 700 ms followed by a 600 ms blank screen. Participants were instructed to press the space bar on a computer keyboard whenever the letter on the screen did *not* match one of the memory set letters (Go trials) and to withhold responding to trials featuring letters that were part of the memory set (NoGo trials).

The decision trials in each run included 76 Go (75%) and 25 NoGo trials (25%), a ratio that would ensure a bias towards Go responses, a bias that we expected would be particularly strong because of the natural tendency to respond whenever a match occurred. Three percent of NoGo trials immediately followed a previous NoGo trial so as to prevent participants from developing the rote response of always expecting a Go if a NoGo trial had just occurred. When the set of decision trials concluded, a window identical to that from the start of the run appeared, and participants were instructed to type in the memory set letters once again in order to ensure that any errors made during that run were the result of poor inhibitory control rather than memory failure over the course of the run. Again, no time limit was imposed for this recall period, and trials based on misremembered items were excluded from analysis. Once the participant typed in the memory set letters, the run was complete. The task involved 18 runs in total, 6 for each memory load size of 2, 4, or 6 letters resulting in a total of 456 Go and150 NoGo trials at each level of WM load.

Experimental runs were presented to each participant in an identical sequence, with the order of presentation counterbalanced for memory load requirements (2, 4, 6, 4, 6, 2, 6, 4, 2, 4, 6, 2, 2, 6, 4, 6, 4, 2). A 30-second break was provided between each run, with a longer 5 minute break at the half-way point (between runs 9 and 10). The task, including practice and breaks, took approximately 1 hour to complete.

2.3. Procedure

Upon arrival in the lab, participants completed a health history questionnaire, the SCOLP vocabulary test (Baddeley, Emslie, & Nimmo-Smith, 1992), and a simple, self-report mood screening measure. Participants then completed the modified WMIC while seated in a dimly lit, electrically and acoustically shielded room. Stimuli were presented using E-Prime research software (Psychological Software Tools, Inc.). Electroencephalography (EEG), electrocardiography (ECG), and respiration were recorded throughout the session, and resting blood pressure was measured before and after the task.

2.3.1. Electrophysiological Measures

EEG was collected using a 128 channel Active Two BioSemi system (BioSemi, Amsterdam). Signals were sampled at a rate of 512 Hz, digitized with a 24 bit ADC, and time-locked to the response (i.e., space bar press) starting 600 ms before the response and continuing 1,000 ms post-response (epoch=1,600 ms). A bandpass filter from 1 Hz to 30 Hz was used, and all electrodes were re-referenced offline to averaged mastoids for analysis. Trials that included moderate eye movements or blinks were corrected using a regression procedure developed by Gratton, Coles, and Donchin (1983). For correct Go trials, all epochs with midline amplitudes exceeding ±50 µV were automatically rejected. Because there were fewer NoGo error trials, each epoch was individually inspected and artifact rejection was performed manually. Response-locked, artifact-free EEG recordings were then averaged relative to a -400 ms to -100 ms pre-response baseline. For the ERN, response-locked correct Go and NoGo error trials were measured as the average amplitude of the voltage data between -50 and 100 ms at site FCz. For the Pe, response-locked correct Go and NoGo error trials were measured as the average amplitude between 100 ms and 325 ms post-response at site FCz. The sites and timing windows described above represented where and when the ERN and Pe components were maximal in our participants, patterns which align well with other research (e.g., Schreiber, Pietschmann, Kathmann, & Endrass, 2011). Brain Electrical Source Analysis (BESA, version 5.0; Megis Software, 2005) was used to examine voltage shifts in scalp topography across the recording period for the ERP responses, and a four shell ellipsoidal head model was used to fit the generator site of the ERN.

2.3.2. Cardiac measures

Basic heart rate (HR) was monitored throughout the testing session. Blood pressure readings (systolic: SBP; diastolic: DBP) using an automated sphygmomanometer were taken following a 5-minute rest period that preceded testing and again following another final 5-minute rest period that concluded the session. Both pre and post BP measures were taken to ensure that participants remained within normal BP range during the test situation, and two BP measures were taken each time for increased stability and reliability. ECG was monitored throughout the entire task and during the 5-minute pre-task and post-task resting periods. ECG signals were recorded from two electrodes placed on the participant's chest; about 2.5 cm below the right clavicle and between the 2 bottom-ribs on the person's left side. ECG signals were sampled at 512 Hz by the acquisition program (BioSemi) and digitized with a 24-bit ADC, then analyzed using a commercial software package (MindWare Heart Rate Variability Scoring Module 2.51, Mindware Technologies Ltd., Columbus, OH). R-R (interbeat) intervals were visually inspected and edited where necessary according to principles advocated by Berntson and Stowell (1998). Minute-by-minute estimates of RSA (heart rate variability at the respiratory frequency, 0.12- 0.4 Hz) were calculated via spectral analysis of the heart beat series using fast Fourier transformation and a Hamming window based on 1-minute epochs. A sample rate of 250 ms (4/sec) provided 240 samples (120 FFT bins), resulting in a frequency resolution of .01667 Hz. RSA is then expressed as the natural log transform of this frequency band, $ln(\text{ms}^2)$. Estimates of RSA, heart rate, and respiration were then averaged for the pre-task baseline and post-task resting periods. Again, pre and post-task measures were taken to ensure that participants remained within normal ranges during the test situation. For on-task RSA, 2 minute time frames from each of the 18 runs were selected, analyzed, and then averaged together. Pre and post-task RPP measures were calculated by multiplying resting systolic blood pressure and mean resting heart rate for that period, and dividing by 100.

2.3.3. Analyses

To investigate the effects of group and condition, data were subjected to a series of ANOVAs with interactions followed up by simple effects analyses. These were corrected for violations of Mauchley's Test of Sphericity, where necessary, utilizing the Huynh-Feldt correction for estimating the F-Statistics with the original degrees of freedom and corrected *p*-values reported in the text. Simple within-group correlational analyses were used to examine relations among autonomic, electrocortical and behavioural measures. All effects are based on two-tailed tests.

3. Results

3.1. Performance Data

Accuracy and response time data for the inhibitory control errors (Table 2-1) were analyzed using a 2 (age group) x 3 (load: low, medium, high) mixed model analysis of variance (ANOVA). For the proportion of NoGo errors, there was a main effect of load, $F(2, 76) = 148.71$, $p < .001$, $\eta^2 = .80$, indicating that NoGo errors increased in conjunction with the increasing working memory load. There was also a main effect of group, $F(1,38) = 8.28$, $p = .007$, $\eta^2 = .18$, but not in the expected direction in that older adults made a smaller proportion of NoGo errors (M = .19 ± .02) than younger adults (M = .27 ± .02). Finally, the interaction between load and group did not reach significance (p > .08), indicating that error rates increased across load in generally the same manner for the two groups.

Table 2-1.
Proportion of NoGo Errors, Go Corrects, and Average Go RT (in milliseconds) for Younger and Older Adults

	Younger Adults			Older Adults		
Load	NoGo Errors (SE)	Go Corrects (SE)	Correct Go RT (SE)	NoGo Errors (SE)	Go Corrects (SE)	Correct Go RT (SE)
Low	.20 (.02)	.99 (.001)	396 (11)	.10 (.02)	.99 (.004)	512 (16)
Med	.25 (.02)	.98 (.004)	463 (11)	.16 (.02)	.97 (.005)	598 (18)
High	.36 (.02)	.95 (.007)	502 (12)	.31 (.03)	.89 (.017)	646 (21)

Go accuracy levels were generally the inverse of the error level data. There were main effects of load and group (*p*s < .01), but, in the case of correct hits, these main effects were superseded by a load by group interaction, $F(2, 76) = 10.08$, $p = .002$, $\eta^2 = .21$. Follow-up analyses indicated that the groups did not differ markedly on Go accuracy for the low or medium loads (all *p*s > .07); however, when the WM load was high, older adults (M = .89 ± .02) were less likely to respond on Go trials than were younger adults (M = .96 ± .01), $t(38) = 3.43$, $p = .001$, suggesting a more cautious approach on the part of the older participants at that level of task difficulty. Analyses of RTs for correct Go trials indicated main effects for load and group (*p*s < .001); however, these were superseded by a group by load interaction, $F(2, 76) = 4.27$, $p = .033$, $\eta^2 = .10$, that showed a linear increase in Go RT for both groups across load but with a steeper increase for older relative to younger adults.

Given the longer RTs and lower NoGo error rate of the older group, we undertook a series of within-group analyses examining the correlations between correct Go RT and NoGo error rate. For younger adults at the low load, faster Go RTs were associated with increased NoGo errors ($r = -.55$, $p = .008$). Although the possibility of a speed-accuracy trade-off cannot be ruled out, we note that no other relations emerged between RT and NoGo error rate at the medium or high loads for younger adults (all *p*s > .35). Furthermore, there were no within-group relationships between RT and error rate for the older group across any of the loads (all *p*s > .47). Thus, with the exception of younger adults at the lowest WM load, there was little evidence that longer RTs alone could account for the ability to avoid inhibitory control errors.

We note here that, in an attempt to reduce confounds associated with age differences in WM, our analysis of inhibitory control errors was based only on trials for which participants accurately recalled the WM items. Although the number of recall errors were small for both groups (necessitating nonparametric analysis), a Mann-Whitney U test indicated that younger adults (M = 1.45 ± .31) had, in fact, made fewer WM set recall errors than older adults (M = 3.83 ± 1.07), $z = 2.46$, $p < .02$, thus justifying our decision to base our analyses only on those trials in which the WM items were accurately retrieved.

3.2 Heart rate, blood pressure, and respiration

HR was analyzed using a 2 (group) x 2 (test phase: pre-task, post-task) repeated measures ANOVA. Results indicated that mean HR did not differ between older (*M* = 66.61 ± 2.00) and younger adults (*M* = 67.26 ± 1.81, $p > .81$). Furthermore, HR was not affected by test phase, nor was there an interaction between test phase and group (all *p*s > .14). Systolic blood pressure (SBP) was higher in older (*M* = 140.01 ± 3.55 mm Hg) relative to younger adults (*M* = 101.46 ± 3.21 mm Hg), $F(1, 38) = 64.99$, $p < .001$, $\eta^2 = .63$, and higher at the end of testing (*M* = 124.77 ± 2.80 mm Hg) than at the beginning (*M* = 116.70 ± 2.35 mm Hg, $F(1, 38) = 17.15$, $p < .001$, $\eta^2 = .31$), with no interaction ($p > .47$). Diastolic blood pressure (DBP) was also higher in the older (*M* = 81.94 ± 1.64 mm Hg) relative to younger adults (*M*

= 65.74 ± 1.48 mm Hg), $F(1, 38) = 53.84$, $p < .001$, $\eta^2 = .59$, and higher at the end (M = 76.29 ± 1.30 mm Hg) compared to the beginning of testing (M = 71.39 ± 1.09 mm Hg, $F(1, 38) = 26.71$, $p < .001$, $\eta^2 = .41$, but again, this did not interact with group ($p > .15$). Finally, respiration rate did not differ between older (M = 12.33 ± .89) and younger adults (M = 14.14 ± .74, $p > .12$), and there was also no main effect of test phase and no interaction between test phase and group (all *p*s > .19).

3.2.1. RSA and RPP

RSA, based on continuous HR data, was calculated for time periods prior to, during, and after the WMIC task. Some participants displayed an irregular (i.e., short-long) HR pattern that prevented accurate assessment of RSA, and therefore, RSA data come from 21 of the 22 younger adults and 15 of the 18 older adults. RSA data were submitted to a 2 (group) x 3 (test phase: pre-task, on-task, post-task) repeated measures ANOVA. As expected, RSA was higher for younger adults (M = 6.46 ± .21 ln ms^2) compared to their older counterparts (M = 4.06 ± .25 ln ms^2), $F(1, 33) = 54.54$, $p < .001$, $\eta^2 = .62$. There was also a main effect of phase, $F(2, 66) = 8.62$, $p = .001$, $\eta^2 = .21$, which indicated that across both groups there was an increase in RSA at post-task (M = 5.48 ± .17 ln ms^2) relative to on-task (M = 5.02 ± .18 ln ms^2, $p = .003$), suggesting a return to increased parasympathetic control upon task completion. However, pretest RSA (M = 5.29 ± .18 ln ms^2) did not differ reliably from either of the other measures. There was also no interaction with group ($p > .37$), indicating that there was no difference between older and younger adults in their pattern of RSA responses across test phases.

RPP computations, (HR x SBP)/100, depended on blood pressure readings that were taken only before and after the WMIC, thus only pre- and post-task scores were available.

These were entered into a 2 (group) x 2 (test phase: pre, post) repeated measures ANOVA. As expected, RPP was markedly higher in older (*M* = 92.85 ± 2.75) compared to younger adults (M = 67.84 ± 2.49), *F*(1, 38) = 45.54, $p < .001$, $\eta^2 = .55$. There was also a main effect of test phase, *F*(1, 38) = 5.02, $p = .031$, $\eta^2 = .12$, indicating that RPP increased from pre-task (*M* = 78.35 ± 1.97) to post-task (*M* = 82.34 ± 2.14), but again, there was no interaction ($p > .28$), indicating that this shift occurred to the same degree for both groups. Thus, the cardiovascular functioning of the older relative to the younger group was characterized by higher overall BP, reduced phasic vagal cardiac control (RSA), and increased cardiac workload (RPP). Taken together, these results suggest the presence of mild autonomic dysregulation in the older group.

3.3. Predicting Inhibitory Control from Autonomic Variables

We originally hypothesized that within both age groups, higher pre-task RSA and lower pre-task RPP would relate to better response control. Thus, higher vagal cardiac control and lower cardiac workload would be reflected in fewer NoGo errors. We also expected these relations to increase in a graduated way across the three WM loads such that these associations would be greatest at the highest load. In addition to our examination of pre-task RSA, we attempted to predict error rate from on-task RSA directly. Thus, in the present analysis on-task RSA refers to on-task RSA adjusted for pre-task levels, which, in effect, provides an index of RSA reactivity, such that the lower the residual, the greater the reactivity.

Contrary to expectations, pre-task levels of RSA did not relate to the number of NoGo errors at any of the three WM loads for older (*p*s > .68) or younger adults (*p*s > .64).

Furthermore, no consistent associations emerged between on-task RSA and NoGo errors across loads for older (all *p*s > .06) or younger adults (all *p*s > .66).

Interestingly, although RPP is not typically examined with respect to cognitive performance, it proved to be more robust and consistent in its relationship with participants' responses to the WMIC task. However, the nature of these relationships differed as a function of age. For younger adults, pre-task RPP was positively related to correct Go RT, indicating that higher levels of cardiac workload were associated with slower response tendencies in general and this association increased with load (Figure 2-2). Although this relationship was just a trend at the low load (*r* = .40 *p* = .062), it became more robust at the medium (*r* = .43 *p* = .046) and high loads (*r* = .52 *p* = .013). However, cardiac workload within the younger group did not relate to error rate at any level of task difficulty (all *p*s > .36).

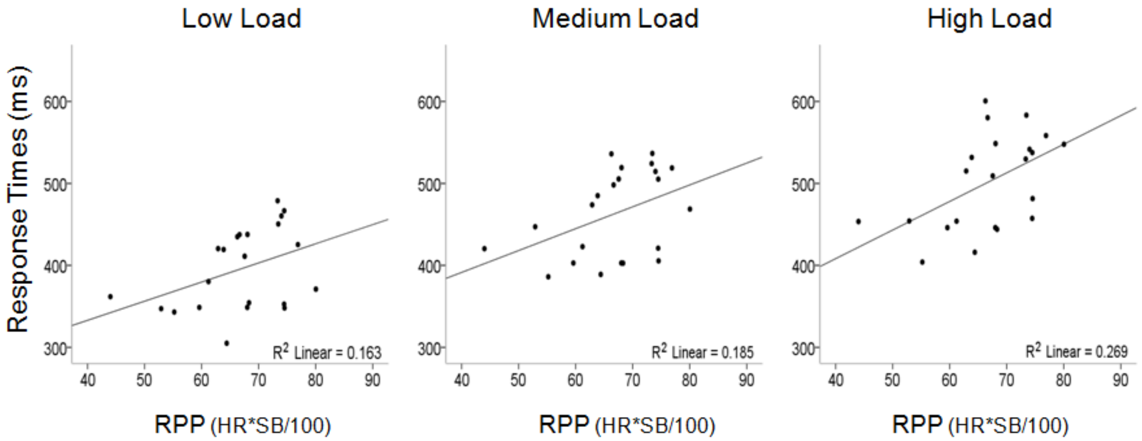

Figure 2-2. Relations between pre-task resting cardiac workload (RPP) and response times across the three levels of working memory load for younger adults.

Older adults, on the other hand, demonstrated a fairly consistent pattern of association between pre-task RPP and NoGo errors (Figure 2-3). Specifically, older adults with higher pre-task RPP made more NoGo errors at low (*r* = .59, *p* = .009) and high WM loads (*r* = .49, *p* = .038), with a borderline relationship at the medium load (*r* = .45, *p* = .059). RPP did not relate to RTs at any load for older adults (all *p*s > .24). Thus, in both groups, the level of cardiac workload prior to the onset of the task did have implications for task performance with pretest RPP being reflected in RTs for the younger group and in actual error rates for older adults.[2]

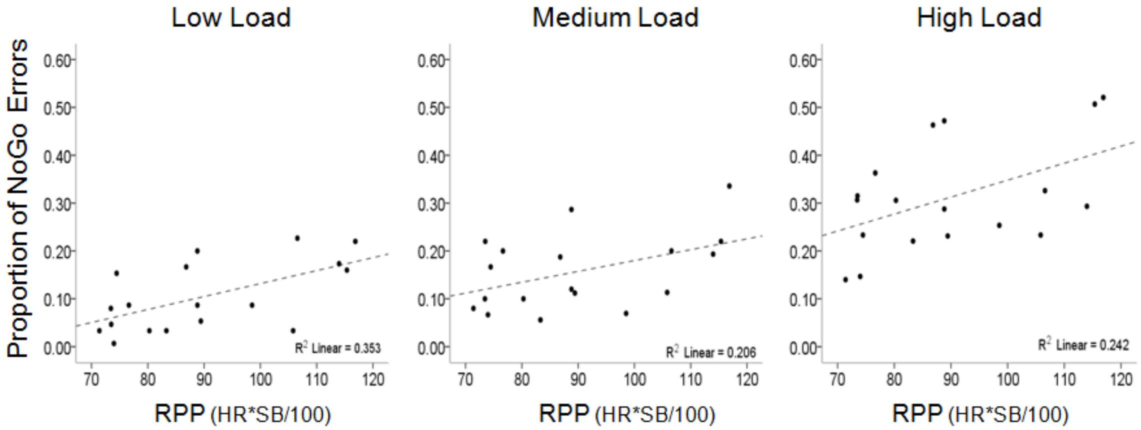

Figure 2-3. Relations between pre-task resting cardiac workload (RPP) and the proportion of NoGo errors across the three levels of WM load for older adults.

Table 2-2.
Correlations between Autonomic and Behavioural Performance Measures for Younger and Older Adults

		NoGo Errors			Correct Go RT		
		Low	Medium	High	Low	Medium	High
Younger Adults	Pre-task RSA	*r* = .11	*r* = -.06	*r* = .07	*r* = -.01	*r* = -.06	*r* = -.12
		p = .648	*p* = .792	*p* = .772	*p* = .998	*p* = .801	*p* = .613
	On-task RSA	*r* = .05	*r* = .07	*r* = .09	*r* = -.16	*r* = -.13	*r* = -.02
		p = .828	*p* = .772	*p* = .680	*p* = .493	*p* = .581	*p* = .930
	Pre-task RPP	*r* = -.20	*r* = .01	*r* = -.073	*r* = .40	*r* = .43	*r* = .52
		p = .364	*p* = .951	*p* = .747	*p* = .062	*p* = .046	*p* = .013
Older Adults	Pre-task RSA	*r* = -.50	*r* = -.08	*r* = -.11	*r* = -.10	*r* = -.07	*r* = -.11
		p = .858	*p* = .781	*p* = .686	*p* = .713	*p* = .805	*p* = .686
	On-task RSA	*r* = -.29	*r* = -.49	*r* = -.039	*r* = -.39	*r* = -.35	*r* = -.09
		p = .288	*p* = .060	*p* = .891	*p* = .143	*p* = .202	*p* = .728
	Pre-task RPP	*r* = .59	*r* = .45	*r* = .49	*r* = -.01	*r* = -.24	*r* = -.29
		p = .009	*p* = .059	*p* = .038	*p* = .993	*p* = .347	*p* = .246

3.4. ERP responses

Grand average ERP waveforms associated with error commission are shown in Figure 2-4. ERPs were calculated only for participants who made a minimum of 7 errors in order to

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[2] Pre-task RSA, on-task RSA, and pre-task RPP were also examined to determine whether they predicted the effect of load (difference in NoGo errors across loads), but no relationships reached significance (all ps > .09).

ensure stable ERP component averages (see, for example, Olvet & Hajcak, 2009; Pontifex et al., 2010). Thus, ERP analyses were based on data from 21 of the 22 younger adults and 17 of the 18 older adults.

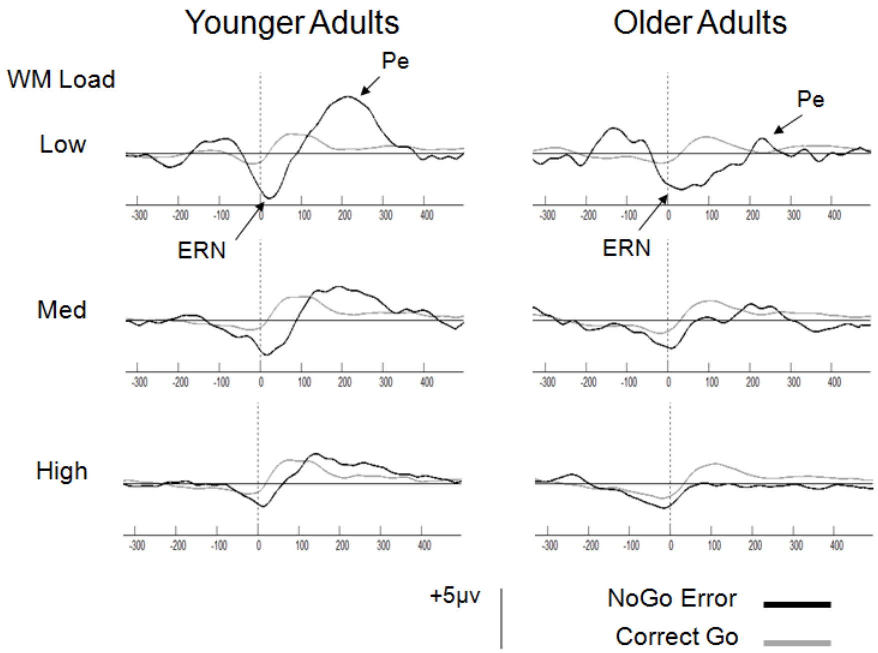

Figure 2-4. Response-locked event-related potentials (ERNs, Pe's) depicted at frontal-central site (FCz) associated with errors and correct trials at three levels of WM load for younger and older adults.

ERN analyses were carried out in a 2 (group) x 3 (load) x 2 (accuracy: correct Go vs. incorrect NoGo) repeated measures ANOVA. Although there were main effects of accuracy and of load (all *p*s < .02), these were superseded by an accuracy by load interaction, $F(2, 72) = 6.63$, $p = .003$, $\eta^2 = .16$. Follow-up analyses indicated that, whereas the amplitude of the ERN decreased in a linear fashion with load (-2.49 ± .47 µV; -1.70 ± .32 µV; -1.00 ± .30 µV), the ERP following correct Go responses maintained a relatively stable amplitude as load-size increased, with only a slight increase at the medium level (.27 ± .27 µV; .36 ± .25 µV; .27 ± .25 µV). Additionally, there was no main effect of group ($p > .53$), and group did not interact with accuracy ($p > .46$) or load ($p > .53$) in predicting the amplitude of the ERN.

There was a main effect of group indicating that younger adults produced larger Pe responses (1.85 µV ± .24 µV) than older adults (.44 ± .27 µV), $F(1, 36) = 15.34$, $p < .001$, $\eta^2 = .30$. There was also an interaction between accuracy and group, $F(1, 36) = 18.35$, $p < .001$, $\eta^2 = .34$, indicating that the Pe response was larger on NoGo relative to Go trials for the younger group, $F(1, 20) = 32.55$, $p < .001$, $\eta^2 = .62$, a differentiation that was not present for the older adults ($p > .15$).

Thus it would appear that the ERN response to inhibitory control errors was not diminished in our older adults. It was the Pe response that differed most between groups. It was generally diminished in amplitude and less responsive to error in the older group.

3.5 Predicting Behavioural Performance from ERPs

We created residual measures of the ERN and Pe by removing the shared variance in ERP amplitudes associated with correct Go responses from those associated with NoGo errors. These residuals represented the ERP response to NoGo errors adjusted for the ERP response on correct Go trials. It is these residuals that were then subsequently entered into correlational analyses with behavioural responses and indices of cardiac function.

Only a few modest relations emerged between ERPs and behavioural performance. We found that smaller, less negative ERNs (residualized on correct trials) were associated with slower behavioural RTs, ($r = .44$, p = .05). Smaller Pe residuals were also associated with slower RTs ($r = -.48$, $p = .03$) (See Figures 2-5a and 2-5b). However, these associations between ERN/Pe and RTs occurred only for younger adults and only at the medium load (all other ps > .06). There were no strong or consistent relationships between the ERN or Pe and the actual NoGo error rate across any of the WM loads for older (all ps > .14) or younger adults (all ps > .10).

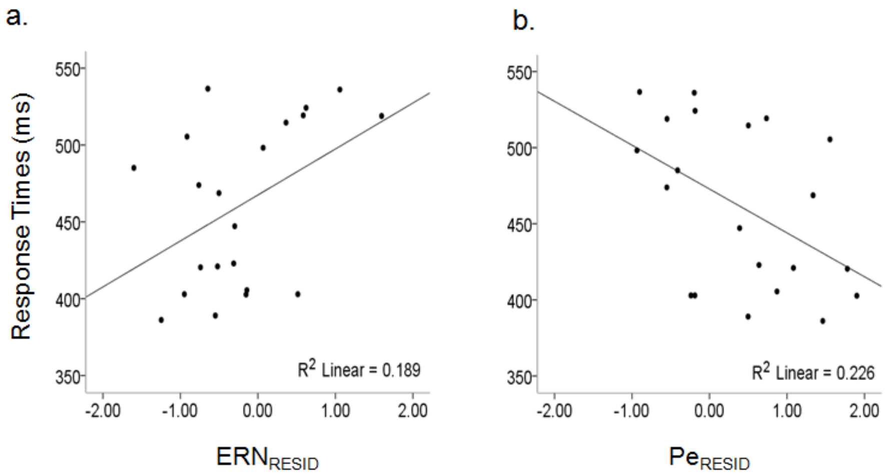

Figure 2-5. Relations at the medium WM load between response times and amplitude of (a) the error-related negativity (ERN) and (b) the error positivity (Pe), adjusted for amplitude on correct trials, for younger adults.

3.6 Predicting ERPs from Autonomic Variables

When it came to associations between RSA and error-related ERPs (residualized on the basis of correct trials), effects were again modest. Among younger adults, higher pre-task RSA was associated with larger Pe amplitudes (Figure 2-6), but again, only at the medium load ($r = .46$, $p = .043$; all other ps > .33). These relationships were not evident in the older adult data (all ps > .21), and there were no relations between pre-task RSA and the ERN for either group (all ps > .14). Furthermore, on-task RSA was not associated with ERN or Pe amplitude for the older (all ps > .82) or younger (all ps > .20) group. We note that the RSA and ERP associations were often most apparent at the medium WM load. It might be because the medium WM load allows for the most variance associated with individual differences thus enabling these subtle associations to emerge.

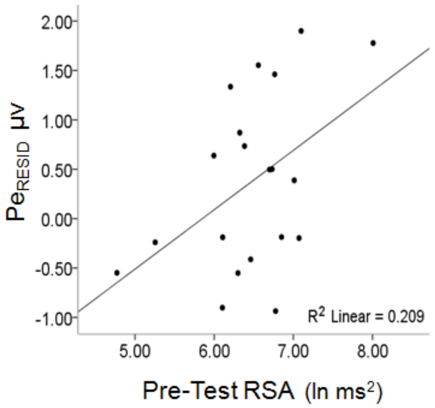

Figure 2-6. Relations at the medium WM load of pre-task resting RSA with the amplitude of the error-related positivity (Pe), adjusted for amplitude on correct trials, for younger adults.

RPP was the autonomic variable that demonstrated the most consistent pattern of association with the ERPs. Specifically, younger adults demonstrated a positive relationship between pre-task RPP and the size of the ERN across two of the three loads. Although only marginally related at the easy load, $r = -.07$, $p > .75$, the relationship became evident at the medium load, $r = .43$, $p = .05$, and was even more robust at the high load, $r = .64$, $p = .001$. Thus, for young adults, higher cardiac workload at the start of the task was associated with smaller ERNs in response to errors at medium and high loads (Figure 2-7). RPP did not relate to the amplitude of either the Pe or ERN (all *p*s > .18) for older adults.

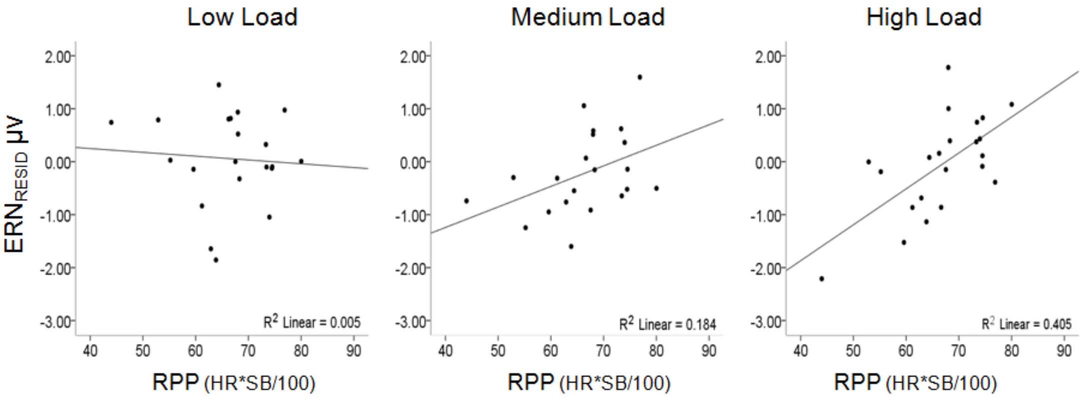

Figure 2-7. Relations across the three levels of WM load between pre-task resting cardiac workload (RPP) and the amplitude of the error-related negativity (ERN), adjusted for amplitude on correct trials, for younger adults.

3.7 Source modeling of the ERN

The ERN was the electrocortical component most consistently associated with autonomic function as measured by pretest RPP but, even so, it was not associated with either error rate or RSA. Further examination of this component revealed typically-observed voltage scalp distributions across both groups across all three WM loads (Figure 2-8). We averaged responses across all three loads and modeled the dipoles for each group based on this average ERN effect, i.e., error relative to correct responses. As can be seen in Figure 2-9, our models resulted in satisfactory fits that localized primary dipoles for both groups in the region of the ACC with less than 10% of the variance unaccounted for in each case. Thus, our ERNs appeared to adequately reflect an ACC-based error-monitoring response but, nonetheless, were associated only with pretest cardiac workload and not with indices of parasympathetic control or performance accuracy, as one might have expected.

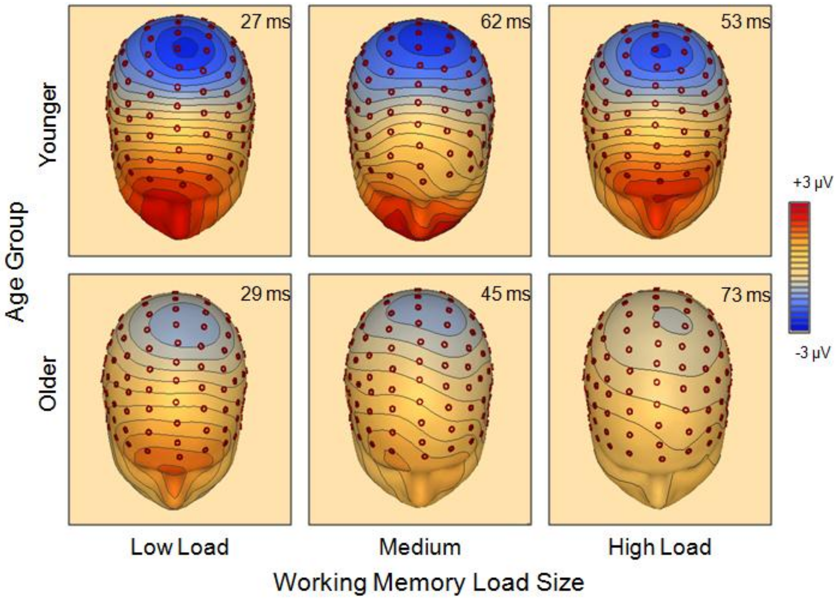

Figure 2-8. Voltage scalp distribution maps representing the scalp topography of the error-related negativity (ERN). Maps are derived from average difference waveforms (error NoGo trials – correct Go trails) for each working memory load and represent the ERN effect within each age group.

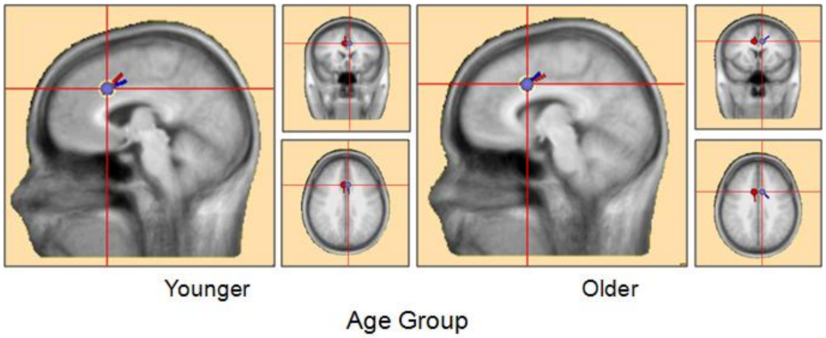

Figure 2-9. Saggital, transversal, and coronal views of major dipoles associated with the error-related negativity (ERN) based on average difference waveforms (error NoGo trials – correct Go trials) across all three working memory loads for each age group.

4. Discussion

Our goal was to determine whether certain autonomic variables (phasic vagal cardiac control and cardiac workload) related to behavioural and electrophysiological indices of executive function, and whether these associations changed with age. Thus, RSA and RPP were examined as older and younger adults performed a complex Go/NoGo task at low, medium, and high levels of WM load. Results indicated that Hester et al.'s (2004) WMIC task was successfully translated from an fMRI to an ERP paradigm. As expected, within both age groups RTs and NoGo errors increased systematically from low to medium to high WM load conditions. Less expected was the fact that older adults made fewer NoGo errors across all three WM loads compared to their younger counterparts. Older adults were also slower, which was likely adaptive for them but follow-up analyses did not suggest a strong relationship between RT and accuracy within groups. Thus, despite the fairly consistent view that aging is associated with impaired inhibitory control, our data indicate that older adults do not always make more inhibitory control errors. There are other such reports in the literature (e.g., Schreiber et al., 2011) despite demonstrated age-related change in attentional allocation (Vallesi, Stuss, McIntosh, & Picton, 2009), suggesting that failed inhibitory control on the part of older adults may be highly dependent on task-specific characteristic (Feyereisen & Charlot, 2008).

Autonomic measures demonstrated the predicted pattern in that they were strongly and consistently sensitive to age. For instance, resting RSA was markedly lower in older relative to younger adults as is typically observed (e.g., De Meersman & Stein, 2007). The inverse was also true, with baseline RPP, our index of cardiac workload, being markedly higher in the older relative to the younger adults. These results are consistent with the idea that aging can result in a form of mild autonomic dysregulation, whereby the balance shifts from parasympathetic to sympathetic predominance in older adults.

Our central finding, however, was that autonomic variables were in fact associated with behavioural and electrocortical indices of inhibitory control, and that these associations differed as a consequence of age. More importantly perhaps was that fact that the most robust and consistent relations with cognitive performance occurred, not with ERP components reflecting an actual brain response to having made an error, but rather, with indices of autonomic regulation, particularly, cardiac workload (RPP). Interestingly, while RSA has received more attention than RPP in the cognitive literature, no strong, consistent relationships emerged between RSA and behavioural performance within the older or younger group. For this task, most of the variance in performance for older and younger adults was associated with RPP. Older adults with higher levels of resting RPP made more inhibitory control errors on NoGo trials. Our findings complement recent results reported by Mathewson et al. (2011) who found that higher pre-task levels of resting RPP among older adults were associated with increased performance monitoring errors on a touch-screen maze task.

Higher cardiac workload, as reflected in RPP, is known to be associated with a host of cardiovascular complications including acute myocardial infarction, angina pain, and overall risk of cardiovascular mortality (Atkinson, Leary, George, Murphy, & Jones, 2009; Deedwania & Nelson, 1990). However, our data and those of Mathewson et al. (2011) demonstrate that the risks of increased cardiac workload among older adults extend beyond cardiovascular health and include cognitive performance as well. Relevant to this, Backs and Seljos (1994) have shown that individuals who performed most poorly on a continuous memory task were the ones who demonstrated the greatest energy expenditure during the task itself. Our results along with Mathewson et al.'s work (2011) extend these findings by demonstrating that those older adults whose cardiovascular systems were more active at rest, i.e., before the task even began, tended to perform more poorly on the cognitive task that followed. Also relevant is the demonstrated link between hypertension and diminished cognitive function (Breteler, 2000; Robbins et al., 2005; Saxby, Harrington, McKeith, Wesnes, & Ford, 2003; Waldstein, 2003; Waldstein, Brown, Maier, & Katzel, 2005). Hypertension has been shown to adversely affect a broad range of cognitive functions, but importantly, executive functions seem to be particularly susceptible (Raz, Rodriquez, & Acker, 2003). This may be due to the fact that the PFC seems particularly vulnerable to structural manifestations of hypertension, including increased white matter hyperintensities (WMHs) and reduced overall white matter volume (Raz et al., 2003; Raz, Rodriquez, Kennedy, & Acker, 2007). For instance, Raz and colleagues (2003) reported associations between greater frontal WMHs, smaller PFC volume, and increased perseveration errors among hypertensive older adults. We note, however, that in our study, it was neither the rate (HR) nor the force (systolic BP) of contractions alone that were associated with NoGo performance, but rather, it was the product of these two measures together, representing the heart’s overall workload, that demonstrated the strongest, most consistent associations with performance.

Although resting levels of RPP were not related to NoGo error rate in the younger group, RPP was consistently related to both RTs and ERN size. For instance, those younger adults with higher RPP at the start of the task had slower RTs and produced smaller electrocortical responses on error trials during the task itself. In effect, those younger adults with higher levels of cardiac workload at pre-task baseline were in some ways more like older adults with respect to RT and with respect to our usual expectations regarding an age-related reduction in the size of the ERN.

Of particular note is the range of RPP within and between the two age groups. Specifically, those younger adults who were in the upper range of RPP within their age group demonstrated RPP levels that were similar to those of older adults who were at the lower range of RPP within their age group. We refer to the point where RPP intersected for older and younger adults as the ‘moderate’ RPP level. Again, lower (moderate) levels of RPP were clearly beneficial to performance in the older group and would, of course, be indicative of better cardiovascular health within this group of participants (Atkinson et al., 2009; Deedwania & Nelson, 1990). Similarly, one could conclude that moderate RPP within the younger group (i.e., RPP at the upper range within their age group) was also adaptive in the present task. Responding more slowly in general may have reflected an adaptive level of cautiousness. Similarly, it may be that among young individuals, those who appreciated the high likelihood of making a NoGo error and thus demonstrate a higher level of caution, would be less surprised when they made an error resulting in smaller ERNs and Pe’s.

Nonetheless, with the exception of these associations, we note that neither the ERN nor the Pe was consistently related to actual accuracy rates.

The ERN and Pe were, nonetheless, differentially affected by age. ERNs, thought to represent low-level registration that an error has occurred (Bettcher & Giovannetti, 2009), were of similar amplitude and became smaller with each increase in WM load (Dywan et al., 2008; Mathewson et al., 2005), a pattern that has been attributed to greater uncertainty regarding accuracy of responses under more demanding task conditions (Pailing & Segalowitz, 2004). Eppinger, Kray, Mock, and Mecklinger (2008) have argued that reduced ERNs (e.g.,Band & Kok, 2000; Falkenstein et al., 2001; Mathewson et al., 2005; Nieuwenhuis et al., 2002; West, 2004) are not a reflection of age *per se.* Rather, they reflect the less efficient learning of the correct response on the part of older adults. When Eppinger and colleagues equated performance levels among older and younger adults, they observed similar ERN amplitudes in both groups. The Pe's, however, often thought to reflect further conscious processing of the error (Falkenstein, 2000; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001), were smaller in older adults, showing the typical decline with age. Thus, it would appear that these distinct electrocortical aspects of error monitoring (i.e., the ERN and Pe) can be differentially affected by age and task parameters (see also, Bettcher & Giovannetti, 2009).

We recognize that the present study is limited by its small sample size, especially in the older group. Nonetheless, these data revealed a consistent relationship between RPP and behavioural and electrophysiological indices of cognitive performance. It will be important, however, to follow up with a larger sample of older adults who demonstrate a broader range of hypertensive profiles. It would also be beneficial to examine on-task RPP and RPP reactivity to determine whether dynamic changes in cardiac workload throughout the task would provide additional insight regarding the association between cardiac workload and higher levels of executive control.

Conclusion

The central result from the present study was that the most robust and consistent relations with cognitive performance occurred, not with ERP components reflecting an actual brain response to having made an error, but rather, with indices of autonomic regulation, particularly RPP, an index of myocardial oxygen consumption. The present study, therefore, provides additional support for the idea that the success of complex mental operations cannot be explained solely on the basis of cortical activity but that they are highly dependent on more broadly-based neurophysiological systems (Porges, 1995; Thayer & Lane, 2000; 2009). In fact, our results extend the discussion beyond the role of RSA in cognitive performance and highlight the importance of cardiac workload, a measure which is seldom considered within general cognitive and/or aging research. Thus, our data provide support for the growing consensus that attentional control must be considered from a broader perspective that better integrates cognition and autonomic regulation and that acknowledges how these relationships may be affected by age.

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Chapter 3: Factors influencing the role of cardiac autonomic regulation in the service of cognitive control[3]

1. Introduction

Models of neurovisceral integration (Benarroch, 1993, 1997; Critchley, 2005; Porges, 1995; Thayer & Lane, 2000, 2009) posit the simultaneous engagement of autonomic, attentional, and emotional systems in the support of self-regulation and adaptive behaviour. Respiratory sinus arrhythmia (RSA) is the high frequency variation in the beat-to-beat interval of heart rate that accompanies normal respiration. It is considered an index of parasympathetic cardiac control and a marker of autonomic flexibility in adapting to environmental demands (Beauchaine, 2001; Berntson, Bigger Jr., et al., 1997; Porges, 1995; Thayer & Lane, 2000, 2009). RSA is modulated by a set of midbrain and higher cortical regions that include the insular cortex, anterior cingulate cortex (ACC), the ventromedial prefrontal cortex (PFC), the central nucleus of the amygdala, and the hypothalamic nuclei (Benarroch, 1993, 1997; Critchley et al., 2000; Critchley, 2005; Matthews et al., 2004; Ter Horst & Postema, 1997). Together, these structures are considered part of a central autonomic network (CAN), and several of these structures also play a critical role in the implementation of cognitive control over attentional resources (e.g., Benarroch, 1993, 1997; Critchley, 2005). It is this observation that has fuelled a growing interest in specifying the role that RSA plays in supporting cognitive performance, especially when the need for cognitive control is high.

There is some confirmation, particularly in child research, that individual differences in RSA are associated with various indices of performance in situations where cognitive

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[3] A version of this chapter has been reviewed, revised, and resubmitted for publication to Biological Psychology (MS # BIOPSYC-D-13-00386).

control is required (Chapman, Woltering, Lamm, & Lewis, 2010; Marcovitch et al., 2010; Staton, El-sheikh, & Buckhalt, 2008). Research with adults is still in its early stages, but some studies have provided evidence of associations between RSA and cognitive performance. For example, higher baseline (resting) RSA in younger adults has been shown to relate to enhanced performance on sustained attention tasks that require the identification of various target stimuli (Hansen, Johnsen, & Thayer, 2009) and on n-back tasks that require the use of working memory (Hansen, Johnsen, Sollers III, Stenvik, & Thayer, 2004; Hansen et al., 2003, 2009). Higher baseline RSA in both older and younger adults has also been shown to relate to enhanced performance on a spatial touch-screen maze task in which performance on one trial is relevant to performance on the next trial for that maze (Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2011). In addition, recent work with middle-aged men demonstrated that those with higher resting RSA performed better on a verbal selective reminding task (Shah et al., 2011). Thus, there is some support for the view that higher baseline RSA is associated with enhanced performance on a range of cognitive tasks, not just in children, but in other age groups as well. Furthermore, such findings support the idea that higher baseline RSA may represent a resource that an individual can draw on to support performance during cognitively demanding situations (Thayer & Lane, 2009).

We note, however, that baseline measures of RSA have not always proved relevant to cognitive performance. In fact, rather than higher baseline RSA, the best predictors can be lower levels of on-task RSA or greater RSA reactivity (i.e., greater reductions in RSA from baseline to task). Children and adolescents with lower on-task RSA were shown to perform more accurately on an affectively arousing Go/NoGo task (Chapman et al., 2010). Similarly, younger adults with lower on-task RSA and greater RSA reactivity made fewer mistakes on a rapid visual search task that required the use of both selective and sustained attention (Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009). In addition, younger and middle-aged adults with greater RSA reactivity were also found to execute correct responses more quickly in the context of an emotional Stroop task (Mathewson et al., 2010). This pattern of results suggests that lower on-task RSA and larger decreases in RSA from baseline to task are associated with enhanced cognitive performance. This on-task reduction in RSA may be beneficial to performance because it represents a reduction in parasympathetic influence so as to allow for the mobilization of resources necessary to meet the demands of the cognitive challenge at hand.

There is some evidence that relations between RSA and performance are most likely to emerge when tasks require higher level executive functions. For instance, Hansen et al. (Hansen et al., 2003) reported a relationship between higher baseline RSA and better performance on tasks that required sustained attention and working memory, an association that did not emerge in the context of a simpler response time task. However, we note that even when executive functions are involved, relationships between RSA and performance are not always seen. For instance, we found no apparent influence of pre-task RSA in a sample of older and younger adults who were asked to complete the Working Memory Inhibitory Control (WMIC) task (Capuana, Dywan, Tays, & Segalowitz, 2012). The WMIC task, initially developed by Hester and Garavan (2005), is a Go/NoGo task that requires participants to withhold responding to items they are currently maintaining in working memory. We manipulated task difficulty by utilizing increasingly larger working memory (WM) loads. We did find that higher pre-test levels of cardiac workload, as measured by Rate Pressure Product (RPP), were related to inhibitory control errors in older adults, which is consistent with there being some general role for cardiac autonomic regulation in supporting task performance; however, relations with RSA did not emerge (Capuana et al., 2012). This was the case for both older and younger adults at all three levels of task difficulty. Similarly, Britton and colleagues (Britton et al., 2008) found that resting RSA was not related to the performance of middle-aged adults on a cognitive battery that included tests of verbal meaning and inductive reasoning. Of course, since RSA is known to decline with age (e.g., De Meersman & Stein, 2007), it may be more difficult to demonstrate such relations in middle to older-aged adults. Even so, inconsistencies in relations between various baseline measures of RSA (pre-task, resting) and performance suggest that the specific nature of the cognitive challenge may be relevant to this association (see also, Morgan, Aikins, Steffian, Coric, & Southwick, 2007; Pu, Schmeichel, & Demaree, 2010) and, as such, a more strategic approach to task design might help clarify the conditions in which associations between RSA and cognitive function are likely to emerge.

1.1. Increasing Response Contingencies

Whether cardiac autonomic regulation contributes in a meaningful way to (or is a result of) better executive control, one might expect this relationship to become increasingly evident as the difficulty of an executive control task increases. We note, however, that tasks often involve only one level of difficulty, so this hypothesis is rarely tested. Furthermore, in those cases when difficulty level has been manipulated, the relationship between autonomic regulatory control and performance remained constant. For instance, Mathewson et al. (2011) examined the relationship between RSA and spatial memory performance as participants navigated their way through a maze that was hidden in a square grid. In order to determine whether the association between RSA and performance increased in response to enhanced spatial memory requirements, they increased grid sizes from 4 x 4 to 6 x 6 to 8 x 8. Mathewson et al. confirmed that higher baseline RSA was associated with better performance on all three levels of the task; however, the size of the relationship between task performance and RSA did not change in response to the augmented spatial memory load.

Importantly, there are other ways to enhance task difficulty. One route involves manipulating the number of rules or contingencies that guide appropriate response selection within a task (Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Bunge & Zelazo, 2006; Bunge, 2004). Effective rule use is a hallmark of adaptive cognitive control in that it facilitates the selection of actions compatible with current goals (Bunge & Zelazo, 2006). Several neuroimaging studies have demonstrated that, as the representations required for response selection become increasingly abstract, activation within the PFC increases systematically in more anterior regions (Badre & D’Esposito, 2007, 2009; Badre, Kayser, & D’Esposito, 2010; Koechlin & Jubault, 2006; Koechlin, Ody, & Kouneiher, 2003). In one particularly elegant study, Badre and D’Esposito (2007) examined frontal activation while participants completed four different types of response-control tasks. Difficulty was manipulated *between* the four tasks by gradually increasing the number of rules required for response selection. Difficulty was also manipulated *within* each task by systematically increasing response competition or load. Results confirmed that, as the number of response contingency rules increased across the four tasks, activation primarily within premotor cortex expanded to include regions of the frontal polar cortex. Importantly, as response competition (i.e., load) increased within each task, the level of activation within a given region increased but remained fixed in terms of its location.

We found this dissociation between “within-task load” versus “between-task complexity” intriguing in that it might help explain some of the puzzling results in the RSA-cognition studies. Recall that Mathewson et al. (2011) reported a relationship between RSA and performance during a spatial maze task, but note that this relationship did not increase in response to larger spatial memory loads. Thus, rather than increasing the size of the memory load within a task, perhaps a more meaningful way to examine relations between RSA and performance would be to manipulate the number of contingency rules that need to be maintained in order to execute an appropriate response in a given task context.

1.2. The Role of Arousal

In addition to manipulating response contingency rules, we were interested in examining whether the relationship between RSA and cognitive performance would increase in strength when we increased the level of arousal elicited by the task. The ability to maintain cognitive control under arousing circumstances would require appropriate emotion regulation which, in turn, would be expected to involve an even greater dependence on cardiac autonomic regulation (Beauchaine et al., 2007; Chapman et al., 2010; Hagemann, Waldstein, & Thayer, 2003; Porges, 1995; Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012; Thayer & Lane, 2009). Moreover, increasing the arousal within a task has been shown to result in greater engagement of regions within the PFC that also play a role in the cortical modulation of RSA, including the dorsomedial PFC and ventromedial PFC (Thayer et al., 2012). Thus, to examine the relationship between RSA and performance in a more emotionally arousing context, we included a monetary incentive phase whereby the amount of money lost for an error was significantly greater than the amount won on the basis of a correct response.

1.3. The Current Study

We had a group of young adults complete a modified Stroop task (Hester, Foxe, Molholm, Shpaner, & Garavan, 2005) but varied both the number and type of contingencies involved in response selection. Based on recent work by Braver and colleagues (e.g., Braver, Gray, & Burgess, 2008) we set up our contingencies such as to encourage a more proactive versus a more reactive response control strategy. So, besides a Basic Stroop task where an individual is required to determine their response on the basis of whether the colour-word is presented in a congruent versus an incongruent colour, we developed two other tasks. One task, the Memory Stroop, required the individual to reject incongruent colour-words, as in the Basic Stroop, but also to reject a particular memory lure that consisted of a congruent colour-word that was also to be rejected whenever it appeared. It has been shown that having a target in mind can facilitate the processing of stimuli even at the earliest stages (see, for example, Bar et al., 2006), and thereby, enable the individual to engage in a more efficient, proactive, response control strategy. The other task, the Repeat Stroop, also required individuals to reject standard incongruent colour-words, as in the Basic Stroop, as well as any congruent colour-words that repeated immediately in the stimulus stream. Because any congruent item could be a cue for a repeat item, the most efficient response strategy would presumably be a reactive one wherein an individual would simply wait for the probe to appear and then rely on inhibitory control to reject it, rather than proactively screen for a different word on each trial. Each Stroop task was followed by a monetary incentive phase wherein correct responses were rewarded but errors resulted in losses much larger than potential gains.

Cardiac autonomic regulation, as indexed by RSA, was assessed prior to and during completion of the three Stroop tasks. We expected that higher pre-task RSA and perhaps greater RSA reactivity (i.e., greater decreases in RSA from pre-task to on-task) would be associated with better performance. Furthermore, we expected that as response rule contingencies increased from the Basic Stroop task to the Memory and Repeat tasks, the role of cardiac autonomic regulation would increase as well. As such, the strongest relations between RSA (pre-task and reactivity) and performance were expected to emerge in the context of the Memory and Repeat tasks, where the number of response rules was greatest and, as such, the need for effective cognitive control most essential. We were also interested in whether a proactive or reactive response strategy would be differentially dependent on cardiac autonomic regulation but felt a hypothesis regarding this distinction would be premature. Finally, we expected that, as the need for emotion regulation increased, the role of cardiac autonomic regulation would increase as well. For this reason, we expected our measures of RSA (pre-task and reactivity) to relate most strongly to performance in the context of the monetary incentive phases of the Stroop tasks, where appropriate emotion regulation, and therefore, cardiac autonomic regulatory control, would be most essential.

2. Method

2.1 Participants

Participants were recruited from Brock University via flyers posted around campus and an electronic advertisement posted on the Psychology Department Research Pool website. Through initial phone contact, participants were provided with a general description of the study and screened for eligibility. The final sample included 17 undergraduate students (11 women, 18 – 26 years, *M* = 21.1). All were right-handed, had normal or corrected to normal vision, and were fluent in English. They were also free of self-reported neurological, psychiatric, and cardiac conditions, as well as psychoactive medications or those with cardiovascular side effects. The project received clearance from Brock University's Research Ethics Board, and all participants gave informed consent and were provided with a small honorarium, as well as any extra money earned during the incentive phases, in appreciation for their participation.

2.2 Stroop oddball paradigm

Participants completed a modified Stroop oddball paradigm (Hester et al., 2005) that required them to make "accept" or "reject" responses to a serial stream of colour-words (BLUE, GREEN, PURPLE, RED, WHITE, and YELLOW) presented on a computer screen. Font colour and word congruency were manipulated such that the stream consisted of congruent trials, where the word and its font colour matched (e.g., the word BLUE printed in blue font), and incongruent trials, where the word and its font colour did not match (e.g., the word BLUE printed in red font). The paradigm included three different tasks (Basic, Memory, and Repeat), and participants completed several blocks of each task during both standard and monetary incentive phases. Participants used their right hand to press a response button indicating "accept" and their left hand to press a response button indicating "reject" (counterbalanced) following the relevant rules for the particular task context.

2.2.1 Manipulating task contingencies

For the Basic task (Figure 3-1a), participants were asked to hit the "accept" key in response to congruent trials (e.g., BLUE in blue font) and the "reject" key in response to incongruent trials (e.g., BLUE printed in red font). Although the tasks were presented in random order (see section 2.2.3 below), the Basic task served as a baseline when analyzing data from the other two contingency tasks.

For the Memory task (Figure 3-1b), participants responded the same way they did during the Basic task (*accept congruents, reject incongruents*), only this time they were also required to reject a specific congruent item (e.g., RED in red font). This *memory lure* was presented prior to the start of a block, and participants were given as much time as they wanted to memorize it. Once participants felt they knew the memory lure, they pressed a button which triggered the start of the block. Each Memory block included its own specific memory lure. To ensure that participants had maintained the correct memory lure throughout the duration of the block, upon the block's completion participants were asked to select it from a list of congruent colour-words.

In the Repeat task (Figure 3-1c), participants were also asked to respond the same way they did during the Basic task (*accept congruents, reject incongruents*), only this time participants were also required to reject the second occurrence of any consecutively repeated congruent item, also known as a *repeat lure*. For instance, if the congruent item GREEN (in green font) was followed directly by GREEN (in green font), the repeated congruent word was to be rejected (i.e., the 2nd appearance of GREEN in green font). Repeat lures could occur equally often for any colour.

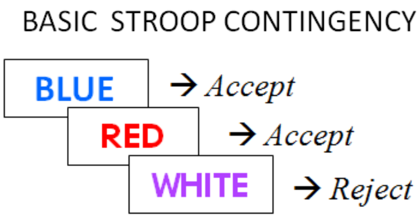

Figure 3-1a. The Basic Stroop required acceptance of congruent colour-words and rejection of incongruent colour-words.

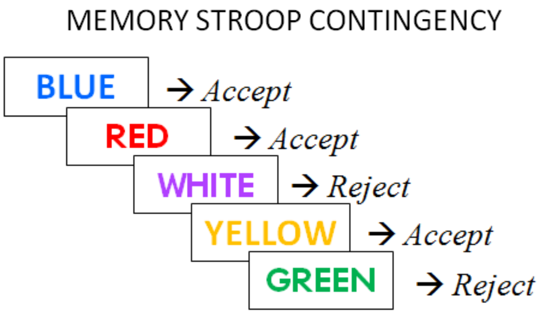

Figure 3-1b. The Memory Stroop required Basic Stroop responses plus rejection of a specific congruent item (i.e., GREEN in green font), which differed for each block.

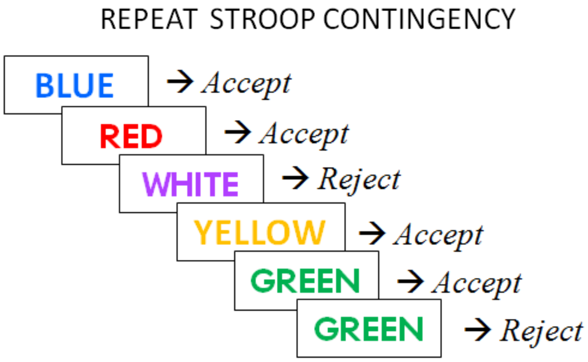

Figure 3-1c. The Repeat Stroop required Basic Stroop responses plus rejection of the second occurrence of any consecutively repeated congruent item (i.e., the second GREEN in green font shown above).

In summary, both the Memory and Repeat tasks added an extra response contingency rule to the Basic Stroop response decision (i.e., *accept if congruent, reject if incongruent*). During the Memory task, participants had to maintain a particular congruent colour-word in working memory while still adhering to the Basic Stroop contingency rules. The identity of the memory lure changed for every block, thus increasing the likelihood of interference from previous blocks as the Memory task progressed. The Repeat task, on the other hand, required the maintenance of a general rule in working memory (*accept unless repeated*) and the ability to externally monitor incoming colour-words for violations of this rule, again, while also adhering to the Basic Stroop contingency rules.

2.2.2 Manipulating emotional arousal

Prior to the first incentive phase, participants were told that during this game-like portion of the task they would win 30 points for each correct response but lose 120 points for each error. This disproportionate trade-off made errors particularly costly which we assumed would increase participants' concern over their performance and hence their level of emotional arousal. Additionally, in order to ensure that participants did not slow down in order to avoid making errors, they were told that there would be a response time penalty which would result in the loss of additional points if their responses were deemed too slow. The response time penalty was calculated based on the average response time of each block of 100 trials. Participants lost 30 points for every 10 ms that their average response time exceeded 600 ms (e.g., a response time of 640 ms would cost an additional 120 points). Participants were told that their points would be tracked throughout each of the three incentive phases and converted to additional earnings following completion of the study (up to $20 CAD). Feedback regarding accuracy rates and response speed were provided after each block of trials indicating the number of points gained for correct responses and the number of points lost for errors or for responding too slowly.

2.2.3 Task details

These data were collected as part of a larger study which involved the investigation of error-related electrocortical activity, which required maximizing the number of errors to provide stable event-related potentials. Thus, we followed the example of O'Connell et al.

(2007) and had participants complete a variable number of blocks (4 to 6) for each of the 3 tasks, during both standard and monetary incentive phases. Each block included 100 decision trials. Seventy-five of the trials consisted of congruent colour-words that required an “accept” response. The remaining 25 trials consisted of colour-words that required a “reject” response. In the case of the Basic task (standard and incentive), all 25 trials consisted of incongruent colour-words. In the case of the Memory and Repeat tasks (standard and incentive), these 25 trials included a combination of both incongruent colour-words and contingency items relevant for the particular task. Thus, each block of the Memory task included 12 incongruent colour-words and 13 occurrences of the memory lure, whereas the Repeat task included 12 incongruent colour-words and 13 repeat lures.

Prior to starting the task, everyone completed one practice block (50 trials) of the Basic task. The order in which the three tasks were completed was counterbalanced across participants, although the monetary incentive phase always followed the standard phase. Colour-words appeared in uppercase on a pale grey background. They were presented for 600 ms followed by a variable inter-trial interval of 700, 800, or 900 ms. Each block, therefore, was approximately 2 minutes and 20 seconds in length. Within each of the 3 tasks, participants controlled the length of their breaks between blocks. A 2-minute break was provided between the standard and incentive phases of the tasks, and a longer 5-minute break was provided before transitioning to a new task. The entire paradigm, including practice and breaks, took approximately 1.25 hours to complete.

2.3 Procedure

Participants completed the three Stroop tasks during standard and monetary incentive phases while seated in a dimly lit, electrically and acoustically shielded room. Stroop colour-words were presented using E-Prime research software (Psychological Software Tools, Inc.). Electroencephalography (EEG), electrocardiography (ECG), and respiration were recorded throughout the session, and resting blood pressure was measured prior to and following the completion of the Stroop tasks.

2.3.1 Cardiac Measures

Using an automated sphygmomanometer, two blood pressure readings (systolic: SBP; diastolic: DBP) were taken following a 5-min rest period that preceded the start of the testing session and again following another final 5-min rest period that concluded the testing session to ensure that participants remained within normal BP range during the test situation. ECG and respiration were monitored throughout the entire task and during the 5-min pre-task and post-task resting periods. In order to monitor respiration, a flexible respiration belt was placed around the participant's upper chest (MindWare Technologies Ltd., Columbus, OH). ECG signals were recorded from two electrodes placed on the participant's chest; one affixed about 2.5 cm below the right clavicle, the other placed between the 2 bottom-ribs on the person's left side. ECG signals were sampled at 512 Hz by the acquisition program, BioSemi (Amsterdam), which provided the grounding for the ECG signal through the ground electrode formed by the Common Mode Sensor (CMS) active electrode and the Driven Right Leg (DRL) passive electrode system associated with our simultaneous collection of EEG data. ECG signals were digitized with a 24-bit ADC, and then analyzed using a commercial software package (MindWare Heart Rate Variability Scoring Module 2.51, Mindware Technologies Ltd., Columbus, OH). R–R (interbeat) intervals were visually inspected and edited where necessary according to principles advocated by Berntson and Stowell (1998). Minute-by-minute estimates of RSA (heart rate variability at the respiratory frequency, 0.12–

0.4 Hz) were calculated via spectral analysis of the heart beat series using fast Fourier transformation and a Hamming window based on 1- min epochs. A sample rate of 250 ms (4/s) provided 240 samples (120 FFT bins), resulting in a frequency resolution of 0.01667 Hz. RSA was then expressed as the natural log transform of this frequency band, ln(ms^2). Estimates of RSA, heart rate (HR), and respiration rate (RR) were averaged for the pre-task baseline and post-task resting periods. For on-task measures, time frames from each block of a particular task and phase were selected, analyzed, and then averaged together. Finally, as a follow-up to Study 1 (Chapter 2), we calculated a measure of pre-task RPP for all participants to examine whether cardiac workload related to accuracy in the context of the current Stroop tasks (multiplying pre-task SBP and pre-task HR, and dividing by 100).

2.3.2 Analyses

To investigate the effects of task (Basic, Memory, Repeat) and phase (standard, monetary-incentive), data were subjected to a series of ANOVAs, and interactions were followed up with simple effects analyses. All analyses were corrected for violations of Mauchley’s Test of Sphericity, where necessary, using the Huynh–Feldt correction for estimating the F Statistics with the original degrees of freedom and corrected p-values reported in the text. All significance values are based on two-tailed tests.

Correlational analyses were used to examine relations between autonomic and performance data. Due to our reduced sample size, we wanted to ensure the reliability of any significant parametric correlations that emerged from our analyses. Therefore, we utilized a bootstrap approach which involves sampling with replacement. For each of our original parametric correlations, we computed two sets of robust r correlation coefficients: one Winsorized at 10% (r_w 10%) and the other Winsorized at 20% (r_w 20%). In the case of r_w

10%, one individual was moved in from each tail of the distribution, and in the case of r_w 20%, three individuals were moved in from each tail. We then sampled with replacement 1,000 times to generate the Winsorized correlation coefficients. Finally, we examined whether the resulting pattern of Winsorized correlation coefficients were consistent with the original parametric correlation coefficients.

3. Results

3.1 Performance data

Behavioural accuracy rates to congruent and incongruent trials (see Table 3-1) were entered into a 3 (task: Basic, Memory, Repeat) x 2 (congruency: congruent, incongruent) x 2 (phase: standard, incentive) repeated measures analysis of variance (ANOVA). First, there was no main effect of task type ($p > .28$). As expected, accuracy was higher for congruent ($M = .99 \pm .002$) relative to incongruent ($M = .68 \pm .03$) trials, $F(1,16) = 143.80$, $p < .001$, $\eta^2 = .90$, and adding a monetary incentive increased accuracy ($M = .85 \pm .02$) over the standard phases of the tasks ($M = .82 \pm .014$), $F(1,16) = 8.26$, $p < .02$, $\eta^2 = .34$. There was also a congruency by phase interaction, $F(1,16) = 7.30$, $p < .02$, $\eta^2 =.31$, indicating that it was only the incongruent trials that were affected by incentive, with accuracy increasing from the standard ($M = .66 \pm .03$) to the incentive phase ($M = .71 \pm .03$), an effect not observed for the congruent trials ($M_{standard} = .98 \pm .003$ vs. $M_{incentive} = .99 \pm .002$) due to accuracy on those trials being near ceiling. It appeared that incongruent accuracy was reduced in the Memory and Repeat tasks compared to the Basic task; however, the task by congruency interaction failed to reach significance ($p > .07$).

Table 3-1

Proportion of Correct Responses to Congruent and Incongruent Items for Basic, Memory, and Repeat Stroop Tasks during Standard and Incentive Phases.

	Congruent Accuracy (SE)		Incongruent Accuracy (SE)	
Task	Standard Phase	Incentive Phase	Standard Phase	Incentive Phase
Basic	.98 (.01)	.98 (.01)	.69 (.04)	.75 (.03)
Memory	.99 (.01)	.99 (.01)	.64 (.03)	.67 (.04)
Repeat	.99 (.01)	.99 (.01)	.64 (.03)	.69 (.03)

Response times (RTs), analyzed in the same manner, revealed the expected main effects of congruency, task, and phase (all *p*s < .05), but these were superseded by interactions between congruency and task, $F(2,32) = 36.56$, $p < .001$, $\eta^2 = .70$, and congruency and phase, $F(1,16) = 10.68$, $p < .01$, $\eta^2 = .40$. Simple effects analyses indicated that RTs were larger for incongruent compared to congruent trials for all three Stroop tasks, with the largest differences occurring in the Memory and Repeat tasks. As well, adding monetary incentives reduced RTs ($M = 566 \pm 10$ ms) compared to the standard phases ($M = 582 \pm 11$ms) for incongruent trials, but the same did not hold true for congruent trials ($M_{standard} = 448 \pm 8$ ms vs. $M_{incentive} = 447 \pm 7$ ms), which appeared to be performed at maximal speed in either phase. Thus, our results are consistent with what one would expect in a Stroop paradigm, i.e., the interference associated with incongruent colour-words increased response time and reduced accuracy. We also see that this Stroop effect was further modified by the addition of contingencies (increasing complexity and reducing accuracy) and monetary incentive (increasing engagement and improving accuracy).

Memory lure trials (congruent items of a particular colour) and repeat lure trials (a congruent word that directly followed the same congruent word) occurred only in the contingency tasks (i.e., Memory Stroop and Repeat Stroop). Entering the accuracy rates for these lures into a 2 (lure type: memory, repeat) by 2 (phase: standard, incentive) repeated measures ANOVA, we found that participants were less accurate for repeat lures (M = .77 ± .02) than memory lures (M = .85 ± .02), $F(1,16) = 13.06$, $p < .01$, $\eta^2 = .45$, but it was performance on the repeat lures that benefitted most from the monetary incentive, $F(1,16) = 9.87$, $p < .01$, $\eta^2 =.38$. Thus, the incentive-based increase in accuracy was more evident for repeat lures ($M_{incentive}$ = .84 ± .02 vs. $M_{standard}$ = .70 ± .03) than it was for the memory lures ($M_{incentive}$ = .87 ± .02 vs. $M_{standard}$ = .83 ± .02). Perhaps the heightened vigilance associated with the incentive phase provided more benefit for a more reactive style of cognitive control. We note, however, that these differences in accuracy level across lure-type and incentive phase were not reflected in RTs (all *p*s > .31), and the lure-type by incentive phase interaction did not reach significance ($p = .07$).

3.2 Physiological Measures

There were no differences between pre-task and post-task measures of SBP or DBP (all *p*s > .34) and neither were reliably related to cognitive performance *(p*s > .11). Our other physiological measures (i.e., HR, RR, and RSA) were recorded prior to, during, and following task completion and were entered into a series of separate repeated measures ANOVAs. As expected, these measures were all related to one another, with HR being most closely aligned with RSA ($r = -.76$, $p < .001$), and other correlations ranging from $r = -.51$, $p < .04$ for RSA and RR, to $r = .43$, $p = .09$ for HR and RR. We next examined the degree to which our physiological variables shifted across periods of the study. HR showed only a marginal effect of period, $F(2, 30) = 2.97$, p = .07, $\eta^2 = .17$, with small shifts in the expected direction from pre-task (M = 72.10 ± 2.24) to on-task (M = 72.40 ± 1.91) to post-task periods (M = 69.08 ± 2.24). RR was similar, with only a marginal main effect, $F(2,32) = 3.09$, $p = .06$, $\eta^2 = .16$, but again, shifts were in the expected direction for pre-task (M = 13.15 ± .71), on-task (M = 14.75 ± .70), and post-task (M = 13.05 ± .90). RSA was most responsive to task period, $F(2,30) = 10.64$, $p < .001$, $\eta^2 = .42$, showing the expected decline from the pre-task (M = 6.78 ± .22 ln ms^2) to the on-task period (M = 6.34 ± .21 ln ms^2) and then increasing again post-task (M = 7.01 ± .19 ln ms^2). These data are consistent with the expected decline in parasympathetic influence during the task and its expected increase following task completion but, of course, subtle shifts in respiration could also have influenced the on-task drop in RSA.

We also examined our on-task physiological measures to determine whether they differed according to the specific task and/or phase. On-task HR, RR, and RSA were all entered into separate 3 (task: Basic, Memory, Repeat) x 2 (phase: standard, incentive) repeated measures ANOVAs. Results indicated that none of these on-task physiological measures differed according to task (all ps > .27), the effect of phase was marginal (all ps > .08), and none of the interactions between task and phase reached significance (all ps > .27). Finally, because research has demonstrated sex differences in RSA, we wanted to determine whether such differences were evident in our current sample. Our results indicated that the men and women in our sample did not differ in terms of their pre-task (p > .94) or on-task RSA measures (p > .28).

3.3 Cardiac Autonomic Regulation and Task Accuracy

Our central question was whether cardiac autonomic control at baseline (i.e., pre-task RSA) or in response to task demands (i.e., RSA reactivity) would increase the likelihood of accurate performance and under which conditions this was most likely to occur. To increase the stability of the test scores, we used overall rejection accuracy within each task as our dependent measure, i.e., the correct rejection of all lure items (incongruent colour-words plus memory or repeat lures) as relevant to each task. Pearson correlation analyses (see Table 3-2, row 1) showed first that, in the standard, non-incentive phases, higher pre-task levels of RSA were only relevant to rejection accuracy in the context of the Memory task ($r = .57$, $p < .02$). RSA appeared to be less relevant to accuracy in the Basic or Repeat tasks (all *p*s > .12) (see Figure 3- 2a). Adding a monetary incentive, however, did reveal a greater role for general levels of phasic vagal cardiac control in predicting performance accuracy. Higher pre-task RSA was associated with greater accuracy for the monetary incentive phase of the Basic task ($r = .51$, $p < .04$). It remained significant for the incentive phase of the Memory task ($r = .54$, $p < .03$) but was still not predictive of rejection accuracy in the incentive phase of the Repeat task ($p > .22$) (see Figure 3-2b). [4] Importantly, application of the bootstrapping procedure (i.e., correlations Winsorized at both 10% and 20%) produced a pattern that was consistent with (and generally strengthened) our original findings regarding associations between pre-task RSA and rejection accuracy (see Table 3-2, rows 2 and 3). We also note that when we controlled for pre-task respiratory rate, all of the relations between pre-task RSA and rejection accuracy described above remained significant (standard phase of Memory task: $r = .56$, $p < .03$; incentive phase of Basic task: $r = .49$, $p = .05$; incentive phase of Memory task: $r = .52$, $p < .04$). This pattern of findings suggests that the level of cardiac autonomic regulatory control that the individual brings with them to the task, as reflected in pre-task RSA, appears more strongly related to performance on some types of cognitive challenge (i.e., maintaining specific cues in memory; increases in arousal that accompany the introduction of monetary incentive) than for others (i.e., the focused monitoring of repeated

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[4] Because participants completed a variable number of blocks (between 4 and 6) during each task or phase, we checked whether our relationships between pre-task RSA and performance replicated when we based all of our participants' accuracy rates on the first 4 blocks only. Results of our analyses confirmed that this was indeed the case (Basic-incentive: $r = .59$, $p < .02$; Memory-standard: $r = .55$, $p < .03$; Memory-incentive: $r = .62$, $p < .01$).

stimuli with or without reward) in this sample. We note that we are not dealing with a clear interaction between RSA and accuracy across tasks. Thus, RSA may be relevant to performance on all tasks, but the effect may be somewhat smaller and require a larger sample to reach levels of statistical reliability. Nonetheless, in the sample size we have here, it was the relationship between RSA and proactive response tendencies that presented the most reliable results.[5]

We also examined other indicators of pre-task arousal (RR and HR) and found that they too related to performance in similar ways. Lower pre-task HR was associated with better rejection accuracy during the standard phase of the Memory task (r = -.54, p = .03) and during the incentive phases of the Basic (r = -.56, p = .02) and Memory (r = -.53, p = .03) tasks (all other ps > .09). Lower pre-task RR was associated with better rejection accuracy during the standard phase of the Repeat task (r = -.49, p = .04); however, no other relations reached significance (all other ps > .45). Thus, relations that emerged with pre-task HR were very similar to those that emerged with pre-task RSA, but pre-task RR, although showing some relations in the expected direction, was neither as consistently nor as robustly related to performance as were the other cardiac variables.

We also examined whether pre-task RPP related to rejection accuracy during any of the tasks. Although pre-task RPP did not relate to rejection accuracy during standard or incentive phases of the Basic or Repeat tasks (all ps > .12), higher pre-task RPP was associated with reduced rejection accuracy on the Memory task during standard (r = -.67, p = .003) and incentive (r = -.65, p = .004) phases. However, these relations were no longer

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[5] Pre-task RSA was also examined to determine whether it predicted the effect of incentive (i.e., change in accuracy from the standard to the incentive phases of the Basic, Memory, or Repeat tasks) and/or the effect of load (i.e., change in accuracy from the Basic to the Memory task and/or the Basic to the Repeat task). None of the correlations reached significance (all ps > .13).

present when Winsorized at 20% (standard: *p* > .20; incentive: *p* > .68) or 10% (standard: *p* > .16; incentive: *p* > .54) and, therefore, will not be discussed further with respect to this study. However, a fuller discussion of the role of RPP will be presented in Chapter 5.

Table 3-2
Parametric and Winsorized Correlations between Pre-Task RSA and Rejection Accuracy for Basic, Memory, and Repeat Tasks during Standard and Incentive Phases.

	Basic		Memory		Repeat	
	Standard Phase	Incentive Phase	Standard Phase	Incentive Phase	Standard Phase	Incentive Phase
Pearson's r	.39 ($p > .12$)	.51 ($p < .04$)	.57 ($p < .02$)	.54 ($p < .03$)	.19 ($p > .44$)	.31 ($p > .22$)
r_w (10%)	.41 ($p = .132$)	.54 ($p = .038$)	.59 ($p = .008$)	.61 ($p = .036$)	.09 ($p = .730$)	.36 ($p = .268$)
r_w (20%)	.44 ($p = .194$)	.52 ($p = .048$)	.59 ($p = .014$)	.50 ($p = .064$)	.05 ($p = .844$)	.36 ($p = .340$)

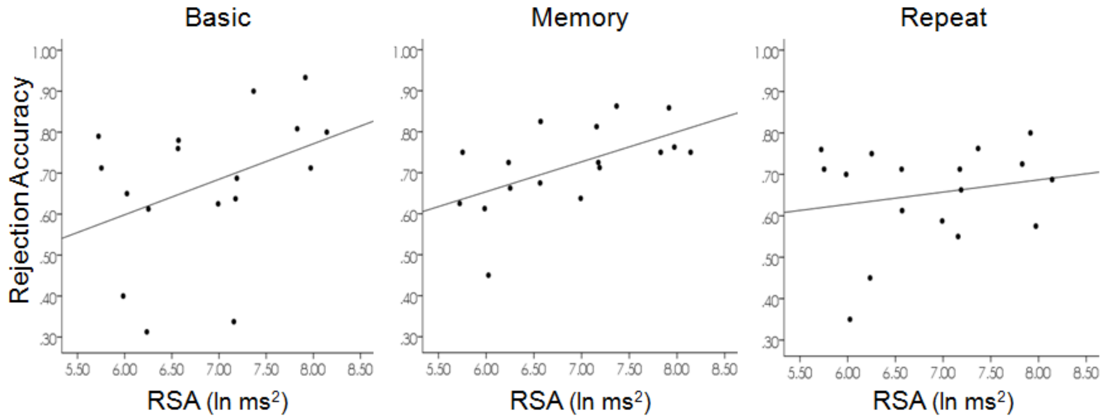

Figure 3-2a. Relations between pre-task RSA and rejection accuracy for the three Stroop tasks during standard (non-incentive) phases.

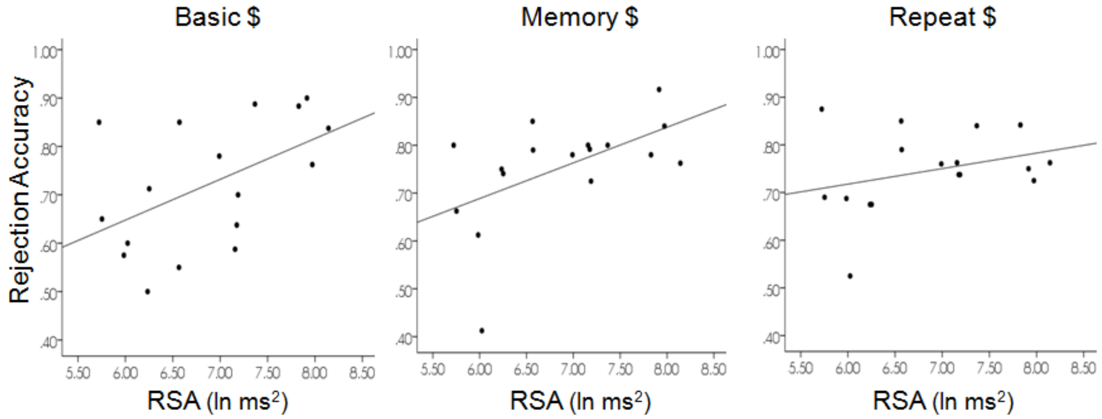

Figure 3-2b. Relations between pre-task RSA and rejection accuracy for the three Stroop tasks during incentive phases.

We were also interested in whether the degree to which RSA shifted in response to attentional demands or changes in emotional arousal (via monetary incentive) would affect performance. An index of RSA reactivity was calculated for each of the six tasks by removing the shared variance in RSA associated with the pre-task period from the RSA recorded during the performance of each task. These saved residuals were then used to predict performance within each relevant task. We originally expected that greater RSA reactivity would be associated with enhanced performance, particularly during monetary incentive phases, where the need for appropriate emotion regulation, and therefore, cardiac autonomic regulatory control, would be most useful. Contrary to expectations, however, RSA reactivity was not consistently related to rejection accuracy. In the standard phases, we found RSA reactivity to be associated with greater accuracy during the Basic (r = -.56, p < .03) and Repeat tasks (r = -.48, p = .05) but not the Memory task (p > .61). During the incentive phases, the only association between RSA reactivity and rejection accuracy that even approached significance occurred in the context of the Memory task (r = -.45, p = .07), with ps > .22 for the other two tasks. In contrast to the relations with pre-test RSA, none of the relations between RSA reactivity and performance survived bootstrapping operations.[6]

4. Discussion

Our goal was to test a model of neurovisceral integration (Benarroch, 1993, 1997; Critchley, 2005; Porges, 1995; Thayer & Lane, 2000, 2009) wherein autonomic, attentional, and emotional systems are dependent on shared underlying neural structures and simultaneously support self-regulation and successful adaptation. The links between phasic vagal cardiac control and emotion regulation have been well documented (Beauchaine, 2001;

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[6] We also examined whether on-task RSA related to accuracy on any of the tasks/phases, but none of the correlations reached significance (all ps > .31).

Hagemann et al., 2003; Thayer & Lane, 2000) but, based on this model, one would also expect that the capacity of an individual to flexibly adapt to changing environmental demands would play an important role in supporting higher-order cognitive control as well. This has been demonstrated quite convincingly in research with children (Chapman et al., 2010; Marcovitch et al., 2010; Staton et al., 2008) but results from adult samples have been mixed (e.g., Britton et al., 2008; Capuana et al., 2012). Thus, we thought that a more careful evaluation of task parameters was in order.

First, we focussed on manipulating the level of complexity involved in three Stroop tasks by increasing the number of contingencies that needed to be considered in order to execute an appropriate response. Badre and colleagues (2007; 2010) have shown that increasing task complexity in this manner results in a pattern of increased frontal activation that does not occur when one simply increases the memory load within a task. We also attempted to manipulate emotional arousal by including a monetary incentive phase for each task. We hypothesized that by increasing both the complexity of response contingency rules and the level of emotional arousal involved in the already attentionally-demanding Stroop task, we would increase the need for phasic vagal cardiac control, and as such, the likelihood of seeing relationships between our index of such control, RSA, and task performance.

We found some support for our expectation regarding the addition of response contingency rules but, importantly, this effect was only evident in the context of the Memory task. It was not observed at all in the Repeat task. Thus, our results are consistent with the view that cardiac autonomic regulation may be particularly relevant for performance when cognitive control demands are increased via the inclusion of an extra response contingency rule. It is also apparent, however, that the inclusion of an additional response contingency, per se, may not be sufficient to ensure a greater dependence on autonomic regulation. The nature of the added contingency appears to be important as well. Thus, it may not be task difficulty, per se, that is at issue (the Repeat task garnered more errors), but rather a qualitative difference in task demands.

We speculate that our response contingency manipulation led participants to engage in distinctly different cognitive control strategies, and that these strategies may have differed in terms of their reliance on cardiac autonomic regulation. According to Braver and colleagues (2008), successful cognitive control can be achieved through the use of both proactive and reactive control strategies. Proactive control is a form of early selection that involves the sustained, active maintenance of goal representations *prior to the onset* of the trigger stimulus, whereas reactive control is a form of late correction that involves the transient re-activation of goal-relevant information *following the appearance* of the trigger stimulus. According to this model, optimal performance is achieved through the combined use of both proactive and reactive strategies, but it has also been shown that specific task parameters can affect which control mode is employed in a given situation. Furthermore, even subtle differences between otherwise similar tasks can shift the cognitive control strategy employed by participants from proactive to reactive and vice versa.

Within this framework, our Memory task would have offered the opportunity to use a more proactive style of cognitive control. According to Braver and colleagues (2008), proactive control is particularly effective when tasks include predictive contextual cues that can guide appropriate response selection. The Memory task included such cues in the form of memory lures (i.e., the specific congruent colour-word that needed to be rejected in each block). Because one memory lure was presented prior to the start of each block, participants could actively maintain the item in working memory throughout the duration of the block in order to facilitate target (i.e., memory lure) identification. Recent research suggests that top-down processing can facilitate object recognition at very early stages (Bar et al., 2006), thereby, enabling more efficient, proactive control over response tendencies.

Another potential push for proactive control (Braver et al., 2008) occurs when sources of proactive interference are high. Because each block of the Memory task required the maintenance of a new memory lure, participants were required to override the tendency to reject the previous block's memory lure when they encountered it in a new block. As such, previous memory lures would have represented sources of interference that may also have encouraged the adoption of a proactive control strategy. We found no direct evidence for this by way of a statistically reliable drop in accuracy for later versus earlier blocks of trials in the Memory task, but this might have been confounded by the random distribution of tasks across the testing session.

Nonetheless, neither of these conditions held for the Repeat task. The Repeat task did not include sources of proactive interference nor did it require actively maintaining a specific cue in working memory as a template against which to compare upcoming stimuli. Instead, participants were required to maintain a general rule (i.e., accept congruent items unless they immediately repeat). In this case, it would be more appropriate to engage a reactive control strategy that relied upon the transient reactivation of the goal (i.e., reject repeat) upon encountering the trigger stimulus (i.e., the repeat itself). One would still need to inhibit responding to the Repeat lure whenever it occurred, but one could not actively anticipate that specific lure on each trial.

Importantly, the ability to actively maintain goal-relevant information online, in anticipation of cognitively demanding response decisions, has been shown to require a high and sustained level of neuronal support from the lateral PFC (Badre et al., 2010; Bunge & Zelazo, 2006). Consequently, the utilization of proactive control places a significant strain on cognitive resources, making this form of control highly metabolically costly (Braver et al., 2008) . As such, cardiac autonomic regulation may be particularly relevant when there is a need for proactive control because it may act as an additional resource that an individual can draw upon to support performance in such contexts (Thayer & Lane, 2009). Our findings appear to support this position. Specifically, the strongest relations between pre-task RSA and performance accuracy emerged during our Memory task, the context that we believe required the greatest need for proactive control.

With respect to our monetary incentive manipulation, it was clear that participants became more focussed since their accuracy increased in response to incentive, but there was little evidence that they became more emotionally aroused. There was no reliable drop in RSA or increase in HR or RR when participants transitioned from the standard to the monetary incentive phases of our tasks. The only hint that incentive may have increased arousal was in the context of the Basic task where, during the monetary incentive phase, an association between pre-task RSA and performance emerged. This relationship was evident, as well, during the monetary incentive phase of the Memory task but, in this case, the relationship was of the same magnitude as it was during the standard phase. Of course, it may be that the level of emotional arousal during the standard phase of the Memory task was already quite high so that the effects of adding the incentive were less obvious. What was clear, however, was that there was no relationship between pre-task RSA and performance on the Repeat task, irrespective of the incentive manipulation.

We were surprised to find so little support for RSA reactivity as a predictor of performance accuracy across our tasks despite the fact that it has been shown to be highly relevant in studies with children (Blair & Peters, 2003; Quas, Bauer, & Boyce, 2004) and even in a few adult samples (Mathewson et al., 2010; Duschek et al., 2009). This may have been a result of power being too low to detect this effect with our relatively small sample. We did see some evidence for relations between RSA reactivity and performance accuracy during the standard phases of the Basic and Repeat tasks. However, these correlations did not survive the bootstrapping strategy we applied to protect ourselves from spurious effects that can emerge with smaller samples.

We note, however, that there are a number of issues that need to be considered when examining RSA reactivity. First, ECG recordings obtained during on-task procedures may be influenced by phasic heart rate responses that can result in violations to the assumption of stationarity (Grossman & Taylor, 2007) rendering the calculation of on-task RSA, and hence RSA reactivity, less stable. Additionally, on careful inspection, we find that studies which have demonstrated associations between RSA reactivity and cognitive performance have taken very different approaches to the calculation of this measure making cross-study comparisons difficult. For instance, Chapman et al. (2010) reported that RSA reactivity in children was related to better performance on an emotional Go/NoGo task, but their measure of reactivity was actually just on-task RSA, and not the degree to which RSA declined from pre-task to on-task conditions. On the other hand, Kimhy et al. (2013) reported that RSA reactivity was related to better performance on inhibitory control and attention switching tasks but, in this case, the cognitive measures and RSA reactivity data were collected at two different time points. Participants completed the cognitive battery and then, after a time lag of 1-61 months, autonomic activity (i.e., RSA reactivity) was assessed. Whereas these data could be used as evidence for the stability of RSA reactivity as a measure, they do not speak to the relations between RSA reactivity and performance on the tasks that had actually elicited those shifts from baseline to on-task levels.

The way in which RSA reactivity has been computed also raises issues. Typically, this is done through the simple subtraction of on-task from pre-task RSA. When this occurs, the variance associated with pre-task (resting/baseline) measures is included in the difference score and may contribute to correlations with other measures. Variance associated with on-task RSA can also be influenced by a number of factors including the subjective experience of doing well or poorly on the task (Lehrer et al., 2010), making it unclear whether this variance predicts or reflects performance. Since baseline (i.e., resting or pre-task) measures of RSA are less susceptible to such confounds, they may provide a more reliable index of cardiac autonomic regulation.

We have acknowledged that our current study is limited by its small sample size, and hence, some caution is in order in interpreting our results. We have tried to rectify the problem by using a bootstrapping technique to further test the reliability of our correlations. We find that, in general, the pattern of relationships holds quite well. Evidence of an association between pre-task RSA and performance was still evident during the incentive phase of the Basic task and both the standard and incentive phases of the Memory task, as was the absence of any associations in the context of the Repeat task. The role of RSA reactivity as a correlate of performance accuracy was not as evident in this study. This may be due to low power, but it may also be that the ability to measure a shift in RSA is more problematic, making this measure somewhat less robust than the pre-task measure, which did predict performance accuracy under theoretically-relevant conditions despite our small sample size. Finally, although sex differences in RSA were not evident in the current study, these results should be interpreted with caution due to our limited sample size and uneven sex distribution.

Conclusion

The central focus of our study was to test a model of neurovisceral integration in which specifically increasing task contingencies as well as monetary incentives would increase the need for cardiac autonomic regulation in order to maintain higher levels of cognitive control. We found that pre-task RSA did seem sensitive to both response rule contingencies and monetary incentives, but that these relationships were further mediated by the nature of the extra response contingency rules. RSA appeared to be more relevant to performance when the contingency required the maintenance of a specific item in memory, allowing for the use of a proactive response strategy. RSA also appeared more relevant to performance when the task context included a monetary incentive, but not in every circumstance, i.e., not when a reactive response strategy was more appropriate to the task. We conclude that the model that best accounts for these results is one put forth by Braver and colleagues (2008) whereby associations between RSA and performance may have emerged when participants shifted toward a more proactive style of cognitive control, a control strategy that is more metabolically costly, and as a result, more reliant upon flexible autonomic regulatory support.

Chapter 3: Addendum

Although Study 2 (Chapter 3) did not include ERPs, Appendix A provides the details of a different analysis we ran on the electrophysiological data that was collected from the younger adults in Study 2. Here, we provide a brief summary of this work.

We used independent component analysis (ICA), a technique we describe in more detail in Study 3 (Chapter 4). By applying ICA to our response-locked error data, we were able to identify the component that accounted for the ERN effect. As expected, dipole analysis of the component confirmed that its source generator was the ACC. Interestingly, further inspection of the response-locked error data revealed a later occurring component with a broad posterior topography that looked similar to the occipital P2 component that is often found following stimulus onset. Subsequent ICA of our stimulus-locked data confirmed that the component that was occurring later in the response-locked error data was in fact the same component accounting for the variance at the time of the P2 following stimulus onset.

We were interested in modeling the event-related brain dynamics of these two source components (the ACC and occipital components); therefore, we submitted our response-locked correct data to time/frequency analysis. We then examined the mean power of these components in the alpha frequency band (8-14 Hz) and found a pattern of ongoing occipital alpha that changed over time as a function of the task. Specifically, the onset of the response seemed to lead to a burst in ACC power and a simultaneous attenuation of ongoing occipital alpha.

Based on this pattern, we were interested in the predictive relationship between these two signals. Thus, we utilized Granger Causality, a unique statistical technique that provides information about the direction of information flow, and therefore, can help identify causal relationships between neural signals. We examine the ACC's Granger causality on occipital alpha and vice versa. The correlation coefficients were calculated across time using a sliding lag. These lagged correlation coefficients were then transformed into waveforms representing the ACC's Granger causality on occipital alpha and occipital alpha's Granger causality on the ACC.

For each participant, we exported the latency and amplitude from each waveform's maximum beta coefficient for statistical analysis. We then examined whether pre-task RSA related to the magnitude of ACC Granger causality on occipital alpha or the magnitude of occipital alpha Granger causality on the ACC. No relations emerged in the context of the Basic or Repeat Stroop (all *p*s > .11); however, an association between RSA and the magnitude of ACC Granger causality on occipital alpha emerged in the context of the Memory Stroop ($r = -.55$, $p < .02$). Specifically, we found that for individuals with higher pre-task RSA, the magnitude of the ACC's prediction on later occipital alpha was greater.

The underlying focus of this thesis is to determine the degree to which cognitive and autonomic functions that are dependent on the ACC can be shown to relate to and influence each other. This would, in turn, test the neurovisceral integration model. We found very little evidence that standard electrophysiological indices of ACC function, i.e., the scalp-based ERN and Pe, related to other ACC-associated functions like phasic vagal cardiac control (RSA) or performance on any of the tasks used in this study (i.e., the Memory Stroop or the Repeat Stroop). It is important to keep in mind, however, that the ACC does much more than produce ERP components at the scalp. In fact, it is part of a vast network of regions that regulate various and distinct aspects of behaviour. One of the more intriguing aspects of regulation that we have been documenting in our lab is the ACC's regulation of activation in the visual cortex (unpublished data). To build on this, what we have shown here is that it may not be the amplitude of ACC activation at the scalp that relates to RSA, but rather, its network function, i.e., its degree of connectivity with other regions. Moreover, this analysis shows us that this connectivity is especially important in the context of the Memory task, the same task where relations between RSA and performance were most evident. Again, we hypothesize that this due to the Memory Stroop eliciting a proactive response strategy that, according to Braver and colleagues (2008), is more metabolically costly and would, therefore, be more dependent on the regulatory functions provided by the ACC network of connectivity. For further details on this analysis, please see Appendix A.

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Chapter 4: The role of age and fitness in cortical and autonomic correlates of cognitive control

1. Introduction

According to the neurovisceral integration model (Thayer & Lane, 2000, 2009), higher level cognitive function can be better understood if mental processes are examined from a broader perspective, one that extends beyond traditional brain-based measures (e.g., electrophysiology, neuroimaging) to encompass the role of cardiac autonomic regulation. Phasic vagal cardiac control, as measured by respiratory sinus arrhythmia (RSA), reflects parasympathetic influence on the heart through the prefrontal cortex via the vagus nerve (e.g., Berntson, Cacioppo, & Grossman, 2007). Cardiac autonomic control is thought to support a broad range of self-regulatory processes and to facilitate an individual's ability to adapt to changing environmental challenges and/or demands (Beauchaine, 2001; Berntson, Bigger Jr., et al., 1997; Porges, 1995; Thayer & Lane, 2000, 2009). Furthermore, some research has shown that cardiac autonomic regulation may be an important factor to consider when assessing cognitive performance (Hansen et al., 2004, 2003, 2009; Mathewson et al., 2011). This finding has particularly important implications for those interested in exploring the mechanisms underlying cognitive aging.

1.1 Aging and Cardiac Autonomic Regulation

The normal aging process is known to lead to declines in both cognitive (Prakash et al., 2009) and cardiac autonomic regulation (De Meersman & Stein, 2007; Umetani, Singer, McCraty, & Atkinson, 1998); however, the degree of decline varies a great deal from person to person (Lupien et al., 2005), providing a broader range in which to examine relations between these measures. To date, relatively little research has been done to examine the proposed link between RSA and cognitive control in older adults. Moreover, results of the few studies in which this relationship has been investigated are mixed (Britton et al., 2008; Capuana et al., 2012; Kimhy et al., 2013; Mathewson et al., 2011), with positive associations between baseline RSA and cognitive performance evident in some studies (Mathewson et al., 2011) and not in others (Britton et al., 2008; Capuana et al., 2012). These discrepancies may stem from important differences that underlie the contextual demands of various cognitive tasks employed. As indicated in Study 2 (Chapter 3), baseline cardiac autonomic regulation may be particularly relevant to performance when a task requires a high level of proactive cognitive control. Thus, our main goal for the current study was to further test this hypothesized relationship between cardiac autonomic regulation and proactive control but to extend it to an older adult population. In fact, Study 2 (Chapter 3) was initially designed to pilot a new experimental procedure prior to recruiting older participants, a much more resource-dependent operation. By having younger and older adults complete three versions of a Stroop task in which we varied both the complexity of response contingencies and level of performance motivation, and therefore, the amount of proactive control needed for performance, we hoped to replicate and extend the results of Study 2 in order to further our understanding of the factors involved in age-related cognitive decline.

There is some evidence that flexible and efficient cardiac autonomic regulation (i.e., higher pre-task or baseline RSA) is positively associated with performance on tasks that tap sustained attention and working memory (Hansen et al., 2004, 2003, 2009; Thayer, Hansen, Saus-Rose, & Johnsen, 2009). One might assume, therefore, that these associations are more likely when executive function is required. However, although support for this notion exists, it is not without exception. As demonstrated in Study 1 (Chapter 2), pre-task RSA did not relate to the performance of older or younger adults who completed an attentionally-demanding Go/NoGo task that required them to withhold responding to items being held in working memory. Furthermore, Britton and colleagues (2008) did not find an association between resting RSA and performance on tests of verbal meaning or inductive reasoning in a large sample of 5375 middle-aged adults. Thus, the relationship between cardiac autonomic regulation and cognitive performance is more complex than previously thought, and so the emergence of this association may be particularly sensitive to the nature of the cognitive challenge at hand.

The results from Study 2 (Chapter 3) suggest that whether or not pre-task RSA relates to performance on a particular cognitive task may be dependent upon the type of cognitive control strategy that the task encourages. In that study we had participants complete three Stroop tasks (Basic, Memory, Repeat) in which we varied the number and type of contingencies involved in response selection, and thereby, the type of cognitive control strategy adopted during the task. In addition to rejecting incongruent colour-words (e.g., the word RED printed in blue font), as was done in the Basic task, the Memory task included an additional contingency that required participants to reject a specific congruent colour-word (e.g., the word RED printed in red font), whereas the Repeat task included a different contingency that required participants to reject the second occurrence of any consecutively repeated congruent colour-word. We expected that the variations on this task would lead participants to recruit different cognitive control strategies that would, in turn, be differentially reliant on a high degree of autonomic regulation.

According to Braver and colleagues (Braver et al., 2008; Braver, Paxton, Locke, & Barch, 2009; Braver, 2012), cognitive control can be considered either “proactive” or “reactive” in nature. Proactive control refers to a form of early selection that involves the sustained, active maintenance of goal representations *prior to the onset* of trigger stimuli. This form of cognitive control can be implemented in situations where a valid task cue can be used to guide upcoming response decisions. By holding a specific task cue in mind over the course of several trials, participants can proactively screen incoming stimuli for relevant targets, which can lead to more effective (i.e., more accurate) and efficient (i.e., faster) responses (Czernochowski, Nessler, & Friedman, 2010). Reactive control, on the other hand, is a form of late correction that involves the transient re-activation of goal-relevant information *following the appearance* of trigger stimuli (Braver et al., 2008, 2009; Braver, 2012). Participants must rely on reactive control when tasks do not include valid cues that can be used to guide upcoming response decisions. The absence of a predictive task cue means that responses cannot be anticipated, and therefore, participants must rely on their ability to detect interference at the time of target presentation and on their ability to exert rapid control over their subsequent motor response.

According to Braver et al. (Braver et al., 2008, 2009; Braver, 2012), the adoption of a particular control strategy is not only dependent on the presence or absence of predictive task cues, but also, on the availability of cognitive resources. Proactive control requires that goal representations in the lateral PFC be sustained over extended periods of time, which, they suggest, makes this an extremely resource-demanding and metabolically costly form of control to use. By contrast, in reactive control, goal representations within the PFC are only activated transiently, as needed, making this form of control less resource-demanding. Research indicates that greater cardiac autonomic regulation at rest would allow for the modulation of arousal and so act as a resource that individuals can draw on to support higher cognitive functions (Thayer & Lane, 2009). Thus, it is our view that autonomic regulation may be most relevant to performance in contexts that encourage the use of a more resource-demanding proactive form of control, an idea which we have found support for in our recent work. Specifically, in Study 2 (Chapter 3) we found that younger adults with higher pre-task RSA demonstrated increased accuracy on a Stroop Memory task that included specific predictive cues that participants could use to proactively screen against incoming stimuli. Conversely, we found no association between pre-task RSA and accuracy on a Repeat Stroop task that we assume encouraged a more reactive style of control since it did not include specific task cues that participants could use to guide their responses.

Thus, one of the main goals of this study was to further test this hypothesized link between cardiac autonomic regulation and proactive control performance. As such, we had participants complete a similar Stroop paradigm to the one described in Study 2 (Chapter 3). Participants again completed the Basic and Memory tasks, but we dropped the Repeat task, where relations between pre-task RSA and performance did not emerge, and instead, replaced it with the Super Memory task. The Super Memory task built off of the demands of the Memory task and included an additional response contingency rule. By including the Basic, Memory, and Super Memory tasks we created an additive factors design within which we could examine associations between cardiac autonomic regulation and performance. We were interested in whether the relations between pre-task RSA and performance from Study 2 (Chapter 3) would replicate in the context of the Memory task and whether they would be even more evident in the Super Memory task, where the specificity of the added contingency was greatest, and therefore, the adoption of a proactive control strategy most likely.

Also central to this research was to examine the above issues from an aging perspective. Increasingly, research indicates that age-related cognitive deficits tend to be most apparent in situations that place significant demands on cognitive control, such as when information must be maintained and manipulated in working memory, when attention must be focused and sustained despite the presence of external distracters, and when prepotent response tendencies must be overridden (Park & Reuter-Lorenz, 2009). Braver and colleagues have suggested that a fundamental mechanism that may underlie the age-related deficits apparent in all of these domains (i.e., working memory, attention, and inhibitory control) may be a reduced ability, on the part of older adults, to actively represent and maintain relevant task goals (Braver & Barch, 2002; Braver et al., 2001; Braver, Satpute, Rush, Racine, & Barch, 2005; Paxton, Barch, Racine, & Braver, 2008).

According to Braver and colleagues, goal maintenance is a critical component of cognitive control and, in particular, proactive control (Braver & Barch, 2002; Braver et al., 2001, 2005). Goal representations not only allow for the planning and execution of appropriate action responses but, by maintaining these representations in an active online state through the use of proactive control, they can actually serve as a source of top-down bias, facilitating very early attentional and perceptual processes. This top-down biasing effect is evident in the work of Bar and colleagues (2003; 2006) who have shown that rapidly-processed low spatial frequency information can enhance the subsequent recognition of an image through the initiation of top-down processes in the orbitofrontal cortex that project back to the visual cortex during the very earliest stages of visual processing. If age reduces the ability to benefit from this top-down enhancement, selective attention will be compromised (e.g., de Fockert, Ramchurn, Van Velzen, Bergstrom, & Bunce, 2009). This is consistent with the position put forth by Jacoby and colleagues who have argued that older adults are less able to engage in early selection, and thus, are more likely to have to rely on late correction, i.e., a more reactive response strategy (e.g., Jacoby, Kelly, & McElree, 1999; Velanova, Lustig, Jacoby, & Buckner, 2007). This aligns with Braver et al.'s observation that older adults tend to shift away from using proactive control in favour of reactive control, even when a proactive strategy may be more effective for a given task context (Braver & West, 2008; Braver et al., 2001, 2008, 2009).

This decline in the utilization of proactive control among older adults is assumed to stem from normal age-related changes in the neural systems that support proactive cognitive control, including the lateral PFC and the dopaminergic system (Braver et al., 2001, 2008; Paxton et al., 2008). However, as indicated by the results of Study 2 (Chapter 3), cardiac autonomic regulation may also play a role in proactive control and this aspect of regulatory control becomes less efficient with age (De Meersman & Stein, 2007; Umetani et al., 1998). Therefore, we were interested in determining whether age-related declines in cardiac autonomic regulation also contributed to poorer proactive control performance among older adults, above and beyond the general decline associated with age. This would be evident if those older adults who demonstrate lower cardiac autonomic regulation (i.e., lower pre-task RSA) were less able to meet the demands of the Stroop contingency tasks, where the need for proactive control, and hence, support from a well-functioning autonomic nervous system, would be most essential.

1.2 The Role of Arousal

In addition to response contingencies, we were also interested in whether the relationship between RSA (pre-task and reactivity) and cognitive performance would increase in strength when we increased the level of emotional arousal elicited by our tasks. The ability to maintain cognitive control under emotionally arousing circumstances requires a high degree of physiological regulation, and as such, it is reasonable to assume that relations between cardiac autonomic regulation and performance might be particularly apparent in such contexts (Beauchaine et al., 2007; Chapman et al., 2010; Porges, 1995; Thayer et al., 2012; Thayer & Lane, 2009). We examined this issue in our previous study by having younger adults complete a similar set of Stroop tasks during both standard and monetary incentive phases (Study 2, Chapter 3). Results indicated that individuals with higher pre-task RSA did, in fact, perform better during the incentive phases of the Basic and Memory Stroop tasks. Thus, greater autonomic regulatory capacity appeared to be relevant for maintaining effective cognitive control when monetary incentive was involved. We note, however, that these relations only emerged with pre-task RSA, not RSA reactivity, i.e., the dynamic shift in cardiac autonomic regulation that occurs in response to task demands (Study 2, Chapter 3). We were surprised by this outcome because we had assumed that RSA reactivity might be particularly relevant for performance during the more emotionally arousing monetary incentive phases of our tasks, when effective regulation of physiological arousal would be most necessary, a pattern which has been demonstrated with children using a negative-affect induction procedure (Chapman et al., 2010).

There are several reasons why associations between RSA reactivity and performance may not have emerged in Study 2. One possibility is that our incentive phase may not have increased arousal sufficiently to elicit relations between RSA reactivity and performance. Evidence for this possibility stems from the fact that participants demonstrated similar levels of RSA during both the standard and incentive phases of our tasks. Thus, for the current study, we again included a monetary incentive phase, but we attempted to heighten physiological arousal by providing more affectively salient feedback at the end of each task block. Specifically, we utilized positive and negative emoticons and a moving thermometer that represented the number of points won for correct responses and lost for errors. We hoped that this strategy would make the number of points lost for errors more salient, thus increasing participants' emotional response to the loss. To the degree that this happened, we expected that relations between RSA reactivity and performance would be more likely to emerge.

1.3 Autonomic Regulatory Control and ACC Function

In addition to associations with task performance, we were also interested in exploring whether cardiac autonomic regulation related to indices of anterior cingulate cortex (ACC) function. The ACC is known to serve as an integration zone for cognitive control and autonomic arousal (Critchley, 2005), and therefore, it is reasonable to assume that RSA might relate to various indices of ACC function. For instance, some researchers have demonstrated a link between RSA and ACC-generated event-related potential (ERP) components. Chapman et al. (2010) found that the NoGo N2 amplitude, an ERP component generated by the ACC, related negatively to on-task RSA in children and adolescents. In Study 1 (Chapter 2) we also found a positive relationship between pre-task RSA and the size of the error positivity (Pe), another ERP component generated in the rostral portion of the ACC and known to be involved in performance monitoring (Taylor, Stern, & Gehring, 2007). Chapman et al. (2010) and Study 1 (Chapter 2) provide evidence of an association between both the cognitive and autonomic regulatory functions of the ACC. For the present study, we again examined whether RSA related to the Pe as well as the error-related negativity (ERN), another ACC-generated ERP component known to be involved in critical aspects of performance monitoring and error processing (Taylor et al., 2007).

In addition to ACC-generated ERP components, we were also interested in examining whether RSA related to ACC global field amplitude (GFA). Although the ERN and Pe are generated by the ACC, the nature of EEG itself and the ERPs that are derived from such recordings represent a mixture of multiple cortical sources or domains (Makeig & Onton, 2009; Onton & Makeig, 2006). Thus, ERPs constitute fairly “noisy” signals, i.e., they include signals that arise from sources other than the one of interest, thereby diminishing the size of potential correlations with other measures. Fortunately, a type of linear signal decomposition known as independent component analysis (ICA) has recently emerged as an effective technique for separating mixed EEG signals (Jung et al., 2001; Makeig et al., 2002; Makeig, Bell, Jung, & Sejnowski, 1996). When ICA is applied to multi-channel EEG data, it produces a set of independent activity patterns, or independent components (ICs), which each represent a separate, specific EEG source. Importantly, some of these sources represent independent activity patterns of distinct cell assemblies, and therefore, ICA can be used to identify and isolate the activity of specific brain sources of interest. By applying ICA in the present study, we can isolate the activity of the IC which accounts for the ACC (i.e., the ACC-IC) in each of our participants. We can then project this activation back to the scalp and measure the GFA of the ACC-IC. This will effectively isolate the ACC’s contribution to global scalp data which in turn will produce a purer index of ACC activation which we can then correlate with our other measures of interest (e.g., RSA, behavioural performance, etc).

1.4 The Role of Fitness

The other main focus of our study was to examine the role of aerobic fitness on our measures. A growing body of research indicates that increased aerobic fitness levels are associated with better performance on cognitive tasks, particularly tasks that involve higher level executive functions. For instance, Hillman et al. (2006) examined the relationship between physical activity and performance on a Flanker task (a task that requires the participant to ignore lures to the right and left sides of a target in order to avoid prepotent response errors) in a group of younger and older adults. They found that increased levels of physical activity within both groups were associated with increased accuracy rates and faster response times, especially for the more challenging incongruent Flanker trials. Recent research has also documented associations between fitness and electrocortical indices of cognitive processing. For instance, older adults who were more physically fit demonstrated faster response times as well as larger P300 amplitudes in the context of a modified Sternberg task, a quick-response short-term memory task (Chang et al., 2013). The authors claimed that this pattern reflected enhanced working memory and attention allocation among more physically fit older adults.

For our current study, therefore, we were interested in exploring the relationship between fitness and performance in both older and younger adults in the context of our three Stroop contingency tasks. Therefore, we had our participants complete a sub-maximal fitness test prior to cognitive testing in order to determine whether fitness level was associated with behavioural and/or electrocortical indices of cognitive control on our tasks, and whether these relationships were strongest during the most challenging of the tasks, the Super Memory Stroop.

Our other goal concerning fitness was to try and determine whether its association with cognitive performance is due to its association with cardiac autonomic regulation. Research has shown that individuals who are more aerobically fit also demonstrate higher levels of RSA compared to their age-matched, sedentary controls (Billman, 2002; Goldsmith et al., 1997, 1992). Furthermore, some researchers have found that participation in aerobic training programs can lead to positive effects on cardiac autonomic regulation (Al Ani, Munir, White, Townend, & Coote, 1996; Hautala et al., 2004; Hautala, Kiviniemi, & Tulppo, 2009; Melanson & Freedson, 2001), though this is not without exception (Boutcher & Stein, 1995). Nonetheless, fitness may be another important factor to consider when examining relations between cardiac autonomic regulation and cognitive control performance.

Perhaps it is the maintenance of greater cardiac autonomic regulation among individuals who are more physically fit that actually underlies the association between fitness and cognitive performance. Conversely, perhaps it is fitness that underlies the association between cardiac autonomic regulation and cognitive performance. Or, perhaps cardiac autonomic regulatory control and fitness both relate with unique variance to cognitive performance. Thus, one of our other goals of the present study was to more carefully understand the interrelations between RSA, fitness, and cognitive performance among younger and older adults.

1.5 The Current Study

Cardiac autonomic regulation (pre-task RSA, RSA reactivity) and fitness level were assessed in a group of older and younger adults to determine whether they related to performance on three Stroop contingency tasks. By increasing the number of contingencies across the three Stroop tasks and the motivation to perform well via the inclusion of a monetary incentive, we aimed to increase the need for proactive cognitive control. In terms of our hypotheses, we expected older adults to perform more poorly than younger adults on our Stroop tasks (e.g., Langenecker, Nielson, & Rao, 2004), particularly the Memory and Super Memory tasks where the need for proactive control would be greatest. In terms of

ERPs, we expected older adults to produce smaller ERN/Pe components in response to making errors, a finding that has been well documented in aging research and is likely due to the reduced availability of dopamine in striate and extrastriate prefrontal systems (Cruz-Muros et al., 2007). We further hypothesized that within each age group, baseline cardiac autonomic regulation (i.e., higher pre-task RSA) would be associated with better performance, particularly during the Memory and Super Memory tasks where the need for proactive control, and hence, autonomic regulatory support, would be greatest. We were also interested in exploring whether relations between RSA reactivity and accuracy would emerge during the incentive phases of our tasks, where the need for appropriate emotion regulation would be even more relevant for task performance. Additionally, we were interested in exploring the relationship between RSA and indices of ACC function (i.e., ERN/Pe and ACC GFA), given the role of the ACC in both cognitive and autonomic regulation (Critchley, 2005). Finally, within both groups, we expected that higher fitness would be related to better performance, especially on the more cognitively demanding Memory and Super Memory contingency tasks.

2. **Methods**

2.1 Participants

Participants included of 23 Brock University undergraduates (18 women, 18-24 years, *M* = 20.0) and 22 healthy older adults from the local community (17 women, 60-78 years, *M* = 68.8). All individuals were right-handed, had normal or corrected to normal vision, and were fluent in English. Participants were also free of self-reported neurological, psychiatric, and cardiac conditions and from use of psychoactive medications and beta-adrenergic blockers.

Older adults scored within the normal range on the Mini-Mental Status Examination (26-30, $M = 28.8$, $SD = 1.1$). In terms of education, participants did differ on the highest level completed, $t(43) = -3.70$, $p = .001$, such that the majority of younger participants had completed less than two years of post-secondary education at the time of testing while the majority of the older participants had completed a post-secondary degree or equivalent. Finally, SCOLP "Spot the Word" performance revealed a typical vocabulary superiority effect for older ($M = 89\%$ correct) compared to younger adults, ($M = 76\%$ correct), $t(43) = -5.69$, $p < .001$. The project received clearance from Brock University's Research Ethics Board, and all participants gave informed consent and were provided with a small honorarium in appreciation for their participation (plus, the extra money earned during the incentive phases of the tasks).

2.2 Stroop oddball paradigm

Participants completed a modified Stroop oddball paradigm (Study 2, Chapter 3; Hester, Foxe, Molholm, Shpaner, & Garavan, 2005) that required them to make "accept" or "reject" responses to a serial stream of 6 colour-words presented in either upper or lower case letters (BLUE/blue, GREEN/green, PURPLE/purple, RED/red, WHITE/white, and YELLOW/yellow) on a computer screen. Font colour and word congruency were manipulated such that the stream consisted of congruent items, where the font colour matched the word (e.g., the word BLUE or blue printed in blue font), and incongruent items, where the font colour did not match the word (e.g., the word BLUE or blue printed in red font). There were three versions of the task (Basic, Memory, and Super Memory), and participants completed several blocks of each task during both standard and monetary incentive phases. Participants used their right hand to press a button indicating "accept" and their left hand to press a button indicating “reject” (counterbalanced) following the relevant rules for the particular task context.

2.2.1 Manipulating task contingencies

For the Basic task (Figure 4-1a), participants were asked to hit the “accept” key in response to congruent trials (e.g., BLUE or blue in blue font) and the “reject” key in response to incongruent trials (e.g., BLUE or blue printed in red font). The Basic task represented the least complex version of the three Stroop tasks because it required the maintenance of a single response contingency rule (i.e., *accept unless incongruent*). The Memory and Super Memory tasks both increased complexity by building on the demands of the Basic task via the inclusion of additional response contingency rules.

The Memory task (Figure 4-1b) represented the middle level of complexity, and as such, built directly off of the Basic task. Specifically, the Memory task required participants to respond the same way they did during the Basic task (*accept unless incongruent*), only this time they were also required to reject a specific congruent item (e.g., RED/red in red font). Importantly, participants were instructed to reject *all* instances of the specified congruent item (the *memory lure*), e.g., both “RED” written in red font and “red” written in red font; however, attention was not directly drawn to case during the instructions. Thus, compared to the Basic task with its single contingency (*accept unless incongruent*), the Memory task required an additional response contingency (*accept unless incongruent OR memory lure*).

The Super Memory task (Figure 4-1c) built directly off of the Memory task, and represented the most complex version of the three Stroop tasks. Participants were again instructed to reject all incongruent trials and the specified memory lure but, this time, only when the lure appeared in a particular case (e.g., “RED” written in red font, but not “red” written in red font). We refer to this as the *super memory lure*. Thus, compared to the Basic task with its single contingency (*accept unless incongruent*), the Super Memory task required the maintenance of two additional response contingency rules (*accept unless incongruent OR Memory lure BUT only in specified case*).

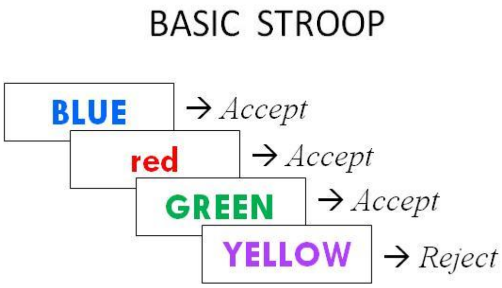

Figure 4-1a. The Basic task required acceptance of congruent colour-words and rejection of incongruent colour-words.

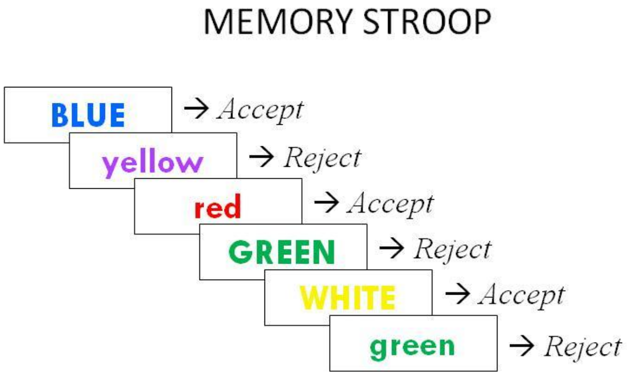

Figure 4-1b. The Memory task required Basic task responses plus rejection of the *memory lure*, a specific congruent item (i.e., both "GREEN" and "green" in green font), that differed for each block.

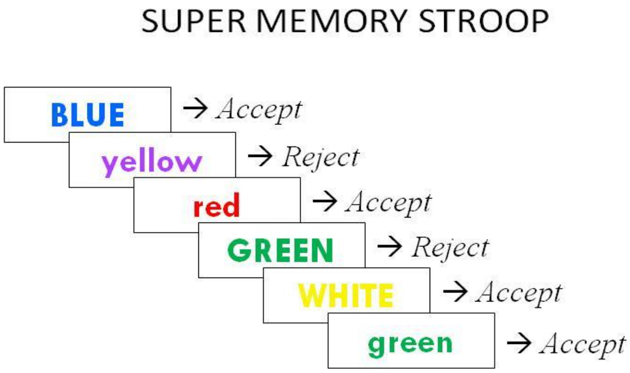

Figure 4-1c. The Super Memory task required Basic task responses plus rejection of the *super memory lure*, a specific congruent item in either upper or lower case (e.g., "GREEN in green font, but not "green" in green font), that differed for each block.

For both the Memory and Super Memory tasks, a specific contingency lure (i.e., the memory lure or super memory lure) was presented prior to the start of each block, and participants were given as much time as they needed to memorize it. Once participants felt they knew the relevant contingency lure (usually about 5 to 10 seconds), they pressed a button which triggered the start of the block's trials. To ensure that participants had maintained the correct memory or super memory lure throughout the duration of the block, they were asked to identify it at end of the block. For the Memory task, where case was not relevant to responses, four colour-words (one of which was the memory lure) were presented in both upper and lower case letters (e.g., RED/red, BLUE/blue, etc). For the Super Memory task, where case *was* relevant to responses, participants were first presented with four coloured squares and asked to identify the colour of the super memory lure. Once they selected the block that represented the colour, they were instructed to indicate whether they had rejected the lower or upper case version of this word during the previous block. Each Memory block included one memory lure (e.g., RED/red), and each Super Memory block included one super memory lure in either upper or lower case letters (e.g., RED). For both tasks, the relevant contingency lure changed from block to block.

2.2.2 Manipulating emotional arousal

In the monetary incentive phase, participants won 10 points for each correct response but lost 20 points for each error. This disproportionate trade-off made errors particularly costly, which, we assumed, would increase participants' concern over their performance and hence their level of emotional arousal. In order to ensure that participants did not slow down in order to avoid making errors in this phase, we also implemented a response time (RT) penalty that resulted in the loss of additional points if responses were deemed too slow.[7] In order to heighten the affective salience of the incentive phase, following the completion of each block, we utilized positive and negative emoticons and a moving thermometer that increased and then decreased according the number of points won and lost during that particular block (Figure 4-2). Participants were told that their points would be tracked throughout the session and converted to additional earnings following the completion of all three tasks (up to $15 CAD).

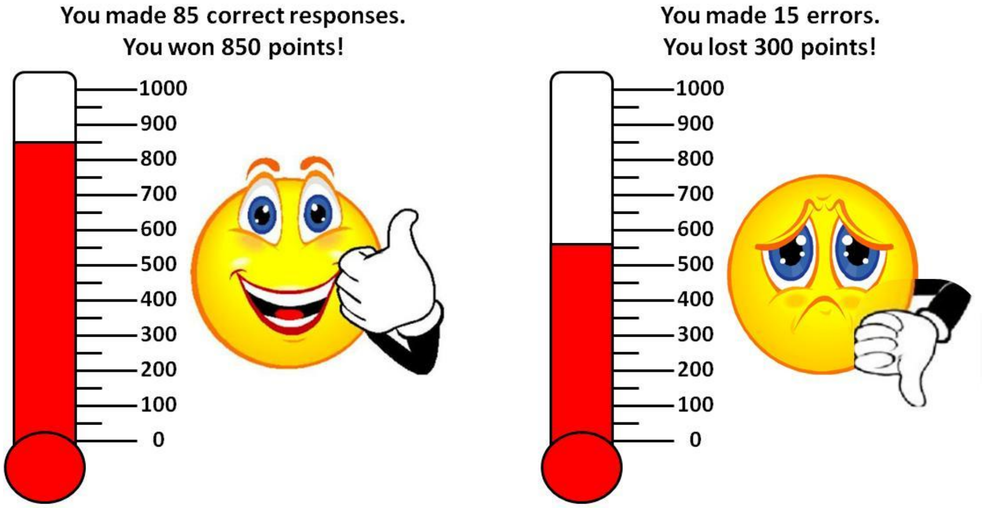

Figure 4-2. Depiction of affective feedback provided at the end each block during incentive phases.

2.2.3 Task details

Because we were interested in investigating error-related electrocortical activity, we attempted to maximize participants' errors in an effort to ensure the production of stable ERPs. As described in Study 2 (Chapter 3), we had participants complete a variable number of blocks (4 to 6) for each of the 3 tasks, during both standard and monetary incentive phases. Each block included 100 decision trials. Seventy-five of the trials consisted of

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[7] The RT penalty was calculated based on the average RT of each block of 100 trials. Younger adults lost 30 points for every 10 ms that their average RT exceeded 600 ms (e.g., an RT of 640 ms would cost an additional 120 points), whereas older adults lost 30 points for every 10 ms their average RT exceeded 700 ms (e.g., an RT of 740 ms would cost an additional 120 points).

congruent colour-words that required an “accept” response. The remaining 25 trials consisted of colour-words that required a “reject” response. In the case of the Basic task (standard and incentive), all 25 trials consisted of incongruent colour-words. In the case of the Memory and Super Memory tasks (standard and incentive), these 25 trials included a combination of both incongruent colour-words and relevant contingency items for the particular task. Thus, each block of the Memory task included 12 incongruent colour-words and 13 occurrences of the memory lure, whereas the Super Memory task included 12 incongruent colour-words and 13 occurrences of the super memory lure.

All participants completed the three Stroop tasks in identical order (Basic, Memory, Super Memory), with the completion of the monetary incentive phase of a task immediately following the completion of its standard phase. Colour-words appeared in uppercase and lowercase letters on a pale grey background. Colour-words for younger adults were presented for 600 ms, whereas colour-words for older adults were presented for 700 ms. In each case, colour-word presentation was followed by a variable intertrial interval of 700, 800, or 900 ms. Each block, therefore, was approximately 2 minutes and 20 seconds in length for younger adults and 2 minutes and 30 seconds in length for older adults. Within each of the 3 tasks, participants controlled the length of their breaks between blocks. A 2-minute break was provided between the standard and incentive phases of the tasks, and a longer 5-minute break was provided before transitioning to a new task. The entire paradigm, including practice trials and breaks, took approximately 1 hour and 35 minutes for younger adults to complete and 1 hour and 40 minutes for older adults to complete.

2.3 Procedure

All participants came to the lab on two different occasions, no more than 1 week apart. Part I was 1 hour in length and consisted of a general introduction to the study, the administration of a health history questionnaire, and the completion of the Modified Canadian Aerobic Step Test, a measure of physical fitness. Part II was approximately 3 hours in length and included the set-up of the psychophysiological equipment and the completion of the Stroop oddball paradigm. Participants completed the three Stroop tasks during both standard and monetary incentive phases while seated in a dimly lit, electrically and acoustically shielded room. Stimuli were presented using E-Prime research software (Psychological Software Tools, Inc.). Electroencephalography (EEG), electrocardiography (ECG), and respiration were recorded throughout the session. Resting blood pressure (BP) was measured prior to and following the completion of the Stroop tasks.

2.3.1 Modified Canadian Aerobic Fitness Test

The Modified Canadian Aerobic Fitness Test (mCAFT) was completed by all participants who were physically able and whose resting BP did not exceed the recommended limit (i.e., 140 mm Hg /90 mm Hg). The mCAFT is a sub-maximal test that provides an estimate of the maximum rate of oxygen consumption (VO_2max) which serves as an index of aerobic fitness. The test includes several levels, each of which requires participants to step up and down two steps for 3 minutes while their heart rate (HR) is recorded. The pace at which participants step during the test is based on a rhythm set by an auditory recording. The level selected on the recording is determined by the participant’s age and sex. Participants complete one or more levels until their predetermined ceiling HR (again, based on their age and sex) is reached. Because the mCAFT is a sub-maximal test, the pre-determined ceiling HR represents 85% of one’s maximum HR. Most participants completed one or two stepping levels. Following completion of the mCAFT, each participant's VO_2max, or aerobic fitness score, was then estimated using the following equation:

$$VO_2max = 42.5 + 16.6(E) - 0.12(M) - 0.12(HR) - 0.24(A)$$

where VO_2max represented aerobic power in ml**.**kg-1**.**min-1, E represented the energy cost of the final Step Test stage reached in liters of oxygen per minute, M represented body mass in kilograms, HR represented heart rate in beats per minute on the last stage of Step Test, and A represented the participant's age in years.

2.3.2 EEG Processing

EEG was collected using a 128-channel Active Two BioSemi system (BioSemi, Amsterdam). Data were sampled at a rate of 512 Hz and digitized with a 24-bit analog-to-digital converter. Before submitting data for ICA, several preprocessing steps occurred including the identification and rejection of bad channels (i.e., noisy and linked channels) and time segments. These preprocessing steps were performed in MatLab using a combination of EEGLab functions (Delorme & Makeig, 2004) and in-house functions designed to facilitate the automatic identification and rejection of artifacts using the Shared Hierarchical Academic Research Computing Network (SHARCNet). See Appendix B for specific details on EEG and ICA processing.

Following two ICA decompositions, dipoles were fit to each IC, and if a dipole set explained less than 85% of the weight variance, that IC was marked for rejection. Each IC was then manually inspected. If an IC that was marked for rejection could be explained by symmetrical bilateral dipoles, it was retained. Those ICs that represented biological artifacts (e.g., eye movements, blinks, muscle tension, heart rate), however, were rejected. Following this manual inspection, the ICA weights were then applied back to the continuous filtered data with periods removed that were flagged during the ICA pruning procedure.

2.3.3 ERP Analyses

In order to examine the ERN and Pe, the response-locked, artifact-free data were averaged relative to a −600 ms to −400 ms pre-response baseline. For the ERN, response-locked correct and error trials were measured as the average amplitude of the voltage data between 0 and 150 ms at site FCz. For the Pe, response-locked correct and error trials were measured as the average amplitude between 150 ms and 325 ms post-response at site FCz.

2.3.4 ACC-IC Analyses

In addition to our ERPs, we were interested in exploring our response-locked errors further to determine whether a component accounting for the ERN could be identified. As such, it was necessary to calculate the mutual variance between the components and the ERN in the corresponding time window. This was done by examining the percent of variance the components accounted for in the time window that corresponded to the ERN (approximately 0 to 150 ms). The topographies and time courses of the ICs produced by this analysis were then inspected. The component that produced an increase in phasic activity following the error along with a fronto-central scalp topography was identified as the IC accounting for the ERN. Further dipole analyses were consistent with a model of the ACC being the source. This component will be referred to as the ACC-IC. We were able to identify an ACC-IC for 21 of our 23 younger adults; however, we were unable to identify this same component for the majority of our older adults. Therefore, all analyses involving the ACC-IC are based on the younger adults only.

For those younger adults with an available ACC-IC, global field amplitude (GFA) ERP overlays were produced for each of the participants' six tasks. Average ERP overlays for each of the six tasks revealed two peaks (see Figure 4-3). The first peak occurred between 0 and 125 ms and likely represents the GFA of the ACC-IC that corresponds with the ERN. The second peak occurred between 125 and 400 ms and likely represents the GFA of the ACC-IC that corresponds with the Pe. Therefore, we computed two GFA measures of the ACC-IC by calculating the average amplitude of the voltage data between 0 and 125 ms (ACC_{GFA1}) and 125 and 400 ms (ACC_{GFA2})

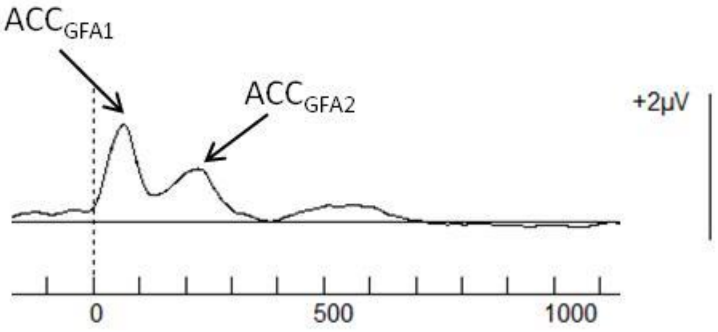

Figure 4-3. Global field amplitude overlay of the ACC independent component.

2.3.5 Cardiac Measures

Using an automated sphygmomanometer, two BP readings (systolic: SBP; diastolic: DBP) were taken following a 5-minute rest period that preceded the start of the testing session and again following another final 5-minute rest period that concluded the testing session. ECG was monitored throughout the entire task and during both the 5-minute resting periods. In order to monitor respiration, a flexible respiration belt was placed around the participant's upper chest (MindWare Technologies Ltd., Columbus, OH). ECG signals were recorded from two electrodes placed on the participant's chest; one affixed about 2.5 cm below the right clavicle, the other placed between the 2 bottom-ribs on the person's left side. ECG signals were sampled at 1000 Hz by the acquisition program (BIOPAC Acq*Knowledge*), and RSA was then analyzed using a commercial software package (MindWare Heart Rate Variability Scoring Module 2.51, Mindware Technologies Ltd., Columbus, OH). R–R (interbeat) intervals were visually inspected and edited where necessary according to principles advocated by Berntson and Stowell (1998). Minute-by-minute estimates of RSA (heart rate variability at the respiratory frequency, 0.12–0.4 Hz) were calculated via spectral analysis of the heart beat series using fast Fourier transformation and a Hamming window based on 1- min epochs. A sample rate of 250 ms (4/s) provided 240 samples (120 FFT bins), resulting in a frequency resolution of 0.01667 Hz. RSA is then expressed as the natural log transform of this frequency band, ln(ms^2). Estimates of RSA, HR, and respiration rate (RR) were averaged for the pre-task baseline and post-task resting periods. For on-task measures, time frames from each block of a particular task and phase were selected, analyzed, and then averaged together. Finally, we calculated a measure of pre-task RPP for all participants to examine whether cardiac workload related to accuracy in the context of the current Stroop tasks (multiplying pre-task SBP and pre-task HR, and dividing by 100).

2.3.6 Analyses

To investigate the effects of group (younger, older), task (Basic, Memory, Super Memory), and phase (standard, monetary-incentive), data were subjected to a series of ANOVAs, and interactions were followed up with simple effects analyses. All analyses were corrected for violations of Mauchley’s Test of Sphericity, where necessary, using the Huynh–Feldt correction for estimating the F Statistics with the original degrees of freedom and corrected p-values reported in the text. Correlational analyses were used to examine relations between autonomic, electrophysiological, and performance data. All significance values are based on two-tailed tests.

Results

3.1 Performance data

Accuracy for congruent trials across all tasks and phases was > 97% for both older and younger groups. More informative was the effect of task manipulations on the ability of participants to correctly reject the various lures: the incongruent lures present in all three tasks and the contingency lures present in the Memory task (i.e., memory lures) and Super Memory task (i.e., super memory lures). First, the proportion of accurate rejections for incongruent lures was entered into a 3 (task: Basic, Memory, Super Memory) x 2 (phase: standard, incentive) x 2 (group: younger, older) repeated measures analysis of variance (ANOVA). Importantly, there was no main effect of group ($p > .12$) nor did any interactions with group emerge ($p > .10$), indicating similar levels of response control across tasks and phases for older and younger adults. However, the ability to accurately reject incongruent lures decreased with the addition of each contingency, $F(2,84) = 33.73$, $p < .001$, $\eta^2 = .45$ (Basic, $M = .81 \pm .02$; Memory, $M = .72 \pm .02$; Super Memory, $M = .68 \pm .03$). Conversely, the addition of monetary incentive resulted in more correct responses to incongruent lures, F $(1,42) = 11.04$, $p = .002$, $\eta^2 = .21$ (standard, $M = .72 \pm .02$; incentive, $M = .75 \pm .02$). An interaction between task and phase, $F(2,84) = 5.32$, $p = .007$, $\eta^2 = .11$, indicated that this effect was reliable only in the context of the Super Memory task, $t(44) = -3.68$, p = .001, with accuracy increasing from the standard ($M = .63 \pm .02$) to the incentive phase ($M = .70 \pm .03$). Thus, using a monetary incentive to enhance motivation had its greatest impact when the task required the highest level of cognitive control (all other *p*s > .09) (see Figure 4-4).

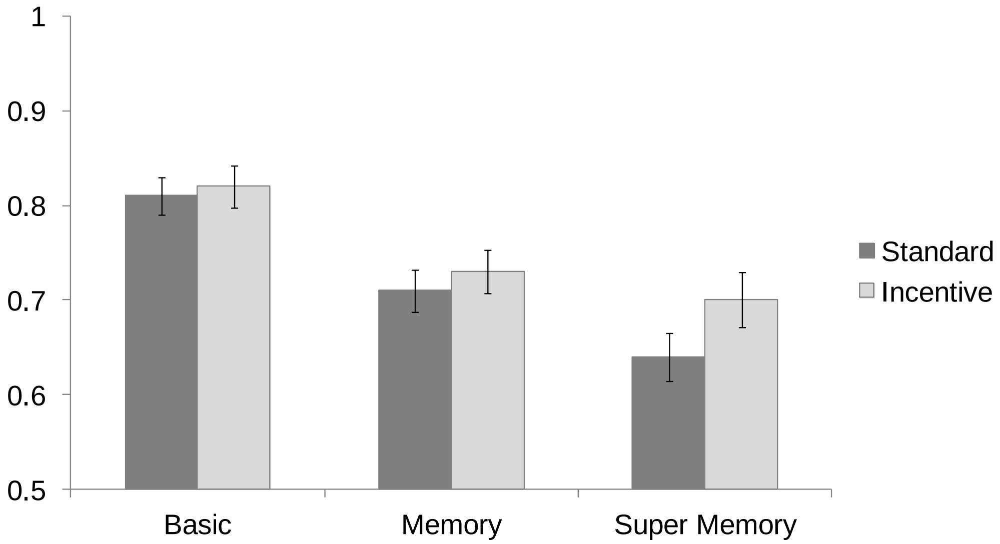

Figure 4-4. Depiction of the interaction between task and phase on incongruent accuracy. Incongruent accuracy increased from the standard to the incentive phase, but this effect was only reliable in the context of the Super Memory task.

RTs for correct incongruent lure rejections were analyzed in the same manner, and revealed the expected main effect of group, $F(1,41) = 31.94$, $p < .001$, $\eta^2 = .44$, with older adults responding more slowly ($M = 670 \pm 12$ ms) than younger adults ($M = 576 \pm 12$ ms). As well, the addition of monetary incentive resulted in faster RTs ($M = 617 \pm 8$ ms) compared to standard phases ($M = 629 \pm 9$ ms), $F(1,41) = 17.69$, $p < .001$, $\eta^2 = .30$. There was also a main effect of task, $F(2,82) = 20.00$, $p < .001$, $\eta^2 = .32$, indicating that participants responded more slowly to incongruent lures during the Memory ($M = 633 \pm 10$ ms) and Super Memory ($M = 637 \pm 9$ ms) tasks compared to the Basic task ($M = 598 \pm 8$ ms). None of the interactions reached significance (all *p*s > .15) (see Figure 4-5).

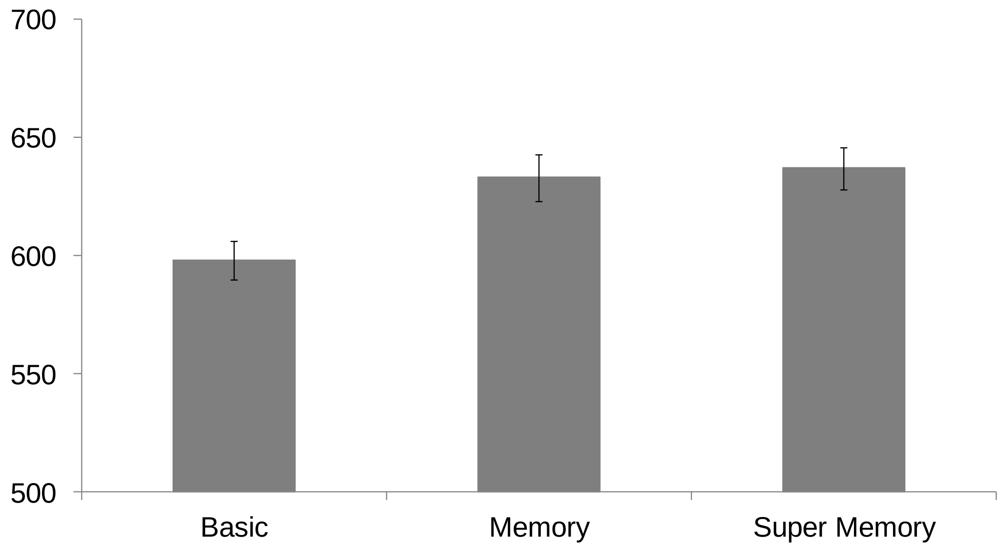

Figure 4-5. Depiction of the main effect of task on incongruent response time. Participants responded more slowly to incongruent lures during the Memory and Super Memory tasks compared to the Basic task.

In order to determine whether super memory lures (i.e., the ability to reject a specific congruent colour-word based on both colour *and* case size) were indeed more challenging to reject than memory lures (i.e., the ability to reject a specific congruent colour-word based on colour *only),* and to determine whether younger and older adults differed in terms of their performance on these items, we entered the proportion of accurate rejections for these contingency lures into a 2 (contingency lure-type: memory, super memory) x 2 (phase: standard, incentive) x 2 (group: younger, older) repeated measures ANOVA. Contrary to expectations, there was no main effect of task (p > .86) or group (*p* > .61). There was, however, a main effect of phase, $F(1,42) = 18.76$, $p < .001$, $\eta^2 = .31$, indicating, as expected, that accuracy for contingency lures increased from the standard ($M = .79 \pm .02$) to the incentive phases ($M = .83 \pm .02$). There was also a three-way interaction between contingency lure-type, phase, and group, $F(1,42) = 4.49$, $p = .04$, $\eta^2 = .10$. Follow-up analyses indicated that the incentive was most effective for younger adults in terms of their accuracy for single-contingency memory lures, $t(22) = -4.19$, $p < .001$ (standard, $M = .76 \pm .02$; incentive, $M = .82 \pm .02$), but not super memory lures (pairwise $p > .73$), whereas the incentive benefitted older adults in terms of their accuracy for super memory lures , $t(21) = -2.45$, $p = .023$ (standard, $M = .77 \pm .04$, incentive, $M = .84 \pm .03$), but not memory lures (pairwise $p > .14$). We have no hypotheses as to why this interaction would have occurred (see Figure 4-6).

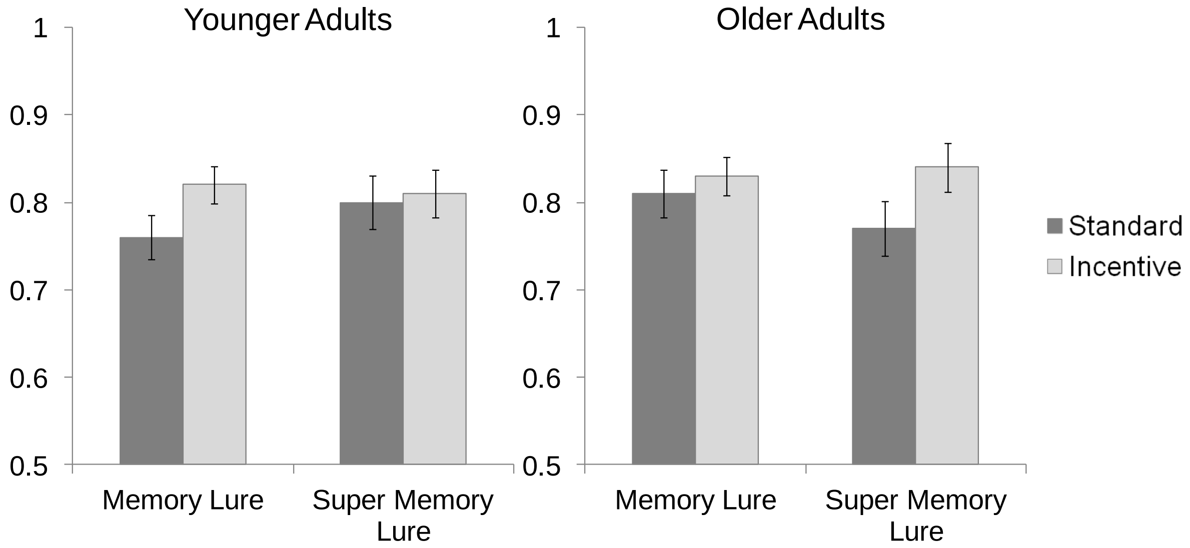

Figure 4-6. Depiction of 3-way interaction between contingency lure-type, phase, and group.

Analyses with contingency item RTs revealed the expected effect of group, $F(1,41) = 27.48$, $p < .001$, $\eta^2 = .40$, with older adults responding more slowly ($M = 568 \pm 11$ ms) than younger adults ($M = 491 \pm 10$ ms). An interaction between contingency type and phase did not reach significance ($p = .063$), but there was a main effect of contingency type, $F(1,41) = 5.08$, $p = .03$, $\eta^2 = .11$, which indicated, as expected, that participants responded faster to the memory lures ($M = 523 \pm 8$) than the super memory lures ($M = 536 \pm 8$ ms), confirming that super memory lures were more costly in terms of cognitive resources.

3.2 BP, HR, RR, and RSA

BP was measured prior to and following completion of the task. Analyses with SBP revealed main effects of both group and phase (*p*s < .001), but these were superseded by a group by phase interaction, $F(1,41) = 17.39$, $p < .001$, $\eta^2 = .30$. Follow-up analyses indicated that for both groups, SBP increased from pre-task to post-task, but this increase was greater for older (pre = 119.74 ± 2.38 mm Hg, post = 133.41 ± 2.50 mm Hg) relative to the younger adults (pre = 99.39 ± 2.32 mm Hg, post = 102.32 ± 2.44 mm Hg). DBP also varied on the basis of group and phase (ps < .02), but again, these effects were superseded by an interaction between group and phase, $F(1,41) = 6.56$, $p = .014$, $\eta^2 = .14$. As was the case with SBP, DBP increased from pre-task to post-task for both groups, but this increase was greater for older (pre = 73.48 ± 1.37 mm Hg, post = 81.21 ± 1.69 mm Hg) relative to younger adults (pre = 64.86 ± 1.33 mm Hg, post = 68.14 ± 1.65 mm Hg). In all, older adults appeared to be more physiologically reactive to the experimental conditions.

HR, RR, and RSA were measured prior to, during, and following completion of the task and were subjected to a 2 (group: younger, older) x 3 (test period: pre-task, on-task, post-task) repeated measures ANOVA. HR (beats per minute) did not differ between older (M = 72.12 ± 1.95 bpm) and younger (M = 71.36 ± 2.04 bpm) adults ($p > .79$). Nor did HR differ between pre-task (M = 72.58 ± 1.46 bpm) and on-task periods (M = 74.20 ± 1.57 bpm), but was lower during the post-task period (M = 68.45 ± 1.44 bpm), $F(2,80) = 24.64$, $p < .001$, $\eta^2 = .38$, suggesting a reduction of arousal at task completion, an effect that did not interact with group ($p > .14$). In terms of RR (breaths per minute), there was no main effect of test period ($p > .30$) and the interaction between test period and group did not reach significance ($p > .12$), but RR was generally lower in the older (M = 11.54 ± .56 bpm) compared to the younger adults (M = 14.28 ± .52 bpm), $F(1,39) = 12.61$, $p < .002$, $\eta^2 = 24$. Finally, and again, as expected, RSA was lower in older (M = 4.55 ± .18 ln ms^2) compared to younger adults (M = 6.47 ± .18 ln ms^2), $F(1,40) = 56.60$, $p < .001$, $\eta^2 = .59$, and it was lower during on-task (M = 5.22 ± .15 ln ms^2) compared to pre-task (M = 5.54 ± .15 ln ms^2) and post-task (M = 5.76 ±

.14 ln ms^2) periods, $F(2,80) = 8.51$, $p < .001$, $\eta^2 = .18$. There was no group by task period interaction ($p > 30$).

3.3 Autonomic Regulation and Total Rejection Accuracy

We were primarily interested in whether parasympathetic influence on cardiac function at baseline (i.e., pre-task RSA) would increase the likelihood of accurate performance and under which conditions this was most likely to occur. As was the case in Study 2 (Chapter 3), we used overall rejection accuracy within each task and phase as our dependent measure, i.e., the correct rejection of all relevant items (incongruent items plus memory or super memory lures) as relevant to each task and phase.

Contrary to expectations, younger adults' pre-task levels of RSA did not relate to their overall rejection accuracy during any of the Stroop tasks or phases (all *p*s > .10). Thus, regardless of task demands or monetary incentive, there was no evidence of an association between pre-task RSA and performance within the younger group. However, relations between pre-task RSA and performance within the older group were more in line with expectations. During the standard phase, there was no relationship between pre-task RSA and rejection accuracy in the Basic task ($p > .35$), but relations did emerge with the added response contingencies. Higher pre-task RSA was related to better overall rejection accuracy in the context of both the Memory ($r = .52$, $p < .02$) and Super Memory ($r = .53$ $p < .02$) tasks. During the monetary incentive phase, pre-task RSA was still not relevant to rejection accuracy in the Basic task ($p > .25$). It was evident again in the context of the Memory task ($r = .59$, $p < .006$) but did not reach significance for the Super Memory task ($p < .13$), although it was in the same direction. Thus, for older adults, pre-task RSA was relevant to overall rejection accuracy, but this relationship was most consistent in the context of the Memory task.

3.4 Comparing Incongruent and Contingency Lures

We were surprised that relations did not emerge between pre-task RSA and total rejection accuracy in the younger group, especially since we had observed such relations during Study 2 (Chapter 3). To explore this further, we separated lures on the basis of whether they would be more or less likely to elicit a proactive response strategy. As stated previously, we would expect relations between pre-task RSA and accuracy to be most apparent when participants are relying on a more resource-demanding proactive form of control. One could argue, however, that the incongruent colour-words would elicit a more reactive response strategy because one can only hold a general rule in mind (i.e., *reject if incongruent*) to guide response preparation. In other words, there is no predictive cue that can be held in mind in order to facilitate early selectivity (Bar, 2003; Bar et al., 2006) and response preparation (Braver et al., 2008). On the other hand, the contingency lures do allow for the maintenance of a specific relevant target that could facilitate this early selectivity. Hence, the combined rejection accuracy rate may encompass both types of response strategies such that the actual relationship of proactive response strategies with other variables might be obscured.

To test the possibility that participants may have relied upon different control strategies when confronted with incongruent versus contingency lures, we borrowed a concept from Czernochowski, Nessler, and Friedman (2010) who proposed that proactive control should lead to more effective (i.e., more accurate) and efficient (i.e., faster) responding than the use of reactive control.[8] Thus, we ran another set of analyses in which we compared the accuracy rates and RTs associated with incongruent versus contingency lures in both phases of the Memory and Super Memory tasks. Based on Czernochowski et al.'s (2010) model, our incongruent lures should involve more errors and longer RTs than the contingency lures that allow for the maintenance of a specific target item in WM and, hence, a proactive response strategy.

We entered the proportion of accurate lure rejections into a 2 (task: Memory, Super Memory) x 2 (lure-type: incongruent, contingency) x 2 (phase: standard, incentive) x 2 (group: younger, older) repeated measures ANOVA. Importantly, as well as the other main effects of task and phase that have already been reported, we found a main effect of lure-type, $F(1,42) = 37.86$, $p < .001$, $\eta^2 = .47$, which indicated that participants responded more accurately to contingency lures ($M = .81 \pm .02$) than incongruent lures ($M = .69 \pm .02$). Furthermore, an interaction between lure-type and task, $F(1,42) = 8.76$, $p = .005$, $\eta^2 = .17$, suggested that this accuracy difference was somewhat larger for the Super Memory task (incongruent lures: $M = .67 \pm .02$; contingency lures: $M = .80 \pm .02$) than the Memory task (incongruent lures: $M = .72 \pm .02$; contingency lures: $M = .81 \pm .02$). A 4-way interaction also emerged, but this appeared to be driven by interactions with phase that were not relevant to the current question regarding differences in lure-type accuracy.

RTs for correct lure rejections were analyzed in the same manner and, again, revealed a main effect of lure-type, $F(1,42) = 396$, $p < .001$, $\eta^2 = .90$, which showed that participants responded faster to contingency lures ($M = 530 \pm 7$) than incongruent lures ($M = 636 \pm 9$). A further lure-type by group interaction, $F(1,42) = 4.62$, $p < .04$, $\eta^2 = .10$, indicated that the

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[8] Because the Basic task only involved the rejection of incongruent lures, subsequent analyses only pertained to the Memory and Super Memory tasks where the rejection of additional contingency lures was required.

difference seemed to be even larger for older (incongruent lure RT: *M* = 685 ± 13; contingency lure RT: *M* = 568 ± 10) compared to younger adults (incongruent lure RT: *M* = 586 ± 12; contingency lure RT: *M* = 492 ± 10).

Thus, participants, in general, responded faster and more accurately to contingency lures than they did to incongruent lures. This particular pattern suggests that participants may have indeed relied on different forms of control for the various lures, utilizing a more proactive form of control for contingency lures but opting for a more reactive strategy for incongruent lures.

3.5 Autonomic Regulation and Specific Lure Accuracy

We next examined the relationship between pre-task RSA and accuracy for the different lures (i.e., incongruent lures, memory lures, super memory lures). For younger adults, we found that pre-task RSA related to the ability to accurately reject memory lures ($r = .46$ $p < .03$) (Figure 4-7a) and super memory lures ($r = .42$ $p < .05$) (Figure 4-8a). In neither case, however, did pre-task RSA relate to the ability to accurately reject regular incongruents (both *p*s > .34). The addition of the monetary incentive revealed a similar but less consistent pattern. Specifically, pre-task RSA was again related to the ability to accurately reject memory lures ($r = .44$ $p < .04$) (Figure 4-7b), but this time, accuracy for super memory lures was not related ($p > .78$) (Figure 4-8b), and again, there was no relationship with regular incongruents (both *p*s > .71). Thus, for younger adults, pre-task RSA was relevant to rejection accuracy, but specifically, to the rejection of contingency lures, not regular incongruents (See Table 4-1, column 4).

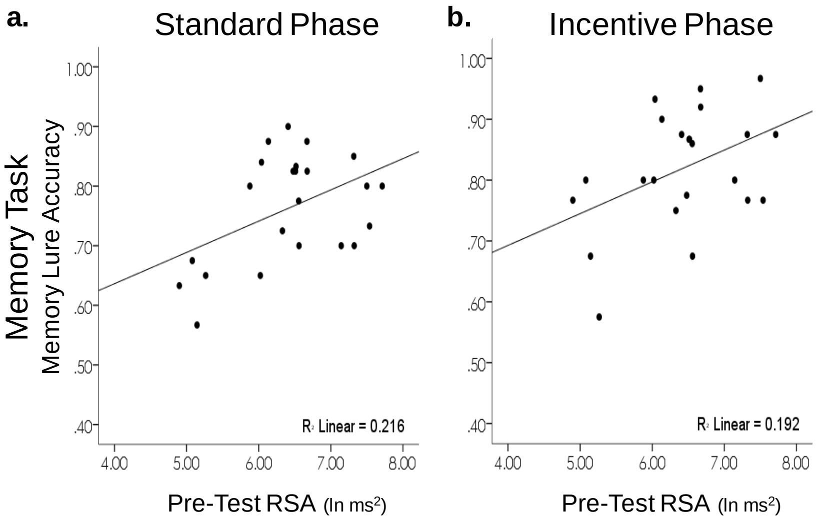

Figure 4-7. Relations between pre-task RSA and memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Memory task for younger adults.

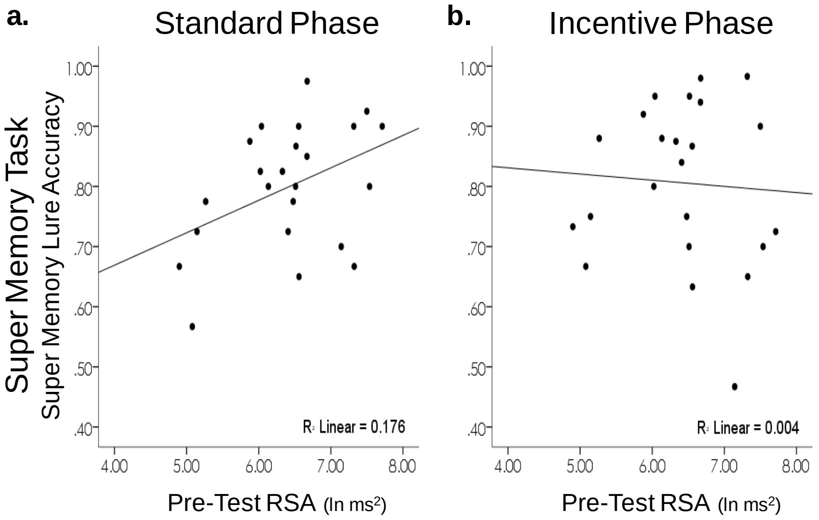

Figure 4-8. Relations between pre-task RSA and super memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Super Memory task for younger adults.

For older adults, higher pre-task RSA was related to the ability to accurately reject both memory lures ($r = .45$, $p < .04$) (Figure 4-9a) and super memory lures ($r = .59$, $p < .01$) (Figure 4-10a). We note, as well, some trends linking pre-task RSA to accuracy in rejecting incongruent colour-words during both the Memory ($r = .39$, $p = .07$) and Super Memory ($r = .37$, $p = .088$) tasks. The addition of the monetary incentive revealed a somewhat similar pattern. Pre-task RSA again related to accuracy for memory ($r = .55$, $p < .01$) and super memory lures ($r = .49$, $p < .03$), and to the accurate rejection of incongruent colour-words in the Memory, ($r = .47$, $p < .04$) but not the Super Memory ($p > .36$), task. Thus, pre-task RSA related to contingency lure accuracy in both older and younger adults, but there was some evidence for relations with incongruent accuracy in the older adults as well (See Table 4-2, column 4).

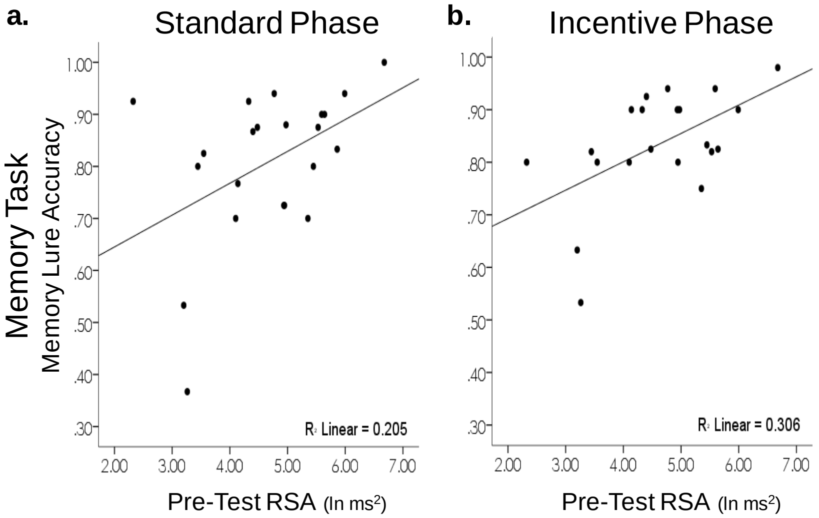

Figure 4-9. Relations between pre-task RSA and memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Memory task for older adults.

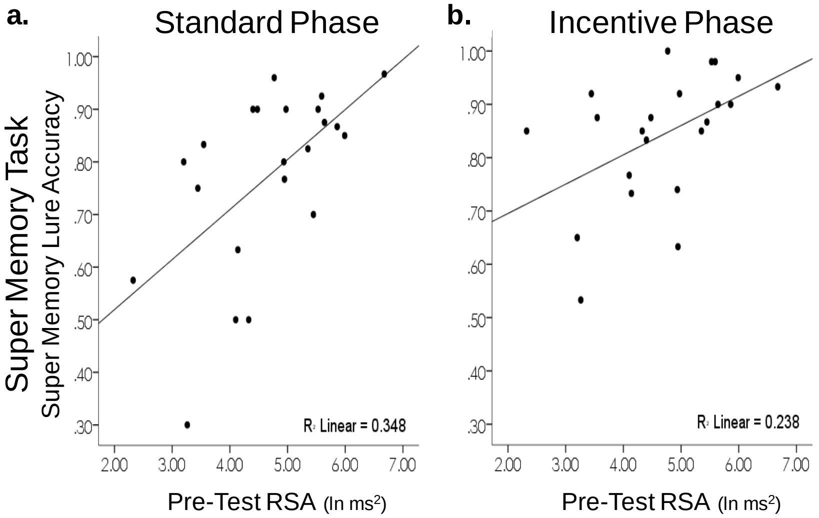

Figure 4-10. Relations between pre-task RSA and super memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Super Memory task for older adults.

3.6 Bootstrapping

Due to our relatively small sample size, we submitted our data to a more robust analysis procedure to ensure reliability (Desjardins & Segalowitz, 2013; Rousselet, Husk, Bennett, & Sekuler, 2008; Wilcox, 2005). For each of our original parametric correlations, we computed two sets of robust *r* correlation coefficients: one Winsorized at 10% (r_w 10%) and the other Winsorized at 20% (r_w 20%). In the case of r_w 10%, one individual was moved in from each tail of the distribution, and in the case of r_w 20%, three individuals were moved in from each tail. We then re-sampled with replacement and Winsorized 1000 times so as to generate 1000 correlation coefficients and their associated p-values. Table 4-1 depicts the original Pearson *r* correlation coefficients (column 4) with their corresponding Winsorized correlation coefficients (columns 5 and 6) for the younger group, and Table 4-2 depicts the original Pearson *r* correlation coefficients (column 4) with their corresponding Winsorized correlation coefficients (columns 5 and 6) for the older group. Relations between pre-task RSA and accuracy in the younger adults did not survive bootstrapping. However, many of the relations within the older group did, particularly relations between pre-task RSA and contingency lure accuracy during the most demanding task, i.e., the Super Memory task, during both standard and incentive phases.

Table 4-1
Parametric and Winsorized Correlations for Younger Adults between Pre-Task RSA and Rejection Accuracy on Incongruents and Contingency Lure Trials during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Stimulus Type	Phase	Pearson's *r*	r_w (10%)	r_w (20%)
Basic	Incongruent	Standard	*r* = .14 (*p* = .530)	*r* = -.02 (*p* = .968)	*r* = -.11 (*p* = .824)
		Incentive	*r* = .13 (*p* = .570)	*r* = -.02 (*p* = .998)	*r* = -.16 (*p* = .790)
Memory	Incongruent	Standard	*r* = .21 (*p* = .342)	*r* = .23 (*p* = .384)	*r* = .14 (*p* = .378)
		Incentive	*r* = .05 (*p* = .830)	*r* = .06 (*p* = .930)	*r* = -.12 (*p* = .840)
	Memory lure	Standard	*r* = .46* (*p* = .026)	*r* = .42 (*p* = .156)	*r* = .15 (*p* = .402)
		Incentive	*r* = .44* (*p* = .037)	*r* = .41 (*p* = .100)	*r* = .22 (*p* = .236)
Super Memory	Incongruent	Standard	*r* = .01 (*p* = .970)	*r* = -.01 (*p* = .912)	*r* = -.05 (*p* = .878)
		Incentive	*r* = -.08 (*p* = .714)	*r* = -.12 (*p* = .538)	*r* = -.22 (*p* = .450)
	Super memory lure	Standard	*r* = .42* (*p* = .046)	*r* = .36 (*p* = .150)	*r* = .21 (*p* = .350)
		Incentive	*r* = -.06 (*p* = .780)	*r* = -.03 (*p* = .832)	*r* = -.17 (*p* = .694)

Table 4-2
Parametric and Winsorized Correlations for Older Adults between Pre-Task RSA and Rejection Accuracy on Incongruents and Contingency Lure Trials during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Stimulus Type	Phase	Pearson's r	r_w (10%)	r_w (20%)
Basic	Incongruent	Standard	r = .21 (p > .350)	r = .13 (p > .580)	r = .11 (p = .686)
		Incentive	r = .25 (p > .250)	r = .26 (p > .450)	r = .16 (p = .508)
Memory	Incongruent	Standard	r = .39 (p = .070)	r = .38 (p = .058)	r = .38 (p = .080)
		Incentive	r = .47* (p = .033)	r = .43 (p = .076)	r = .42 (p = .074)
	Memory lure	Standard	r = .45* (p = .034)	r = .36 (p = .118)	r = .32 (p = .150)
		Incentive	r = .55** (p = .009)	r = .46* (p = .038)	r = .40 (p = .152)
Super Memory	Incongruent	Standard	r = .37 (p = .088)	r = .34 (p = .088)	r = .31 (p = .126)
		Incentive	r = .20 (p = .360)	r = .23 (p = .290)	r = .18 (p = .336)
	Super memory lure	Standard	r = .59** (p = .004)	r = .57** (p = .004)	r = .56* (p = .010)
		Incentive	r = .49* (p = .021)	r = .53* (p = .010)	r = .49* (p = .030)

3.7 RSA Reactivity

We were also interested in whether the degree to which RSA shifted in response to attentional demands or changes in emotional arousal (via monetary incentive) would affect performance. An index of RSA reactivity was calculated for each of the six tasks by removing the shared variance in RSA associated with the pre-task period from the RSA recorded during the performance of each task. These saved residuals were then used to predict rejection accuracy within each relevant task. Instead of looking at total rejection accuracy, we again decided to examine how RSA reactivity related to accuracy for the various rejection items separately (i.e., incongruents, memory lures, super memory lures), which appeared to be more sensitive indicators of performance in our previous analyses.

For younger adults, none of the associations between RSA reactivity and accuracy reached significance, irrespective of task or phase (all ps > .37). Relations between RSA reactivity and accuracy did not reach significance in the older group (all *p*s > .10), except in the context of the Memory task where greater reactivity was associated with better memory lure accuracy during both standard (*r* = .49, *p* < .03) and incentive (*r* = .53, p < .03) phases. However, in contrast to relations with pre-task RSA, associations with RSA reactivity were reduced once bootstrapped (*p*s > .07).

We also examined whether pre-task RPP related to accuracy for the different lures (i.e., incongruent lures, memory lures, super memory lures). None of the associations between pre-task RPP and accuracy reached significance in the younger group, irrespective of task or phase (all *p*s > .35). As for older adults, relations between pre-task RPP and accuracy did not reach significance (all *p*s > .09), expect in the context of the Memory task where greater pre-task RPP was associated with better incongruent accuracy during both standard (*r* = .47, *p* < .03) and incentive (*r* = .50, *p* < .03) phases. Once we employed our more robust statistical procedures, the association in the standard phase was no longer present (*p*s > .14), but the association in the incentive phase remained when Winsorized at 10% (*r* = .47, *p* < .04) and a marginal association remained when Winsorized at 20% (*r* = .48, *p* = .07). This pattern is opposite what we would have expected with respect to RPP and accuracy. However, interpretation requires a comparison across the 3 studies presented in this thesis, which will be reserved for Chapter 5 and Appendix C.

3.8 ERPs

Grand average ERP waveforms associated with corrects and errors are shown in Figure 4-11 and 4-12. Although accuracy for different types of stimuli were examined separately in the behavioural data analyses, all possible errors were included in the ERP analyses to ensure a sufficient number of trials for stable ERP components.

ERN analyses were carried out in a 3 (task: Basic, Memory, Super Memory) x 2 (accuracy: correct, error) x 2 (phase: standard, incentive) x 2 (group: younger, older) mixed measures ANOVA. Results revealed a three-way task by accuracy by group interaction, $F(2,78) = 4.35$, $p = .021$, $\eta^2 = .10$, and a marginal phase by group interaction, $F(1,39) = 3.78$, $p = .06$, $\eta^2 = .09$. Follow-up analyses with the older group indicated a main effect of phase, $F(1,17) = 70.83$, $p = .001$, $\eta^2 = .81$, which showed that the ERN was larger during the incentive ($M = -1.10 \pm .18$ μV) compared to the standard phase ($M = 0.59 \pm .13$ μV). Follow-up analyses with the younger group revealed a main effect of accuracy, $F(1,22) = 7.13$, $p = .014$, $\eta^2 = .25$, and a task by phase interaction, $F(2,44) = 27.75$, $p < .001$, $\eta^2 = .56$. Additional analyses within the younger group indicated that the ERN was largest during the Basic task ($M = -3.16 \pm .30$ μV) compared to the Memory ($M = -1.68 \pm .30$ μV) and Super Memory ($M = -1.70 \pm .29$ μV) task. Thus, the ACC error response of older and younger adults seemed responsive to different aspects of the experimental procedures.

Pe analyses revealed a four-way task by accuracy by phase by group interaction, $F(2,78) = 5.10$, $p = .008$, $\eta^2 = .12$. Follow-up analyses indicated that the task by accuracy by phase interaction reached significance for both older, $F(2,34) = 4.50$, $p = .027$, $\eta^2 = 21$, and younger adults, $F(2,44) = 3.26$, $p = .049$, $\eta^2 = 13$. Further investigation indicated that the addition of incentive resulted in larger Pe's, but the groups differed with respect to the task context in which it occurred. Specifically, the addition of incentive resulted in larger Pe's for older adults during the Basic task, $t(18) = -2.35$, $p = .03$ (standard, $M = .96 \pm .19$ μV; incentive, $M = 1.48 \pm .26$ μV), whereas the same was true for younger adults during the Memory task, $t(22) = -2.60$, $p = .016$ (standard, $M = 1.44 \pm .32$ μV; incentive, $M = 2.22 \pm .43$

µV). So, again, shifts in Pe amplitude suggest between group differences in response to task conditions.

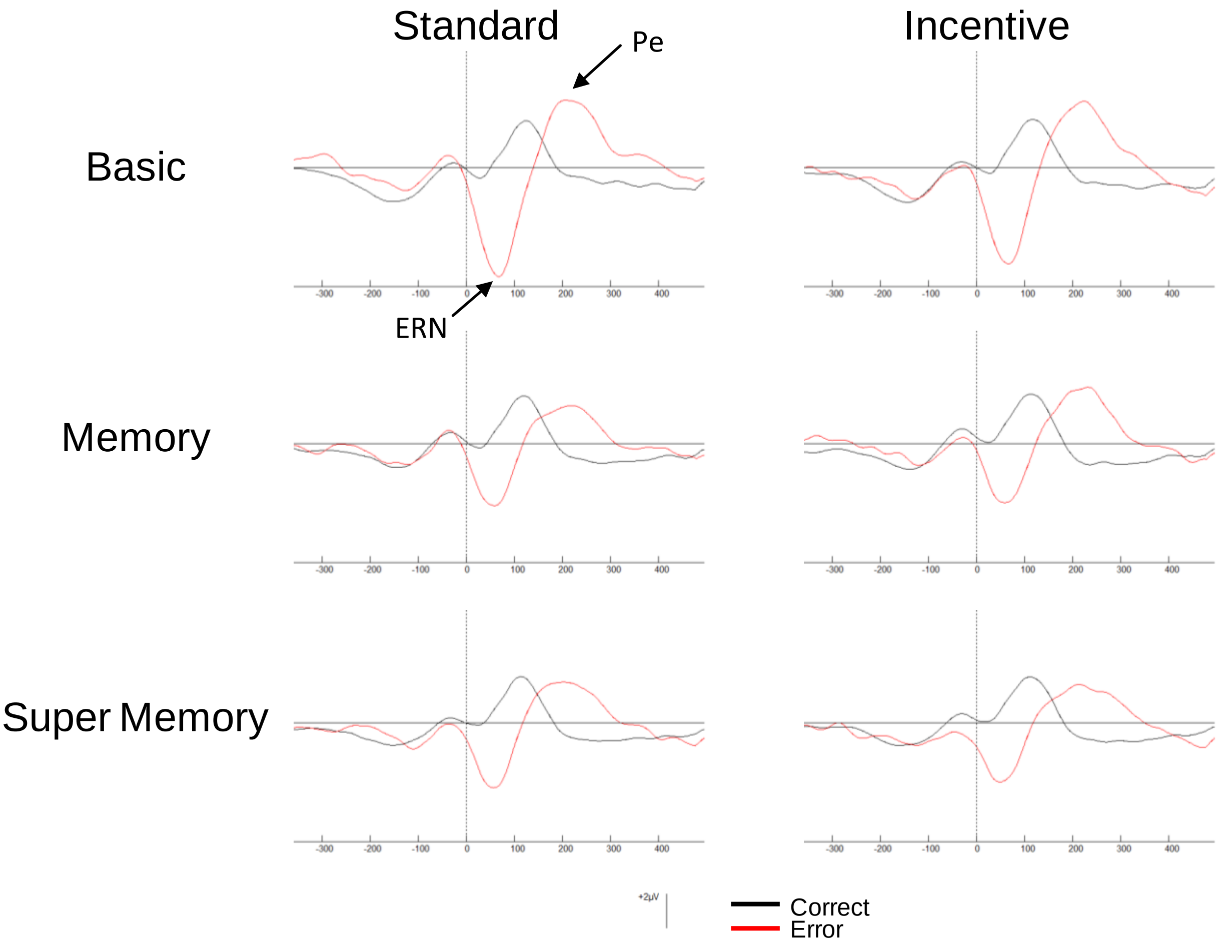

Figure 4-11. Response-locked event-related potentials (ERN, Pe) depicted at frontal-central site (FCz) associated with errors and correct trials for all Stroop tasks and phases for younger adults.

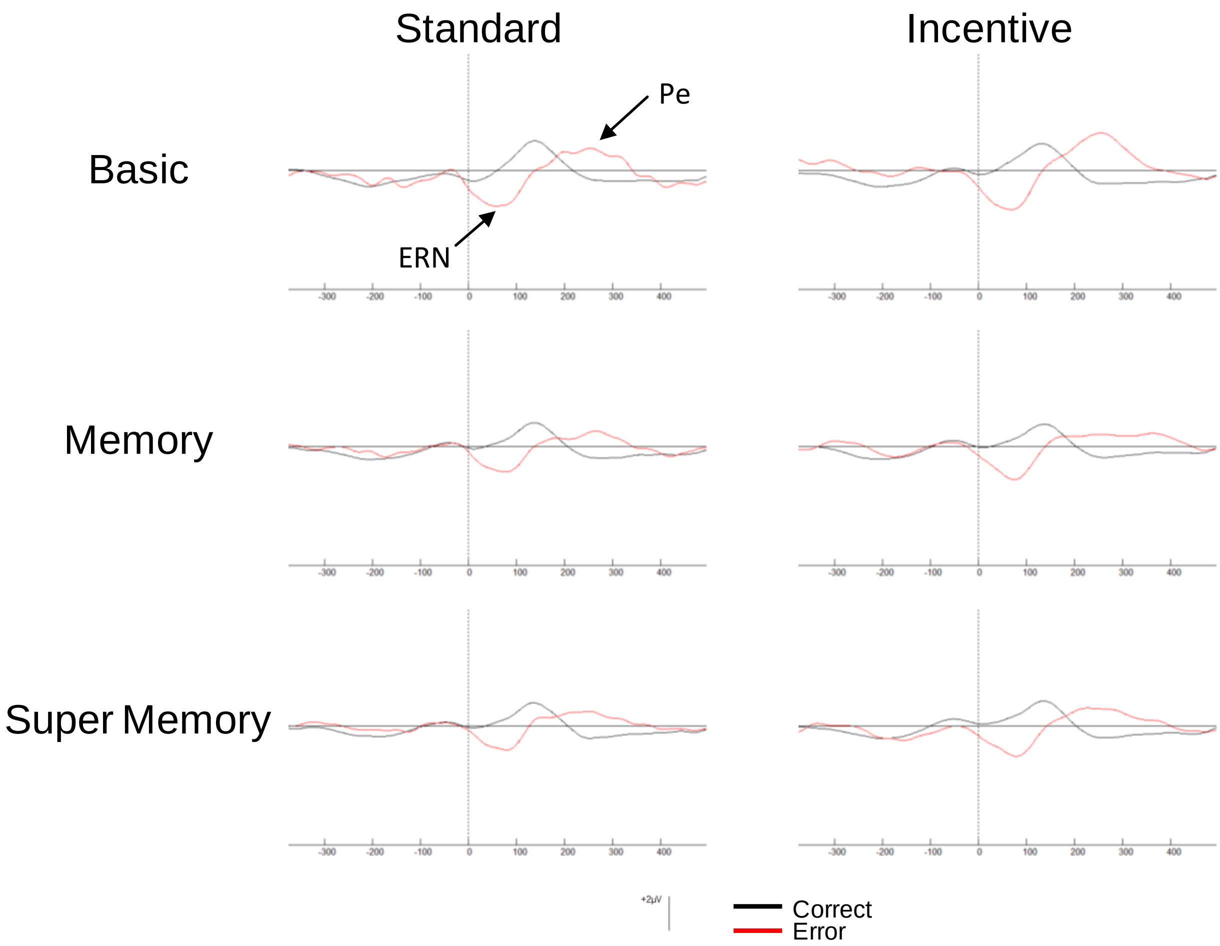

Figure 4-12. Response-locked event-related potentials (ERN, Pe) depicted at frontal-central site (FCz) associated with errors and correct trials for all Stroop tasks and phases for older adults.

3.9 ERPs and Task Accuracy

We created residual measures of the ERN and Pe by removing the shared variance in ERP amplitudes associated with correct responses from those associated with errors. These residuals represented the ERP response to errors adjusted for the ERP response on correct trials. It is these residuals that were then subsequently entered into correlational analyses with rejection accuracy. For our dependent measure, we decided to continue to examine rejection accuracy for specific items separately as relevant to each task (i.e., incongruents in the Basic task; incongruents and memory lures in the Memory task; incongruents and super memory lures in the Super Memory task).

For the younger group, very few relations emerged between ERN size and rejection accuracy. During standard phases, larger, i.e., more negative, ERNs were marginally associated with better incongruent rejection accuracy during the Basic task ($r = -.40$, $p = .052$), not at all during the Memory task ($p > .24$), but this relationship was evident again during the Super Memory task ($r = -.43$, $p = .04$). Once bootstrapped, however, ERN size was no longer significantly related to incongruent accuracy during any of these tasks (all *p*s for r_w 10% and r_w 20% > .10). No relations emerged between ERN size and contingency lure accuracy during any of the standard phases. Furthermore, ERN size did not demonstrate any relations with incongruent or contingency lure accuracy during the incentive phases of any of the tasks (all *p*s > .18).

In terms of Pe size, relations with accuracy in the younger group were even more modest. Pe size seemed unrelated to incongruent or contingency lure accuracy during any of the standard phases of the tasks (all *p*s > .31). During incentive phases, larger Pe’s were unrelated to incongruent accuracy during the Basic or Memory tasks (both *p*s > .24), but a borderline association emerged during the Super Memory task ($r = .40$, $p = .056$). This association weakened when Winsorized at 10% (r_w 10% = .41, $p = .064$) and was no longer present when Winsorized at 20% ($p > .13$). As for contingency lure accuracy during incentive phases, larger Pe size was marginally related to memory lure accuracy ($r = .38$, $p = .067$) with the relationship more evident with respect to super memory lure accuracy ($r = .42$, $p = .04$). However, once bootstrapped, Pe size no longer related to memory lure accuracy (ps for r_w 10% and r_w 20% > .16). A marginal association remained with super memory lure accuracy when Winsorized at 10% (r_w 10% = .35, $p = .082$) but was no longer present when Winsorized at 20% ($p > .18$). Thus there is some evidence for relations between scalp-based ERPs and performance accuracy under some task conditions, but the effects are small and would likely need a much larger sample size to be statistically reliable.

As for older adults, even fewer relations emerged between ERP size and accuracy. Larger, more negative ERNs were associated with better incongruent accuracy during the incentive phase of the Basic task ($r = -.50$, $p= .025$), an association that remained fairly consistent following bootstrapping (r_w 10% = -.52, $p = .008$; r_w 20% = -.53, $p = .06$). No other relations between ERN size and accuracy reached significance, irrespective of task or phase (all ps > .08). As for the Pe, larger Pe size was associated with better incongruent accuracy during the incentive phase of the Memory task ($r = .45$, $p = .052$), an association that weakened slightly after bootstrapping (r_w 10% = .49, $p = .054$; r_w 20% = .53, $p = .078$). Again, no other relations reached significance (all ps > .10), so the amount of variance accounted for is small and the correlations appear to be somewhat unstable.

3.9 ERPs and RSA

As for relations between pre-task RSA and error-related ERPs (residualized on the basis of correct trials), no associations emerged for either age group irrespective of task or phase (all *p*s > .11). This was also the case for RSA reactivity (all *p*s > .21).

3.10 ACC-GFA and Task Accuracy

Although the ERN and Pe are generated by the ACC, the nature of EEG itself and the ERPs that are derived from it represent a mixture of multiple cortical sources or domains. Because multiple sources contribute to ERP averages, the signals include a great deal of noise, and because of this, relationships between these measures and other variables may be more difficult to observe. By using ICA to isolate the activity of the ACC, and then projecting this activation back to the scalp and measuring the global field amplitude (GFA) associated with the region, we were able to isolate the ACC's unique contribution to the global scalp data. This, in turn, provided a purer index of ACC activation which we were then able to correlate with our other measures of interest, including rejection accuracy. As stated earlier, these analyses are based only on data from younger adults.

Tables 4-3 and 4-4 demonstrate how both ACC-GFA measures (ACC_{GFA1}, ACC_{GFA2}) correlated with rejection accuracy for specific items as relevant to each task and phase (i.e., incongruents, memory lures, super memory lures). In contrast to our ERPs, the relationships of both ACC_{GFA1} and ACC_{GFA2} with rejection accuracy were somewhat stronger. During the standard, non-incentive phases of the tasks, greater ACC_{GFA1} and ACC_{GFA2} related to the ability to accurately reject incongruent items in the context of the Basic task (r = .58, p = .006; r = .53; p = .013) (Figures 4-13a and b) and super memory lures in the context of the Super Memory task (r = .47, p = .034; r = .60, p = .004) (Figures 4-14a and b). No other associations emerged during any of the standard phases of the tasks (all other *p*s > .09).

During the incentive phases, greater ACC_{GFA1} and ACC_{GFA2} related to the ability to accurately reject memory lures in the context of the Memory task (r = .48, p = .027; r = .45, p = .04) (Figures 4-15a and b). No other associations emerged during the incentive phases of the tasks (all other ps > .08). Furthermore, once we subjected our data to bootstrapping, all relations between ACC_{GFA1} and accuracy remained significant, and two out of the three relations between ACC_{GFA2} and accuracy remained significant.

Table 4-3

Parametric and Winsorized Correlations for Younger Adults between ACC_{GFA1} and Rejection Accuracy on Incongruents and Contingency Lure Trials during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Stimulus Type	Phase	Pearson's r	r_w (10%)	r_w (20%)
Basic	Incongruent	Standard	r = .58** (p = .006)	r = .62** (p = .002)	r = .67** (p = .002)
		Incentive	r = .37 (p = .097)	r = .40 (p = .028)	r = .46 (p = .082)
Memory	Incongruent	Standard	r = .26 (p = .253)	r = .29 (p = .282)	r = .22 (p = .296)
		Incentive	r = .33 (p = .150)	r = .33 (p = .196)	r = .17 (p = .43)
	Memory lure	Standard	r = .35 (p = .121)	r = .35 (p = .084)	r = .39 (p = .130)
		Incentive	r = .48* (p = .027)	r = .52* (p = .012)	r = .48* (p = .016)
Super Memory	Incongruent	Standard	r = .35 (p = .120)	r = .30 (p = .196)	r = .27 (p = .290)
		Incentive	r = .30 (p = .183)	r = .21 (p = .41)	r = .09 (p = .674)
	Super memory lure	Standard	r = .47* (p = .034)	r = .53* (p = .026)	r = .54* (p = .026)
		Incentive	r = .36 (p = .109)	r = .36 (p = .110)	r = .31 (p = .180)

Table 4-4

Parametric and Winsorized Correlations for Younger Adults between ACC$_{GFA2}$ and Rejection Accuracy on Incongruents and Contingency Lure Trials during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Stimulus Type	Phase	Pearson's *r*	r_w (10%)	r_w (20%)
Basic	Incongruent	Standard	*r* = .53* (*p* = .013)	*r* = .56* (*p* = .036)	*r* = .50* (*p* = .032)
		Incentive	*r* = .21 (*p* = .372)	*r* = .30 (*p* = .214)	*r* = .35 (*p* = .198)
Memory	Incongruent	Standard	*r* = .03 (*p* = .905)	*r* = .12 (*p* = .630)	*r* = .13 (*p* = .562)
		Incentive	*r* = .38 (*p* = .086)	*r* = .41* (*p* = .034)	*r* = .56* (*p* = .046)
	Memory lure	Standard	*r* = .32 (*p* = .160)	*r* = .30 (*p* = .112)	*r* = .36 (*p* = .158)
		Incentive	*r* = .45* (*p* = .04)	*r* = .46 (*p* = .092)	*r* = .35 (*p* = .134)
Super Memory	Incongruent	Standard	*r* = .22 (*p* = .332)	*r* = .23 (*p* = .300)	*r* = .23 (*p* = .294)
		Incentive	*r* = .30 (*p* = .189)	*r* = .40 (*p* = .168)	*r* = .41 (*p* = .160)
	Super memory lure	Standard	*r* = .60** (*p* = .004)	*r* = .60** (*p* = .000)	*r* = .62** (*p* = .004)
		Incentive	*r* = .30 (*p* = .184)	*r* = .43 (*p* = .104)	*r* = .48 (*p* = .094)

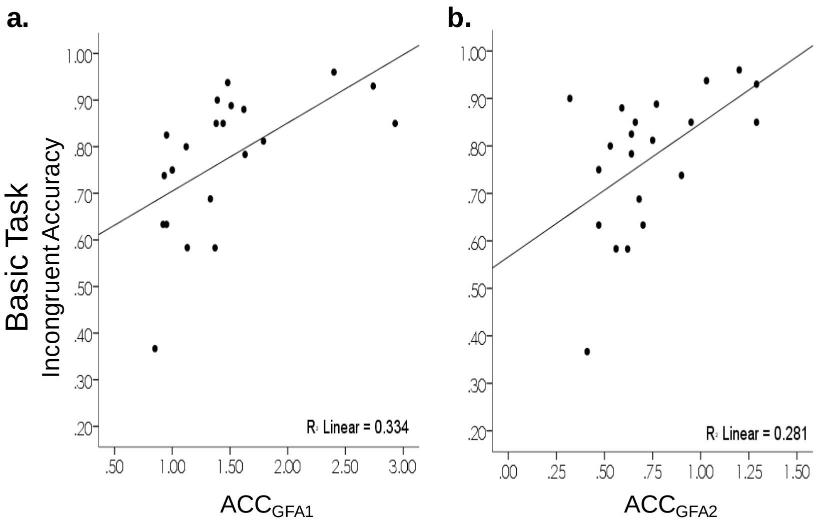

Figure 4-13. Relations between **(a)** ACC$_{GFA1}$ and **(b)** ACC$_{GFA2}$ and incongruent accuracy during the standard phase of the Basic task for younger adults.

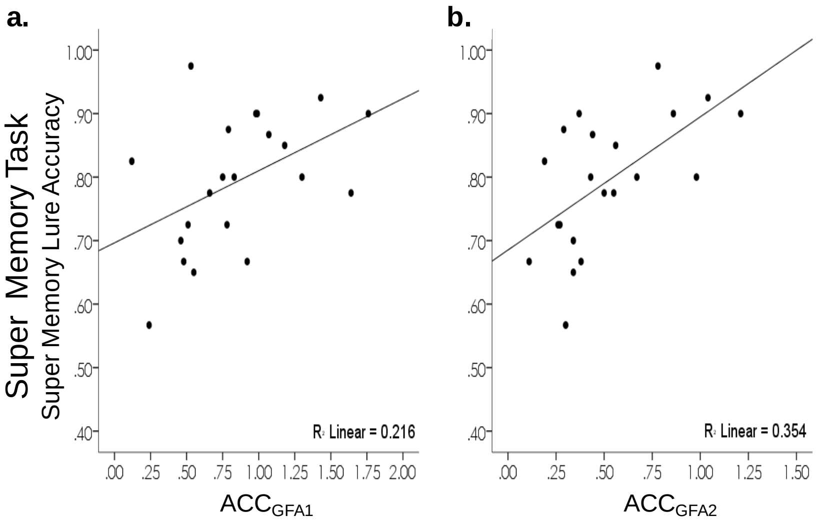

Figure 4-14. Relations between **(a)** ACC$_{GFA1}$ and **(b)** ACC$_{GFA2}$ and super memory lure accuracy during the standard phase of the Super Memory task for younger adults.

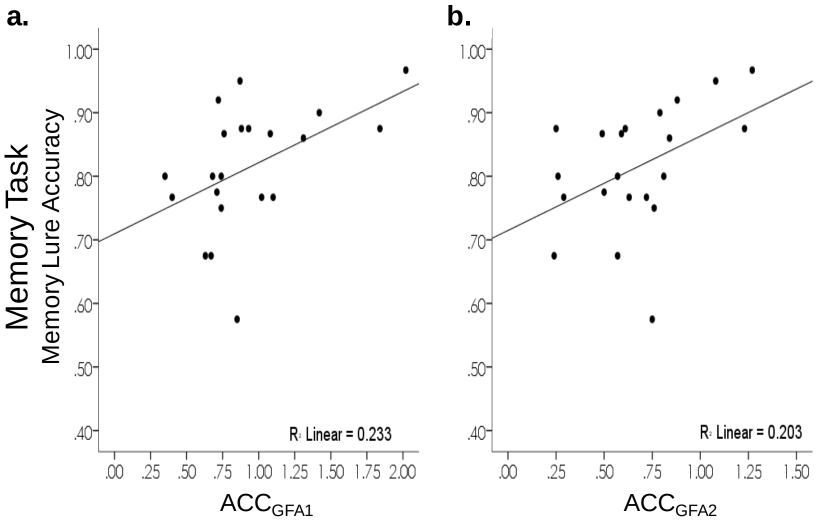

Figure 4-15. Relations between **(a)** ACC$_{GFA1}$ and **(b)** ACC$_{GFA2}$ and memory lure accuracy during the incentive phase of the Memory task for younger adults.

3.11 ACC-GFA and RSA

Next, we examined whether pre-task RSA related to either of our ACC-GFA measures. Although no associations between ACC$_{GFA1}$ and pre-task RSA reached significance (all *p*s > .08), relations between pre-task RSA and ACC$_{GFA2}$ did emerge. Specifically, individuals with higher pre-task RSA also demonstrated greater ACC$_{GFA2}$ during both the standard ($r = .57$, $p = .007$) and incentive phases ($r = .47$, $p = .03$) of the Super Memory task (all other *p*s > .079) (Figure 4-16a and b). Once we employed our more robust statistical procedures, however, pre-task RSA only related to ACC$_{GFA2}$ during the standard (r_W10% = .61, p = .036; r_W20% = .58, p = .042), not the incentive (r_W10%: p = .146; r_W10%: p = .330), phase of the Super Memory task.

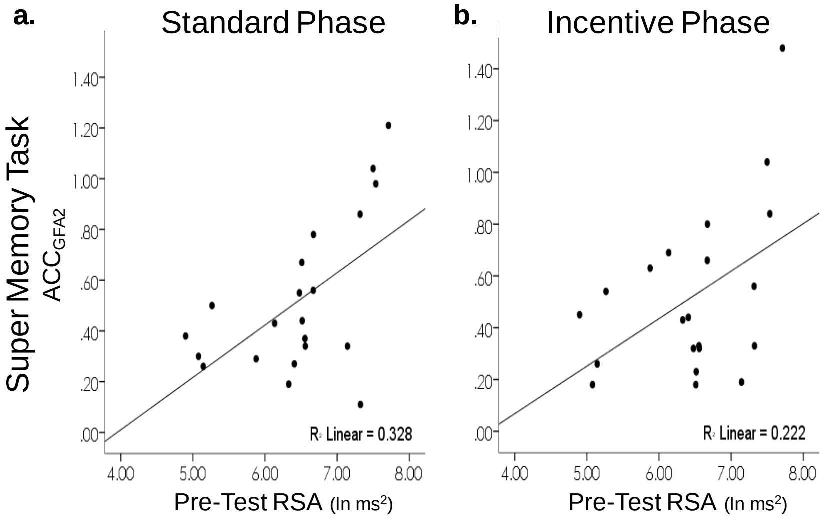

Figure 4-16. Relations between pre-task RSA and ACC$_{GFA2}$ during **(a)** standard and **(b)** incentive phases of the Super Memory task for younger adults.

We then looked at RSA reactivity and found that the only place it related to ACC-GFA was during the standard phase of the Memory task (all other *p*s > .08). Specifically, greater RSA reactivity related to greater ACC$_{GFA1}$ (r = -.50, p = .021) and ACC$_{GFA2}$ (r = -.52, p = .056). A similar pattern of relations with both ACC$_{GFA1}$ (r_W10%= -.51, p = .016; r_W20% = -.60, p = .014) and ACC$_{GFA2}$ (r_W10% = -.45, p = .02; r_W20% = -.48 p = .058) remained after bootstrapping.

3.12 VO$_2$max

All 23 younger adults and 20 of the 22 older adults completed the mCAFT. As expected, estimated VO$_2$max was greater for younger (*M* = 55.10 ± 1.60) compared to older adults (*M* = 35.55 ± 5.44), *t*(41) = 9.51, *p* < .001. Furthermore, VO$_2$max was higher for older men (*M* = 42.75 ± 3.28) compared to older woman (*M* = 33.75 ± 0.85), *t*(18) = -3.92, *p* = .001, and for younger men (*M* = 65.43 ± 4.29) compared to younger women (*M* = 52.23 ±

0.89), *t*(21) = -3.01, *p* = .036. This pattern is well in line with other research which has demonstrated higher VO_2max in men compared to women (Arciero, Goran, & Poehlman, 1993).

Sex differences in VO_2max are a product of body composition differences between men and women that influence basal metabolic rate (Arciero et al., 1993). Men consume more energy for the same basal activities due to their higher muscle mass, whereas women consume less because of their higher fat mass. Thus, the energy requirements used to estimate VO_2max for men and women will differ, even when performing identical physical activities such as the Step Test. For instance, the energy requirements for a man who reaches stage 6 of the Step Test will be 2.35 liters of oxygen per minute, whereas the energy requirements for a woman who reaches the same stage will be 1.79 liters of oxygen per minute. As a result of these energy requirement differences, the values produced when estimating VO_2max will usually be considerably higher for men compared to women, even for those who reach the same level of performance, and thus, VO_2max scores for men will often distort the overall distribution. Because of these sex differences, all correlations with VO_2max for both age groups were based on data from female participants only.[9]

3.13 VO_2max and Task Accuracy

Contrary to expectations, no relations emerged between VO_2max and rejection accuracy for older women, irrespective of task or phase (all *p*s > .20). However, several relations emerged within the group of younger women. Correlational analyses (see Table 4-5, column 4) showed that during standard, non-incentive phases, higher VO_2max was related to the ability to accurately reject incongruent items during the Basic (*r* = .51, *p* = .031) (Figure 4-17a), Memory (*r* = .72, *p* = .001) (Figure 4-18a), and Super Memory tasks (*r* = .56,

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[9] There were not enough male participants in either age group to analyze their relations with VO_2max separately.

p = .017) (Figure 4-19a). Higher VO_2max among younger women was also related to the ability to accurately reject contingency lures during both the Memory (*r* = .53, *p* = .025) (Figure 4-20a) and Super Memory tasks (*r* = .61, *p* = .008) (Figure 4-21a). A similar, but slightly less robust pattern emerged during the incentive phases of the tasks. Higher VO_2max among younger women was related to the ability to accurately reject incongruent items during both the Basic (*r* = .66, *p* = .003) (Figure 4-17b) and Super Memory tasks (*r* = .51, *p* = .032) (Figure 4-19b), and marginally related during the Memory task (*r* = .46, *p* = .055) (Figure 4-18b). Higher VO_2max was also related to the ability to accurately reject contingency stimuli in the context of the Super Memory task (*r* = .59, *p* = .01) (Figure 4-19b), and a marginal association emerged with accuracy for contingency stimuli in the context of the Memory task (*r* = .45, *p* = .062) (Figure 4-20b). In order to test the reliability of our effects, we again submitted these analyses to a bootstrapping procedure. These analyses indicated that the pattern of bootstrapped correlations was consistent with our original parametric correlations (see Table 4-5, columns 5 and 6). Thus, VO_2max proved to be a robust correlate of task accuracy in younger women across a range of tasks and phases.

Table 4-5
Parametric and Winsorized Correlations for Younger Women between VO2max and Rejection Accuracy on Incongruents and Contingency Lure Trials during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Stimulus Type	Phase	Pearson's *r*	r_w (10%)	r_w (20%)
Basic	Incongruent	Standard	*r* = .51* (*p* = .031)	*r* = .47 (*p* = .066)	*r* = .47 (*p* = .148)
		Incentive	*r* = .66** (*p* = .003)	*r* = .72** (*p* = .002)	*r* = .68* (*p* = .012)
Memory	Incongruent	Standard	*r* = .72** (*p* = .001)	*r* = .75** (*p* = .000)	*r* = .75** (*p* = .002)
		Incentive	*r* = .459 (*p* = .055)	*r* = .45 (*p* = .072)	*r* = .46 (*p* = .074)
	Memory lure	Standard	*r* = .53* (*p* = .025)	*r* = .58* (*p* = .046)	*r* = .65* (*p* = .030)
		Incentive	*r* = .45 (*p* = .062)	*r* = .44 (*p* = .064)	*r* = .41 (*p* = .110)
Super Memory	Incongruent	Standard	*r* = .56* (*p* = .017)	*r* = .54* (*p* = .012)	*r* = .49 (*p* = .070)
		Incentive	*r* = .51* (*p* = .032)	*r* = .54 (*p* = .056)	*r* = .44 (*p* = .072)
	Super memory lure	Standard	*r* = .61** (*p* = .008)	*r* = .63** (*p* = .002)	*r* = .67* (*p* = .012)
		Incentive	*r* = .59* (*p* = .010)	*r* = .57* (*p* = .026)	*r* = .51* (*p* = .050)

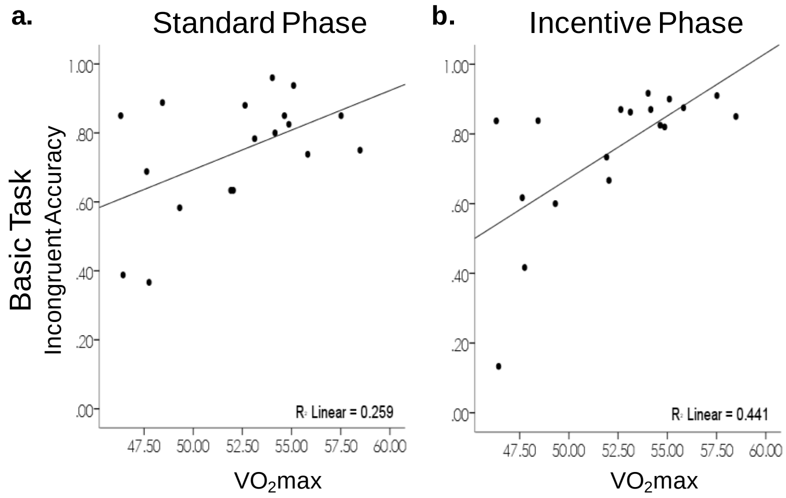

Figure 4-17. Relations between VO2max and incongruent accuracy during **(a)** standard and **(b)** incentive phases of the Basic task for younger adults.

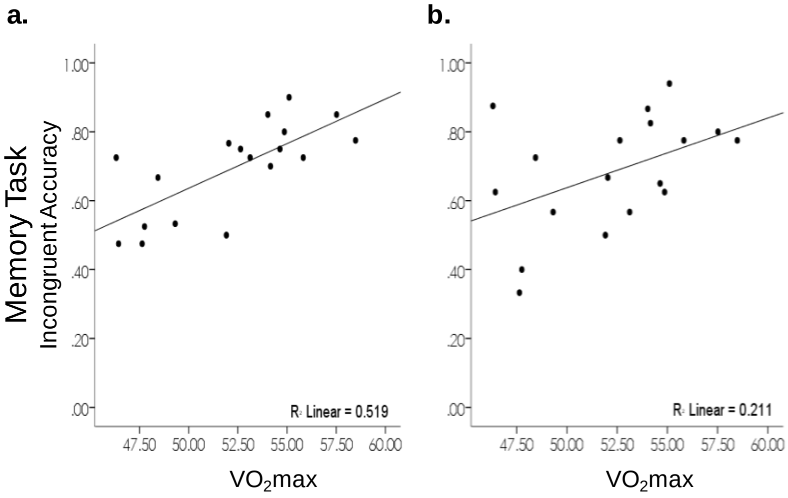

Figure 4-18. Relations between VO2max and incongruent accuracy during **(a)** standard and **(b)** incentive phases of the Memory task for younger adults.

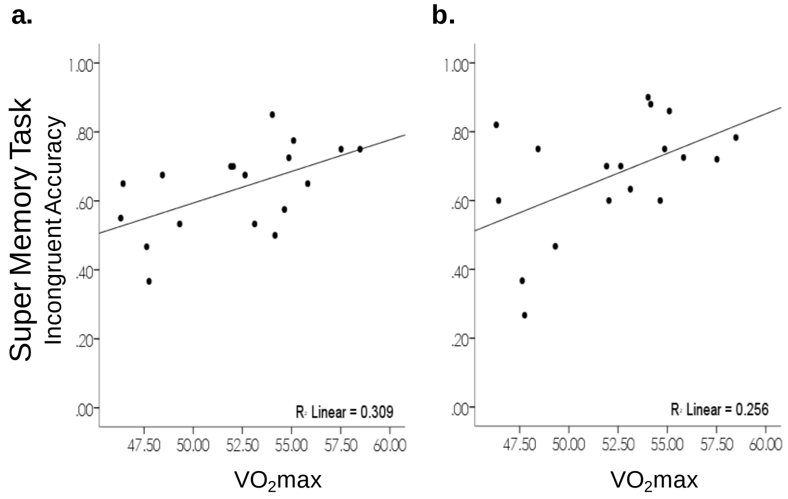

Figure 4-19. Relations between VO2max and incongruent accuracy during **(a)** standard and **(b)** incentive phases of the Super Memory task for younger adults.

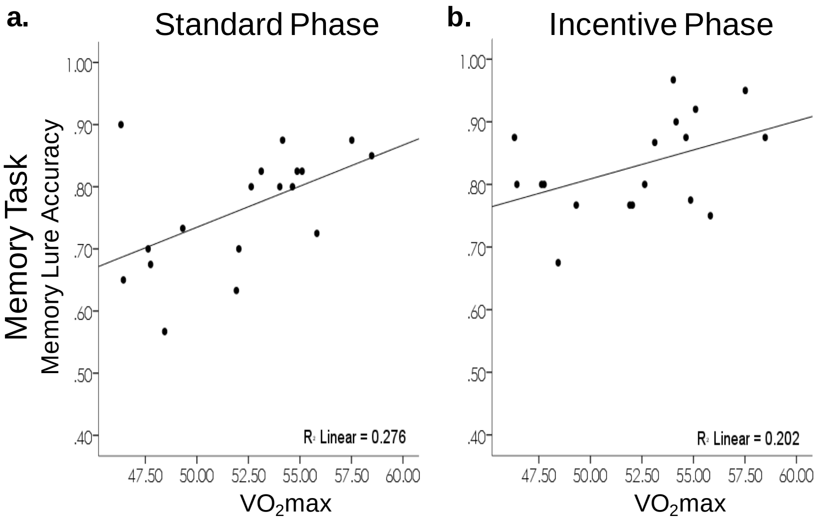

Figure 4-20. Relations between VO2max and memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Memory task for younger adults.

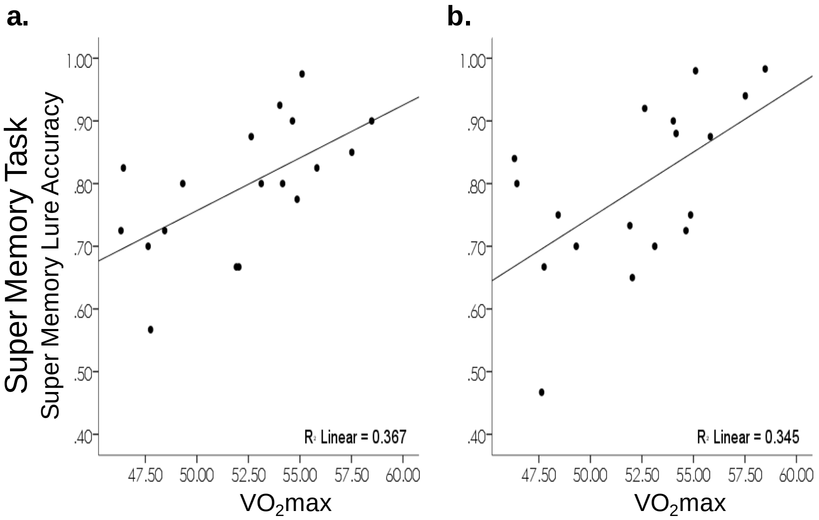

Figure 4-21. Relations between VO2max and super memory lure accuracy during **(a)** standard and **(b)** incentive phases of the Super Memory task for younger adults.

3.14 VO_2max and RSA

We examined whether VO_2max related to RSA in both the older and younger group of women. In neither case, however, did VO_2max relate to pre-task RSA (all *p*s > .16) or RSA reactivity (all *p*s > .09).

3.15 VO_2max and ACC_{GFA2}

We were also interested in whether VO_2max related to ACC activity. Because our measure of ACC-GFA demonstrated more robust relations with both accuracy and RSA than did our scalp ERPs, correlations with VO_2max were based on ACC-GFA. Furthermore, we examined ACC_{GFA2}, specifically, since it correlated best with both accuracy and RSA. Again, due to our inability to identify an ACC-IC for older adults and our sex differences in VO_2max, only younger women were included in the following analysis.

The only evidence of a relationship between VO_2max and ACC_{GFA2} emerged during the incentive phase of the Memory task. Specifically, younger women with higher VO_2max produced a greater ACC_{GFA2} response in this context ($r = .62$, $p = .008$, all other ps > .12), and this association remained after bootstrapping (r_w10% = .69, p = .014; r_w20% = .70 p = .018). In other words, the GFA response of the ACC during the incentive phase of the Memory task was greater among those young women who were more aerobically fit (see Table 4-6).

Table 4-6
Parametric and Winsorized Correlations for Younger Women between VO2max and ACC_{GFA2} during Basic, Memory, and Super Memory Tasks across Standard and Incentive Phases.

Task	Phase	Pearson's *r*	r_w (10%)	r_w (20%)
Basic	Standard	*r* = .32 (*p* = .208)	*r* = .39 (*p* = .194)	*r* = .39 (*p* = .300)
	Incentive	*r* = .28 (*p* = .271)	*r* = .32 (*p* = .194)	*r* = .35 (*p* = .200)
Memory	Standard	*r* = .10 (*p* = .695)	*r* = .11 (*p* = .562)	*r* = .17 (*p* = .582)
	Incentive	*r* = .62 (*p* = .008)*	*r* = .69 (*p* = .010)*	*r* = .70 (*p* = .016)*
Super Memory	Standard	*r* = .39 (*p* = .121)	*r* = .41 (*p* = .090)	*r* = .47 (*p* = .094)
	Incentive	*r* = .39 (*p* = .126)	*r* = .46 (*p* = .062)	*r* = .46 (*p* = .092)

3.16 Predicting accuracy from Pre-task RSA, ACC_{GFA2} and VO_2max

Pre-task RSA, ACC_{GFA2} and VO_2max were all related to accuracy measures so we were interested in determining the proportion of variance accounted for by each variable when they were included in the same analysis. First, because our original correlations between accuracy and RSA and accuracy and ACC_{GFA2} were based on all younger adult participants, we re-ran these correlations using our 18 younger women only, i.e., those whose VO_2max scores we could use, to ensure that the relations of interest held with this reduced sample. Analyses indicated that all three measures, RSA, ACC_{GFA2}, and VO_2max, related to super memory lure accuracy during the standard, non-incentive phase. We then conducted a three-stage hierarchical regression analysis with super memory lure accuracy as our dependent variable. RSA was entered on the first step, followed by ACC_{GFA2} on the second step, and VO_2max on the third step. The hierarchical regression revealed that RSA contributed significantly to the model, $F(1,15) = 5.74$, $p = .030$, and accounted for 27.7% of the variance in super memory lure accuracy. Introducing ACC_{GFA2} explained an additional 18.0% of the variation in Super Memory lure accuracy and this change in R^2 was significant, $F(1,14) = 4.63$, $p = .049$. Finally, the addition of VO_2max to the model explained an additional 20.7% of the variation in super memory lure accuracy, and this change in R^2 was also significant, $F(1,13) = 7.97$, $p = .014$. When all three predictors were examined for their unique contributions to the model, it was evident that there was considerable overlap with respect to the contributions of RSA and ACC_{GFA2} (both *p*s > .09). VO_2max, however, accounted uniquely for a significant 21% of the variance in Super Memory lure accuracy, $t = 2.83$, $p = .014$.

Because the association between pre-task RSA and super memory lure accuracy did not originally survive bootstrapping, we also performed the above hierarchical regression using only ACC_{GFA2} and VO_2max (variables which did survive bootstrapping) as predictors. $ACC_{GFA2}$was entered on the first step, followed by VO_2max on the second step. This hierarchical regression revealed that ACC_{GFA2} contributed significantly to the model, $F(1,15) = 11.47$, $p = .004$, and accounted for 43.3% of the variance in super memory lure accuracy. Introducing VO_2max explained an additional 21.9% of the variation in super memory lure accuracy, and this change in R^2 was significant, $F(1,14) = 8.80$, $p = .01$. It was also clear that, when examining their unique contribution to the model, each remained significant (both *p*s < .02), with ACC_{GFA2} and VO_2max accounting uniquely for 18% and 22% of the variance in super memory lure accuracy respectively, clearly accounting for somewhat separate but important sources of variance.

Discussion

A major goal for this study was to examine the degree to which cardiac autonomic regulation related to behavioural and electrocortical indices of cognitive control, and to determine whether these relations changed as a function of age. Cognitive control is thought to be more metabolically costly when it involves “proactive” rather than “reactive” response strategies (Braver et al., 2008, 2009; Braver, 2012). We assumed, therefore, that increasing the need for proactive control would lead to an increased reliance on flexible cardiac autonomic regulation. This hypothesis was based on a model of neurovisceral integration (Thayer & Lane, 2000, 2009) that posits an interconnection between the ability to regulate arousal, emotion, and attentional resources in the service of adaptive behaviour, that this regulatory system involves a central autonomic network (CAN) that coordinates autonomic, endocrine, and behavioural responses, and that RSA provides an important index of the efficiency of this regulatory system (e.g., Benarroch, 1993; Devinsky, Morrell, & Vogt, 1995; Porges, 1995; Thayer & Lane, 2000, 2009). In order to determine how well this model accounted for variance in the control of cognitive resources, we examined RSA in older and younger adults as they completed a modified Stroop task in which we strategically increased the need for proactive control by manipulating both the number of contingencies required for appropriate response selection and the level of motivation elicited by the task context itself.

Analyses of performance data indicated that, as expected, older adults responded more slowly to both regular incongruent colour-words and contingency lures (i.e., “memory” and “super memory” lures) compared to their younger counterparts. However, older adults demonstrated accuracy rates similar to those of younger adults in rejecting regular incongruent lures across all three Stroop tasks as well as for the more cognitively challenging memory and super memory lures. Although the lack of age-differences might seem surprising, our findings, in fact, align well with previous work demonstrating similar, sometimes even superior, accuracy rates among older adults in performance-monitoring paradigms (Falkenstein, Hoormann, & Hohnsbein, 2001; Nieuwenhuis et al., 2002). More recently, Czernochowski et al. (2010) found that interference errors occurred more frequently for younger compared to older adults on a cued task-switching paradigm that involved three levels of response conflict. Similarly, Schreiber, Pietschmann, Kathmann, and Endrass (2011) found that older adults made fewer errors than younger adults on a modified flanker task. In Study 1 (Chapter 2), we also found that older adults made fewer errors than younger adults across all three levels of an inhibitory control task that required the maintenance of increasingly larger working memory loads.

In all of the above studies, and our current work, older adults responded more slowly than younger adults. Therefore, it is possible that the response accuracy of our older adults was maintained by their having adopted a more cautious approach to the task wherein they emphasized accuracy over speed, a long-standing observation in aging research (see Rabbitt, 1979). If that were so, we would expect that longer RTs within each age-group would also correlate with greater accuracy, but additional post-hoc analyses provided no evidence for such associations (all *p*s > .11).

Despite the lack of group differences, our two experimental manipulations produced their intended effects. Specifically, increasing response contingency rules from the Basic to the Memory to the Super Memory tasks led to increased interference and subsequent decrements in performance. These were evident for both groups in longer RTs and increased error rates. Conversely, the addition of the monetary incentive to each of the three Stroop contexts resulted in increased task engagement and concurrent improvements in performance with shorter RTs and fewer errors.

Our main question, of course, was whether higher levels of pre-task RSA related to better proactive cognitive control performance. Proactive cognitive control can be implemented when a valid cue can be used to guide upcoming response decisions (Braver et al., 2008; Czernochowski et al., 2010). Both the Memory and Super Memory tasks included such cues in the form of the specific lure (memory lure, super memory lure) that participants could hold in mind and reject whenever they encountered it in the stimulus stream. By maintaining a specific lure in working memory over the course of several trials, we assumed that participants would be able to utilize a proactive form of control that would allow them to respond more effectively (i.e., more accurately) and efficiently (i.e., faster) when encountering these items, and that is indeed what happened. Our results indicated that both older and younger adults responded faster and more accurately to contingency lures than they did to incongruent lures. Moreover, our results indicated that higher pre-task RSA among older adults related most strongly and consistently to accuracy for memory and super memory lures. Thus, our results indicate that greater cardiac autonomic regulation may be particularly beneficial when subsequent performance is dependent upon a more proactive style of cognitive control. Moreover, since proactive control generally declines with age (Braver & West, 2008; Braver et al., 2001, 2008, 2009), the presence of greater cardiac autonomic regulation may be especially beneficial to older adults in maintaining a high level of performance.

Electrophysiological Effects

The ERN and Pe are scalp-based electrocortical components that have been shown to be generated by the ACC (S. F. Taylor et al., 2007), a region associated with both the control of attention and the modulation of parasympathetic influence on physiological systems (Critchley, 2005). They arise under a number of circumstances but are typically larger in response to an error or, more generally, an increased need for attentional control (van Noordt, Desjardins, & Segalowitz, under review). As we found in Study 1 (Chapter2), these ERP components were less able to account for variance in performance than was our index of pre-task autonomic regulation, in this case as indexed by RSA, and in Study 1, by RPP (our index of cardiac workload), with higher RSA or lower RPP at pre-task relating to better performance.

In addition to our scalp-based ERPs, we also examined the global field amplitude (GFA) associated with the error response of the ACC-IC. We identified two error-related GFA peaks for the ACC-IC. The first, ACC_{GFA1}, appeared to correspond to the ERN effect, and the second, ACC_{GFA2}, appeared to correspond to the Pe effect. Analyses with ACC-GFA measures were restricted to younger adults since a reliable ACC-IC could not be identified for the majority of our older participants.

In general, we found that our ACC-GFA measures (ACC_{GFA1} and ACC_{GFA2}) related more consistently to behavioural performance than did our error-related ERPs, a notable finding given that scalp-based ERPs have formed the basis of electrophysiological research for the past several decades. Moreover, relations always occurred in the expected direction, with greater ACC responsivity relating to increased accuracy, particularly during the more challenging Stroop contexts. Specifically, we found that greater error-related ACC-GFA was associated with increased contingency lure accuracy during the incentive phase of the Memory task and the standard phase of the Super Memory task. Our findings support other work which has demonstrated the importance of the ACC in supporting performance during cognitively demanding situations (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004). Furthermore, because greater ACC-GFA related to accuracy for contingency lures, specifically, our results support the claim that successful proactive control is dependent upon the availability of cognitive resources associated with the ACC.

We also found that greater ACC_{GFA2} was associated with higher pre-task RSA, an effect that was evident during the more demanding Super Memory task (standard phase). Thus, the benefits of higher pre-task RSA may be reflected both in behavioural performance and cortical responsivity as well. Specifically, the presence of greater cardiac autonomic regulation at rest might also relate to the ability to increase activation within regions like the ACC that support cognitive control when the demands of a task increase.

Although the majority of relations with ACC_{GFA1} and ACC_{GFA2} emerged during more cognitively demanding contexts, a positive association also emerged between ACC-GFA and incongruent accuracy during the standard phase of the Basic task. This pattern is less consistent with our model. However, one possibility is that increased ACC activation during the standard phase of the Basic task reflected an adaptive response wherein the brain attempted to increase the number of resources devoted to performance during the very early stages, when the task was least familiar (Banich, 2009; Chaddock et al., 2012). This association may have diminished as the task became more familiar, but then resurfaced later, when demands again increased (i.e., in the Memory Stroop).

Although the above pattern of relations is not entirely clear, our results do provide additional support for the importance of utilizing ICA to separate mixed EEG signals present at the scalp. Recall that when we examined how both cardiac autonomic regulation and accuracy related to our ERP measures, very few associations emerged. However, as we have shown here, by isolating the contribution of the ACC to global scalp data via the application of ICA, more associations emerged with both accuracy and cardiac autonomic regulation.

The Fitness Dimension

Another focus of our study was to examine the role of aerobic fitness with respect to our various measures. Of interest to our work is that individuals who are more aerobically fit also demonstrate higher levels of RSA (e.g., Billman, 2002; Goldsmith et al., 1997, 1992; Hautala et al., 2004, 2009). Thus, fitness may be another important factor to consider when examining relations between cardiac autonomic regulation and cognitive control performance. We asked about physical fitness in previous studies using self-report questionnaires, but data from these reports did not prove to be predictive of performance. Thus, for the present study we decided to collect a direct measure of aerobic fitness by having participants complete the mCAFT. The mCAFT provides an estimate of VO_2max and, as a sub-maximal test, is ideal for research involving both older and younger adults. By having participants complete the mCAFT during their first lab visit, we were able to examine whether VO_2max related to cardiac autonomic regulation, as well as behavioural and/or electrocortical indices of cognitive control, collected during their second visit.

We had expected, based on the literature (Billman, 2002; Goldsmith et al., 1997, 1992), that there would be a relationship between resting RSA and aerobic fitness (i.e., VO_2max), but this was not evident in either of the age groups. What we had not expected was that fitness would prove to be a more powerful predictor of performance accuracy than either our electrocortical or cardiac measures. These analyses were restricted to the young women in our sample, but in that group it was clear that those with higher estimates of VO_2max demonstrated better accuracy for both regular incongruent lures and contingency lures (i.e., memory and super memory lures), and this pattern emerged in almost all task-phase contexts. Thus, our results provide additional support for the growing consensus that increased aerobic fitness may provide benefits to cognitive performance, especially when task contexts require more extensive amounts of cognitive control (Chaddock et al., 2012; Chang et al., 2013; Colcombe & Kramer, 2003; Pontifex et al., 2011). Moreover, if it is the case that incongruent lures relied upon a more *reactive* form of control and contingency lures relied upon a more *proactive* form of control, our findings indicate that increased levels of aerobic fitness benefitted both forms of cognitive control in young women.

Because pre-task RSA and VO_2max were unrelated in the present samples, we did not find evidence indicating that either mediated the other's relationship with accuracy. However, we entered both ACC_{GFA2} and VO_2max into a hierarchical regression analysis to see how each contributed to super memory lure accuracy when considered together. We found that when both predictors were entered into the model, they each contributed significant variance to the accuracy score, and that each also accounted for somewhat separate (unique) sources of variance. Interestingly, when RSA was included in the model, it appeared as though RSA and ACC_{GFA2} accounted for similar variance, and only VO2max accounted for unique variance. The fact that RSA and ACC_{GFA2} shared a sizeable amount of variance is interesting in light of the results of the Granger Causality analysis included in Appendix A. Both sets of results provide evidence of a relationship between RSA and ACC function when ACC function is analyzed as an independent component, but not so much when ACC function is based only on scalp ERP amplitudes.

Surprisingly, no relations emerged between fitness and accuracy among older women. Part of this may have been due to a reduced VO_2max range within our older group. Because of the inherent risks associated with testing physical fitness in older adults, we were very conservative in terms of who we allowed to undergo testing with the mCAFT, i.e., we did not allow anyone to participate whose resting blood pressure was higher than 140/90. Thus, those older adults who would likely have been in the lower end of the distribution of VO_2max scores were not represented in our sample. Our range may also have been further restricted because we were very conservative in terms of the number of levels we allowed our older adults to complete. For instance, if we found that an older adult was close to, but had not technically reached, his or her ceiling at the end of a particular level, we erred on the side of caution and chose not to have the individual complete the next level of the test. The individual may well have been able to do so, and thus, may have achieved a higher VO_2max score, one that more accurately represented his or her fitness level. We chose instead to exercise a more cautious approach in order to ensure the safety of our older participants, which, in turn, would have further reduced our range of VO_2max in the older group, and, with that, our ability to identify relations between fitness and accuracy.

Conclusion

The central focus of our study was to determine the degree to which cardiac autonomic regulatory control affected the performance of older and younger adults in the context of a Stroop paradigm in which we strategically increased the need for proactive cognitive control. We demonstrated support for the role of cardiac autonomic regulation on proactive control performance, particularly among older adults, where pre-task RSA demonstrated relations with contingency items (i.e., pre-task RSA related to accuracy for memory and super memory lures during standard and incentive phases). The performance in a subsample of young women was strongly and consistently associated with aerobic fitness and, interestingly, this was the case for trials involving the use of proactive (i.e., contingency lures) as well as reactive (i.e., incongruent lures) control. Thus, the current study suggests that both cardiac autonomic regulation and aerobic fitness are beneficial to cognitive performance, but the nature of their effects may differ. Specifically, cardiac autonomic regulation may have selective effects that are beneficial for the use of proactive control, whereas aerobic fitness may have more general effects that are beneficial irrespective of the type of cognitive control involved.

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Chapter 5. General Discussion

Evidence suggests that many cognitive functions decline in response to the normal aging process. Specifically, older adults demonstrate declines in cognitive control, or the ability to flexibly modulate thoughts and actions in accordance with internally maintained goals (Park & Reuter-Lorenz, 2009). Of interest to those who study cognitive aging is the fact that these declines vary from person to person (Lupien et al., 2005). Therefore, a major goal of cognitive aging research is to gain an understanding of the mechanisms that underlie the presence of such variability. One potential factor may be individual differences in autonomic regulatory control. Increasingly, research indicates that autonomic regulation may be highly relevant to performance on certain cognitive tasks. The vast majority of research documenting this link has come from work with infants (Linnemeyer & Porges, 1986; Richards, 1985), children (Marcovitch et al., 2010; Staton et al., 2008; Suess, Porges, & Plude, 1994), and more recently, younger adults (Hansen et al., 2004, 2003, 2009). Very few, however, have explored this relationship in older adults, a population known to demonstrate declines in both cognitive and autonomic regulatory control.

The anterior cingulate cortex (ACC) plays a major role in autonomic, affective, and cognitive integration (Critchley, 2005; Devinsky et al., 1995). Through its connections with the vagus nerve to the sinoatrial node of the heart, the ACC exerts modulatory control over cardiovascular arousal (e.g., Ter Horst & Postema, 1997). There is also growing evidence that autonomic states of arousal play an important role in cognitive performance, especially when that performance requires higher levels of cognitive control (Critchley et al., 2003; Matthews et al., 2004). Thus, according to this model of ACC function, it is not only responsible for implementing effective cognitive control, but also for generating autonomic states of arousal that are adaptive for maximal performance. Importantly, the normal aging process is known to lead to declines in both ACC structure and function (e.g., Raz & Rodrigue, 2006; Volkow et al., 2000) and also in cardiac autonomic regulation (e.g., De Meersman & Stein, 2007). A remaining issue, therefore, is whether cognitive performance in older adults may differ as a function of the level of cardiac autonomic regulation that one has managed to maintain during the aging process.

For this reason, we were interested in exploring the degree to which behavioural and/or electrocortical responses would relate to the regulation of cardiac autonomic arousal in tasks that required ACC support. More specifically, we were interested in determining whether trait-like resting measures of cardiac autonomic control, measured via pre-task respiratory sinus arrhythmia (RSA), would reliably predict behavioural performance and/or electrocortical responsivity. We explored these relations in the context of tasks, each of which required increasing levels of cognitive control. The Working Memory Inhibitory Control (WMIC) task (modifed from Hester, Murphy, & Garavan, 2004) increased the need for such control by manipulating working memory load requirements, whereas the two Stroop paradigms (modifed from Hester, Foxe, Molholm, Shpaner, & Garavan, 2005) did so by increasing the complexity of response contingency rules.

We had expected that the ability to modulate cardiovascular activity, as indexed by RSA, would relate to behavioural and electrocortical indices of cognitive control in both the WMIC and Stroop tasks. Event-related potential (ERP) components included the ERN and Pe, ACC-generated components that emerge following the execution of erroneous responses (Dehaene et al., 1994; Falkenstein et al., 1990; Gehring et al., 1993; Miltner et al., 2003), and reflect performance monitoring associated with this brain region (Falkenstein et al., 2000; S.

F. Taylor et al., 2007). Whereas many researchers have examined these components in a variety of cognitive tasks, it is relatively rare that they are examined as they relate to cardiac autonomic control in the same study. We expected any associations between cardiac autonomic control and our behavioural performance and electrocortical measures to strengthen as the need for cognitive control increased within each task, such that the strongest relations would emerge in the most cognitively demanding conditions when the need for effortful attention and response control would be greatest. Documenting such associations would add to the growing consensus that cognitive control must be considered within a broader framework that acknowledges the contributions of both cortical and autonomic influences.

Behavioural Performance in Older and Younger Adults

Age-related differences in behavioural performance were examined in the context of the WMIC and Stroop tasks. In both cases, we expected older adults to demonstrate reduced accuracy compared to their younger counterparts, especially on the most challenging levels of each task, where the need for cognitive control was greatest. Contrary to expectations, older adults performed as well as younger adults on all three Stroop tasks (Study 3, Chapter 4), regardless of the complexity of contingency rules required for response selection, and older adults actually made fewer errors compared to younger adults on all three levels of the WMIC task (Study 1, Chapter 2). Although the lack of age-differences might seem surprising, our findings, in fact, align well with previous work demonstrating similar, sometimes even superior, accuracy rates among older adults in performance-monitoring paradigms (e.g., Falkenstein, Hoormann, & Hohnsbein, 2001; Nieuwenhuis et al., 2002). More recently, Czernochowski et al. (2010) found that interference errors occurred more frequently for younger compared to older adults on a cued task-switching paradigm that involved three levels of response conflict. Similarly, Schreiber, Pietschmann, Kathmann, and Endrass (2011) found that older adults made fewer errors than younger adults on a modified flanker task.

There are, of course, a number of reasons why we may be seeing fairly high levels of performance among older adults. These range from cohort effects (i.e., a more educated and active older population) to the self-selection of those who have more reserve capacity volunteering for aging research studies (Rabbitt, Lowe, & Shilling, 2001). There is also a growing appreciation of the importance of careful screening. We screen, for example, for any signs of dementia and exclude participants on the basis of head injury, a history of end organ disease such as stroke or heart attack, psychiatric or neurological disorders, or any medication that could affect neurocognitive function.

Another factor to consider is that neural aging can be quite selective with respect to the rate of change in specific cortical regions and neurotransmitter systems (Raz & Rodrigue, 2006) and that these changes can affect cognition in a number of highly specific ways (e.g., de Fockert, Ramchurn, Van Velzen, Bergstrom, & Bunce, 2009; Gazzaley et al., 2008; Velanova, Lustig, Jacoby, & Buckner, 2007). These neurocognitive changes can, in turn, interact with the task and testing context (e.g., Feyereisen & Charlot, 2008; Rush, Barch, & Braver, 2006; Shilling, Chetwynd, & Rabbitt, 2002). As an example of this interaction, Hasher and colleagues have shown that whether the processing of distracter information is an impediment or not depends on whether the information disrupts or supports subsequent task demands (Healey, Campbell, & Hasher, 2008). Thus, despite the general assumption that aging is associated with a ubiquitous decline in cognitive functioning, it is apparent that, in some contexts, older adults are able to perform as well as younger adults even on tasks usually considered to depend on “fluid” as opposed to “crystallized” intelligence, with fluid intelligence involving active, on-line problem solving, the kind most susceptible to age-related decline (e.g., Park & Reuter-Lorenz, 2009).

Relations between Autonomic Regulatory Control and Performance

Despite similar performance levels among younger and older adults, we found support for our expectations regarding relations between our measures of autonomic arousal, i.e., RSA and rate pressure product (RPP), and cognitive performance. Although pre-task RSA did not relate to the accuracy of older or younger adults on the WMIC task, pre-task RPP, an index of cardiac workload (Kitamura, Jorgensen, Gobel, Taylor, & Wang, 1972), did relate to performance and error-related electrocortical measures in this context. For older adults, higher pre-task RPP was associated with increased NoGo errors on the WMIC task. In other words, the presence of greater cardiac workload at rest, prior to the start of the WMIC task, was associated with poorer inhibitory control performance among older adults. For younger adults, RPP did not relate to accuracy, but higher pre-task RPP was associated with longer response times and smaller ERNs, especially when working memory loads were highest.

Cardiac workload provides an indication of the amount of oxygen the heart is consuming in order to meet the metabolic demands of a specific mental or physical challenge (Fredericks, Choi, Hart, Butt, & Mital, 2005; Gobel, Norstrom, Nelson, Jorgensen, & Wang, 1978; Nelson, Gobel, Jorgensen, Wang, & Taylor, 1974). Therefore, the findings of Study 1 (Chapter 2) indicate that the amount of energy the heart was consuming at rest, prior to the start of the WMIC task, had important implications for older adults in terms of their behavioural performance and younger adults in terms of their response speed and error-related electrophysiological responses.

Study 2 (Chapter 3) provided our first evidence of a relationship between pre-task RSA and performance accuracy. Specifically, we found that pre-task RSA predicted accuracy when response contingency rules required the maintenance of a specific item in WM (i.e., Memory task) but not when participants relied on a general rule that was activated only after a high interference event had occurred (i.e., Repeat task). According to Braver, Gray, and Burgess (2008), proactive control involves the sustained, active maintenance of goal representations over time, and therefore, is a more resource demanding and metabolically costly form of control to utilize. Interestingly, our results indicate that this was when higher levels of RSA appeared to be most relevant to performance. Thus, our findings from Study 2 align with Thayer and Lane’s (2000, 2009) proposal that cardiac autonomic control may act as a resource that an individual can draw upon to support adaptive behavioural performance, but our results suggest that this resource may be most relevant when the task specifically requires the use of proactive control.

Based on the results of Study 2 (Chapter 3), we had expected that pre-task RSA would relate to the performance of younger adults in Study 3 (Chapter 4) where we strategically increased the need for proactive control across three Stroop tasks (i.e., Basic, Memory, and Super Memory). Although we initially found support for this assumption, it did not survive bootstrapping. It is possible that task order differences between Study 2 (Chapter 3) and Study 3 (Chapter 4) may account for this discrepancy. In Study 2 (Chapter 3), we counterbalanced the order of the Basic, Memory, and Repeat Stroop tasks, whereas in Study 3 (Chapter 4), we had participants complete the tasks in an identical order, starting with the simplest version (Basic task) and progressing to the most complex version (Super Memory task).

Although relations between pre-task RSA and accuracy did not survive bootstrapping in the younger group, they did in the older group. Higher pre-task RSA was associated with better performance on the Stroop paradigm, particularly during contingency trials (memory lures and super memory lures) where the need for proactive control was greatest. Thus, our results indicate that those older adults who have maintained greater cardiac autonomic control may have been in a better position to meet the increased metabolic demands associated with the use of a proactive control response strategy.

Relations between RSA versus Cardiac Workload and Performance

The relationship between pre-task RSA and cognitive performance, although not always reaching levels of statistical significance, was typically in the expected direction in that higher levels of RSA, indicating greater phasic vagal cardiac control, were associated with better performance on tasks. These associations were typically more robust when the task provided greater opportunity for employing a proactive response strategy. We are not arguing that higher levels of phasic vagal cardiac control would be ineffective in other tasks (even those depending on a more reactive response strategy), but those relations were not statistically significant in our samples. It may be that factors that we did not measure also contribute to success when reactive response strategies are used, or that the relationship between RSA and the use of reactive control strategies is present but weaker and would need a much larger sample size to be observed. However, when examining pre-task RPP (our index of the individual’s cardiac workload recorded prior to the onset of the task), the relations with task performance were, on occasion, opposite of what one would have expected. That is, higher levels of pre-task RPP would suggest higher levels of arousal, and these higher levels of arousal were expected to interfere with performance when attentional demand was high.

To understand this better, we reviewed the range of RPP and performance outcomes across our three separate experiments and our two separate age groups (details of these analyses are available in Appendix C). What we concluded is that, in the case of RPP, a moderate level of arousal is maximally effective. Thus, for any group where the range of RPP scores is relatively low, those at the high end of the range do better, i.e., they are at the moderate level of arousal appropriate for the task. However, when the range covers moderate to high levels of RPP, then the correlation with performance will be negative, i.e., those at the lower end of the range are at the appropriate level of arousal to do well, whereas those at the high end of the range (like the older adults in Study 1, Chapter 2), will be at risk for poorer performance. Thus, the relationship between RPP and performance on cognitive tasks likely represents the very well-established Yerkes-Dodson Law (Yerkes & Dodson, 1908) indicating a curvilinear relationship between arousal and performance.

With respect to RSA, although there was no evidence for a curvilinear relationship with performance across these three experiments, there have been suggestions of such relationships in the child literature. Marcovitch et al. (2010) examined baseline RSA and RSA reactivity in a large sample of 3½ year old children who were asked to perform children’s versions of executive tasks that required the control of attention. They found that those with higher baseline levels of RSA did better overall, but with respect to RSA reactivity, the children who showed a moderate drop in RSA relative to their pre-task levels were the ones who were most successful, again suggesting that some reduction in vagal control was beneficial but a complete reduction was not.

Predicting Performance based on ERPs and Cardiac Autonomic Control

One of the most interesting findings from the current thesis was that our measures of autonomic arousal (i.e., RSA and RPP) demonstrated more robust and consistent relations with behavioural performance than did our ERP components (i.e., ERN and Pe) which reflected an actual error-related brain response. This is important because the vast majority of cognitive aging research has focused predominantly on the relationship between behaviour and various measures of cortical activation (ERPs, neuroimaging). Although these studies have undoubtedly advanced our understanding of cognitive aging, models of cognitive aging might be further enriched by taking into account the role of autonomic regulatory control, a physiological component that we have shown in this thesis to also be relevant to performance on higher level cognitive control tasks. Thus, our results provide support for a model of neurovisceral integration (Thayer & Lane, 2000, 2009) that acknowledges the importance of examining cognition from a broader perspective that better integrates central and autonomic regulatory control and acknowledges how changes in these functions may affect cognition in older adults, specifically.

A logical issue that may arise at this point concerns the directional associations among the variables examined in the present thesis. Given that the normal aging process is associated with declines in cognitive control, one may wonder whether this results from age-related changes to the structural and functional integrity of the medial prefrontal cortex (mPFC) or declines in cardiac autonomic regulatory control (i.e., RSA). To address this issue, we must return to the central autonomic network.

As described in the introduction of this thesis, the neurovisceral integration model is based on our understanding of the central autonomic network (Benarroch, 1993, 1997; Critchley, Corfield, Chandler, Mathias, & Dolan, 2000; Critchley, 2005; Matthews et al., 2004; Ter Horst & Postema, 1997), and this is relevant to the current issue of directional predictions for a few reasons. Firstly, the central autonomic network is comprised of many components. For instance, it includes neocortical, midbrain, and brainstem structures as well as peripheral organs such as the heart. Secondly, it is a dynamic, self-regulatory system that is constantly changing and adapting moment-to-moment based on the context in which it is operating. Finally, it includes multiple reciprocal connections that feed both forward and backward throughout the entirety of the system. Thus, the central autonomic network is a complex, intricate, dynamic system.

According to Julian Thayer, a major proponent of neurovisceral integration, RSA, the variability in the beat-to-beat interval of heart rate, is an indicator of the health of this central autonomic network and provides a measure of the integration of central nervous system (CNS) and autonomic nervous system (ANS) function (Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012). Thus, a higher baseline level of RSA is thought to reflect better central autonomic network health and enhanced CNS-ANS integration.

Both the ACC and mPFC play an important role in modulating the central autonomic network (Thayer, Hansen, Saus-Rose, & Johnsen, 2009) in a top-down direction and, hence, one could think of their inputs as “causal” in some way. However, what is critical to recognize is that the actions of these structures are dependent, to a certain extent, on feedback from the cardiovascular system, especially feedback from the baroreceptors. Baroreceptors are specialized mechanoreceptors found on the walls of the carotid arteries and aorta

(Kirkman & Sawdon, 2010; Silverthorn, 2010). These sensory receptors respond to arterial stretching that result from increases and decreases in blood pressure. Carotid baroreceptors are responsible for monitoring changes in the pressure of blood flowing to the brain, whereas aortic baroreceptors are responsible for monitoring changes in the pressure of blood flowing to the rest of the body (Pocock & Richards, 1999; Silverthorn, 2010). Importantly, these receptors provide feedback to the brain so as to buffer the human body against large, dangerous fluctuations in blood pressure.

With age, arteries often become stiffer and, consequently, the vascular system as a whole may become less functional, and the baroreceptors may no longer operate properly (Pocock & Richards, 1999). This can result from multiple causes including a lack of exercise, poor diet, and, of course, general aging. Consequently, afferent signals from the heart may no longer reach the brain as effectively, which means that the brain may not be as able to adjust efferent outputs to the heart to regulate blood pressure appropriately. Therefore, from this perspective, deterioration in the bottom-up pathway of the central autonomic network would be responsible for age-related declines in cognitive control.

Thus, given the presence of both top-down and bottom-up modulatory routes, it is hard to determine the direction of causation within the central autonomic network. However, because RSA is thought to reflect the general health of this system, which includes both efferent and afferent feedback systems, according to our model, it should be a good predictor of cognitive control as indexed via behavioural performance (i.e., accuracy) and error-related ERPs (i.e., ERN, Pe).

Moving Beyond ERPs

The current results also provide support for the importance of moving beyond traditional ERP analysis towards the examination of other cortical measures which can now be quantified through the application of independent component analysis (ICA) to electrophysiological (EEG) scalp data. Although ERPs allow for the examination of rapidly occurring cognitive processes, because they are derived from scalp EEG data, they are inherently mixed measures which represent the contributions of multiple cortical sources and/or other non-brain artifacts (Makeig & Onton, 2009; Onton & Makeig, 2006). Therefore, this may interfere with the ability to document their relations with other measures of interest. Fortunately, with the advent of ICA, mixed EEG signals can now be separated into individual brain sources (Jung et al., 2001; Makeig et al., 2002, 1996). These independent components, or ICs, represent purer cortical measures compared to ERPs, and thus may make it easier to document the relationship between the brain's electrocortical activity and other measures of interest.

Our results from Study 3 (Chapter 4) provide support for this view. Specifically, when we moved beyond our scalp-based ERN and Pe measures and examined the global field amplitude associated with the error response of the ACC-IC, more of the hypothesized relations with accuracy and autonomic regulation did, in fact, emerge. Specifically, greater ACC responsivity related to increased accuracy during some of the more challenging Stroop contexts. We also found that ACC_{GFA2}, the ACC response that likely corresponded to the Pe effect, was positively correlated with pre-task RSA. This is interesting given that ACC_{GFA2} and RSA shared a sizeable amount of variance with each other when entered into a model with VO_2max predicting accuracy (Study 3, Chapter 4). Furthermore, the results of our exploration of connectivity in Appendix A provide evidence of an association between RSA and ACC connectivity. Thus, our findings not only support the utility of using ICA for examining cortical indices of cognitive control, but they also provide support for the neurovisceral integration model (Thayer & Lane, 2000, 2009) by highlighting the interdependence of autonomic, cortical, and behavioural functions of the ACC.

Another interesting finding from the current thesis concerns the fact that a clear ACC-IC could not be identified for the vast majority of older adults, an effect that is not surprising given that a number of researchers have reported the link between age and diminished size and function of the ACC (e.g., Vaidya, Paradiso, Boles Ponto, McCormick, & Robinson, 2007). The ACC is known to play a critical role in the support of higher level cognitive control (Ridderinkhof et al., 2004). As such, it would be logical to assume that the absence of a clear ACC-IC among older adults would be associated with significant impairments in cognitive control. Interestingly, results from Study 3 did not support this generally-held assumption. Despite the absence of a clear ACC-IC among older adults, they demonstrated a level of performance equivalent to that of younger adults, even when the complexity of response contingency rules was greatest. This pattern suggests that older adults may have been able to utilize a unique strategy in the support of cognitive control that was qualitatively different from that of younger adults. Such findings align well with other research which has shown that older adults may be able to maintain equivalent levels of performance on cognitive control tasks by recruiting neural networks that are qualitatively different from those utilized by their younger counterparts (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002; McIntosh et al., 1999; Tays, Dywan, Mathewson, & Segalowitz, 2008). Furthermore, research indicates that neural systems that control performance and error monitoring are often able to function even when the ACC has been damaged. For instance, Stemmer, Segalowitz, Witzke, and Schönle (2004) tested patients who had sustained ACC damage and noted that even though these individuals did not produced reliable ERNs, they still managed to perform reasonably well, and they still produced the expected subjective responses following error commission.

Fitness and Performance

Although cardiac autonomic regulation (i.e., pre-task RSA) was related to cognitive control in younger adults, interestingly, the strongest and most consistent predictor of performance was actually fitness level, as measured by VO2max. These results are consistent with growing evidence that increased fitness is, in fact, related to better cognitive performance, especially when tasks require higher levels of cognitive control (Chaddock et al., 2012; Chang et al., 2013; Colcombe & Kramer, 2003; Pontifex et al., 2011). Moreover, there is growing interest in the physiological mechanisms that may be responsible for this relationship (Alderman & Olson, 2014). For example, higher levels of fitness have been associated with increased grey and white matter volume in the prefrontal and temporal brain regions (Colcombe et al., 2006), increased cell proliferation in the dentate gyrus (Pereira et al., 2006), and enhanced blood vessel growth throughout these regions (Kramer & Erickson, 2007). Although we cannot speak to the underlying mechanism responsible for the hypothesized link between fitness and cognitive performance, we note that our results from Study 3 (Chapter 4) provide additional support for this relationship in younger adults. This finding suggests the importance of considering other measures, such as tests of physical fitness, when exploring potential predictors of cognitive control.

Furthermore, we note that even though both pre-task RSA and VO_2max were related to cognitive control performance, they appeared to demonstrate differential associations with accuracy. Specifically, our results from Study 3 (Chapter 4) indicated that VO_2max was associated with performance on Stroop trials involving the use of both proactive (i.e., contingency lures) and reactive forms of control (i.e., incongruent lures), whereas pre-task RSA appeared to be relevant for performance on trials involving proactive control (i.e., contingency lures), specifically. Thus, VO2max appeared to relate to cognitive performance in a more general manner than did pre-task RSA. It is possible that fitness may provide more general benefits to cognitive control perhaps by increasing stamina and reducing fatigue during task completion. Conversely, cardiac autonomic regulation may demonstrate selective benefits for cognitive control that are most relevant during capacity-demanding contexts that require the sustained, active maintenance of goal representations over time.

Conclusion

Although the methods used and the findings uncovered in present thesis are new, they provide support for an observation made over 150 years ago by Claude Bernard regarding the intimate relationship between the brain and the heart (as cited in Thayer & Lane, 2009). The studies presented here demonstrated, specifically, that autonomic regulation, measured via RSA and RPP, was relevant to cognitive performance, especially when a task required the use of a more proactive form of cognitive control. This was evident in younger adults, but even more so in the older group. Interestingly, fitness demonstrated even stronger relations with performance in the younger group than did autonomic regulation. Our results also demonstrated that the most robust and consistent relations with cognitive performance occurred, not with ERP components reflecting an actual brain response to having made an error, but rather, with indices of autonomic regulation. Thus, the results of this thesis provide support for a model of neurovisceral integration which argues that cognition should be explored from a broader perspective that acknowledges the relevance of both cortical and autonomic influences on performance (Thayer & Lane, 2000, 2009). This model has especially important implications for those interested in better understanding the variability that is characteristic of the cognitive aging process.

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Appendix A

An analysis of ACC Connectivity

Over the last several decades, the use of electroencephalography (EEG) has significantly advanced our understanding of the cortical dynamics that underlie human brain processing. EEG offers a cost effective, non-invasive technique for investigating neural activity. Its greatest strength, however, is its high temporal resolution which allows for the examination of neural processes unfolding in real time (Davidson, Jackson, & Larson, 2000).

Event-related EEG research has generally taken one of two forms, time domain or frequency domain analysis (Makeig, Debener, Onton, & Delorme, 2004). Time domain analysis involves isolating and extracting different time points within the ongoing EEG that are thought to reflect specific brain processes (Luck, 2005; Martin, 1991). It is assumed that by time-locking to specific events of interest and averaging across these sections of EEG, the electrical activity associated with a specific motor, cognitive, or sensory event can be determined. This event-related averaging technique produces a characteristic waveform known as an event-related potential or ERP. The ERP technique has significantly advanced researchers' understanding of human information processing, particularly because many ERPs index cognitive or other processes that often remain unobservable at the behavioural level.

The frequency domain approach involves spectral decomposition of the continuous EEG (Makeig & Onton, 2009). The EEG itself represents the summation of multiple electrical oscillations of varying frequencies. This approach involves examining the power of the various frequency bands that constitute the ongoing EEG. A major advantage of this spectral decomposition is that it can provide a window into the sophisticated connectivity and coordination that occurs across various brain regions (Makeig & Onton, 2009).

Although EEG technology has undoubtedly advanced our understanding of many aspects of human brain processing, careful consideration reveals important limitations of this technique. EEG signals emanate from postsynaptic potentials of cortical pyramidal cells that are arranged perpendicular to the scalp (Fabiani, Gratton, & Federmeier, 2000; Luck, 2005). Simultaneous activation of multiple pyramidal cells results in the summation of postsynaptic potentials that are propagated via volume conduction to scalp electrodes on the surface of the head. While these biophysical properties allow for the measurement of electrical activity at the scalp, the resulting EEG signals recorded at each electrode, consequently, represent a mixture of multiple cortical sources or domains (Makeig & Onton, 2009; Onton & Makeig, 2006). This poses a major caveat for researchers who are interested in using scalp EEG data to examine dynamic brain imaging.

Early ERP researchers hoped that event-related averaging would resolve the source interpretation issue, also known as the inverse problem (Makeig & Onton, 2009). The logic behind this idea was that event-related averaging would provide the spatial filtering necessary so that each ERP peak would represent the activity of one single cortical generator. However, research has shown that multiple sources contribute to ERP averages, and therefore, event-related averaging is not an effective tool for dealing with the issue of source interpretation inherent in EEG data analysis.

Fortunately, a type of linear signal decomposition known as independent component analysis (ICA) has recently emerged as an effective technique for separating mixed EEG signals (Jung et al., 2001; Makeig et al., 2002, 1996). When ICA is applied to multi-channel EEG data, it produces a set of independent activity patterns, or independent components, which each represent a separate, specific EEG source. In a way, each independent component

(IC) produced by ICA represents a filter that, when applied to the multi-channel EEG data, cancels out the contributions of all but one of the source signals. The recovered components can represent both brain and non-brain sources (e.g., eye and muscle artifacts). An important point about ICA is that it separates the signals in a *blind* manner, with the only *a priori* assumption being that the underlying signals are independent of one another.

ICA offers important advantages for EEG data analysis. First of all, it does an excellent job of isolating non-brain artifacts, including eye blinks, eye movements, and muscle tension, into individual sources or ICs (Makeig & Onton, 2009). These ICs can then be removed from the data relatively easily which results in the preservation of more data trials. The most significant advantage of ICA, however, is its potential to separate the individual brain sources responsible for EEG scalp data (Makeig & Onton, 2009). The issues of volume conduction and signal mixing at the scalp have long hindered the use of EEG data in the investigation of dynamic brain imaging (Onton & Makeig, 2006). However, the growing realization that ICA can be used to decompose EEG signals into independent activity patterns that index distinct cell assemblies represents the dawn of a new era in EEG brain imaging research. The following represents an exploration of ICA as applied to a study which focused on attention and response control in a group of younger adults. In addition to examining the application of ICA for EEG data decomposition, we will also discuss the relevance of ICA for time/frequency analysis of EEG data.

Method

Task

Participants completed three versions of a Stroop task (A, B, and C) which required them to make accept and reject responses. In version A (Basic Stroop), participants were presented with match and mismatch Stroop colour-word stimuli, and they were instructed to press an "accept button" (e.g., button #1) for match stimuli (i.e., **BLUE**) and a "reject button" (e.g., button #2) for mismatch stimuli (i.e., **PURPLE**). Version A (Basic Stroop) served as a baseline for the two additional versions of the task (B and C) which each included a specific contingency. For instance, version B (Memory Stroop) required participants to respond the same way they did in version A (accept matches; reject mismatches), only this time participants were also required to reject a specific match word (for example, **GREEN**). Therefore, version B included the original contingency rules from version A plus an extra contingency that required internal monitoring of a specific match item (accept match unless **GREEN**). In version C (Repeat Stroop), participants were again instructed to accept matches and reject mismatches; however, if two identical match stimuli occurred in a row (**RED**, **RED**), the participant had to reject the repeated stimulus (the 2nd "**RED**"). Therefore, version C included the original contingency rules from version A plus an extra contingency that required a more external type of monitoring (accept match unless repeated). Thus, both the Memory and Repeat Stroop included additional task contingencies that were expected to increase task complexity and draw on higher levels of attentional control than the Basic Stroop with its single contingency (accept unless mismatch).

EEG Processing

EEG was collected using a 128-channel Active Two BioSemi system (BioSemi, Amsterdam). Data were sampled at a rate of 512 Hz and digitized with a 24-bit analog-to-digital converter. Before submitting data for ICA, several preprocessing steps occurred including the identification and rejection of bad channels (i.e., noisy and linked channels) and time segments. These preprocessing steps were performed in MatLab using a combination of

EEGLab functions (Delorme & Makeig, 2004) and in-house functions designed to facilitate the automatic identification and rejection of artifacts using the Shared Hierarchical Academic Research Computing Network (SHARCNet).

Before submitting the data for preprocessing, all three of the Stroop task recordings were appended together in EEGLab, and all break periods were then manually removed from each file. Each participant's EEG file was then submitted for automated preprocessing. A bandpass filter from 2 to 30 Hz was used, and all electrodes were re-referenced to a common average reference. The continuous data were then segmented into 50% overlapping windows, each 600 milliseconds (ms) in length.

In order to identify noisy channels, for each time window the maximum correlation coefficient *r* was calculated for each channel and its three nearest neighbours. The 99% confidence interval of *r* values for each window was then determined. Following this, every time window was scanned and those channels with *r* values that fell outside of the 99% confidence interval were flagged. Those channels that were flagged in more than 10% of the time windows were considered noisy and were subsequently rejected.

The next step was to identify linked or bridged channels. In order to do this, the mean and standard deviation *r* values for each channel were calculated across all of the time windows. Each channel's mean *r* value was subsequently divided by its standard deviation. This calculation produced a composite score that, in the case of a linked electrode, indicated a high, relatively invariable correlation with its bridged neighbour. If a channel's composite score turned out to be more than 8 standard deviations away from the 25% trimmed mean of all channel composite scores, that channel was considered problematic. In the case of the correlations being too high, it was rejected along with the channel with which it was linked, and in the case of the correlations being too low, it was considered noisy and was removed.

Following removal of noisy and linked channels, the time windows were investigated. The maximum nearest neighbour coefficient was recalculated for each window. The 99% confidence interval was then calculated across time windows for each channel. Each time window was then inspected, and if a channel's *r* value fell outside of the 99% confidence interval, that cell was flagged. Each of the time windows were then scanned and if 10% or more of the channels in a given window were flagged, the window was automatically rejected.

Once the necessary time windows were removed, the data were put back together and areas with discontinuities were marked as boundaries. In addition, continuous periods of data that were less than 2 seconds in length were automatically removed. At this point, the remaining continuous time intervals were detrended and the data were submitted to the extended Infomax ICA with an N channels – 1 PCA reduction.

Following the initial ICA decomposition, the ICA time course activations were used to identify additional windows of time that needed to be rejected. The ICA weights were projected back to the continuous data, and the data were again segmented into 50% overlapping windows, each 600 ms in length. For each time window, the standard deviation of activation for each IC was computed. The 99% confidence interval of standard deviation scores was then computed for each IC across all time windows. For each time window, if an IC's standard deviation of activation fell above the confidence interval, this cell was flagged. If 10% or more of the ICs in a particular time window were flagged, the window was subsequently removed. Following removal of necessary time windows, the data were reassembled and areas of discontinuity were marked as boundaries. In addition, continuous periods of data that were not at least 2 seconds in length were removed. The remaining time intervals were then detrended and submitted to a second extended Infomax ICA with an N channels – 1 PCA reduction.

Following the second ICA, dipoles were fit to each IC, and if a dipole set explained less than 85% of the weight variance, that IC was marked for rejection. Each IC was then manually inspected. If an IC that was marked for rejection could be explained by symmetrical bilateral dipoles, it was retained. Those ICs that represented biological artifacts (e.g., eye movements, blinks, muscle tension), however, were rejected. Following this manual inspection, the ICA weights were then applied back to the continuous data.

Data Exploration and Results

Exploring the ICs

ICA was used to examine the response-locked data first. Response-locked correct and error trials were selected and segmented into epochs from -1000 to +2000 ms. Initially, we were interested in exploring the response-locked error effect (errors – corrects) to see whether a component accounting for the error-related negativity (ERN) could be identified (Dehaene et al., 1994; Gehring et al., 1993). As such, it was necessary to calculate the mutual variance between the components and the ERN effect in the corresponding time window. This was done by examining the percent of variance the components accounted for in the time window that corresponded to the ERN effect (approximately 0 to 100 ms). The topographies and time courses of the ICs produced by this analysis were then inspected. The component that produced an increase in phasic activity following the error along with a fronto-central scalp topography was identified as the IC accounting for the ERN. Further dipole analysis confirmed that the source generator of this component was indeed the anterior cingulate cortex (ACC), a finding which is well in line with research on the ERN. This component will be referred to as the ACC_{IC}.

Upon further inspection of the response-locked data, an interesting and unexpected pattern emerged. Not only was an ACC_{IC} identified following the onset of the error response, but for some individuals a later occurring component with a broad posterior topography was also present. What was interesting about this component was that it looked very similar to the occipital component that is often found following stimulus onset and may account for the P2. However, we could not be sure that this was the same component because we were dealing with response-locked, not stimulus-locked data. In order to determine whether this component was in fact the occipital component that accounts for the P2, we returned to the stimulus-locked data.

Stimulus-locked correct trials were selected and segmented into epochs from -1000 to +2000 ms. ICA of the stimulus-locked data confirmed that the component that was occurring later in the response-locked data for some participants was in fact the same component accounting for the variance at the time of the P2 following stimulus onset. This component also seemed to be active at the time of the P1, and dipole analysis indicated a bilateral occipital generator. This component will be referred to as the OCC_{IC}.

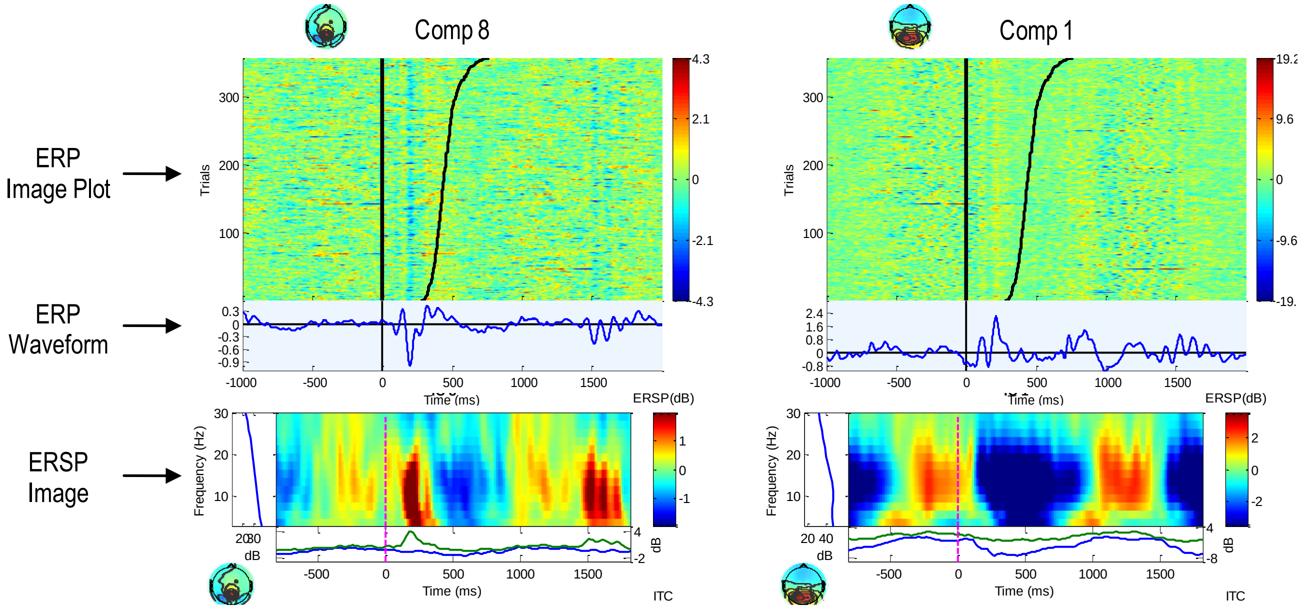
The above analysis indicated that the OCC_{IC} was not only active during the onset of the stimulus, as would be expected, but for some individuals this component became reactivated in the response-locked data following the ACC_{IC} (see end of Appendix A, Figure A-7). This is an interesting and potentially meaningful relationship that warrants further attention. A logical question, therefore, is how to properly follow-up on this particular pattern of relations. The answer lies in a technique called time/frequency analysis. In order to understand why we should use time/frequency analysis in this particular case, let’s return briefly to the traditional ERP averaging technique.

A Closer Look at ERPs

A critical property of ERPs that must be acknowledged is that the very averaging process used to create them results in the preservation of only those features of the EEG data that are partially or completely phase-locked to a specific event of interest (Makeig & Onton, 2009). In other words, the ERP averaging process cancels out all aspects of EEG event-related dynamics that do not happen to be phase-locked. Conventional averaging, therefore, may result in the loss of EEG data that, albeit not phase-locked, could represent potentially important information about underlying brain function. Furthermore, ERP averaging provides merely one view of the event-related data, a view that may be informative in some cases but misleading in others.

Figure A-1 provides an insightful illustration of this issue. ERP image plots, ERP waveforms, and event-related spectral power (ERSP) time/frequency images are depicted for 2 visual ICs, 8 and 1. The ERP image plots provide a visual representation of almost 400 single trials locked to the onset of the stimulus (solid black vertical line) and sorted according to the latency of the participant’s button response (curving black line). The blue waveform below each ERP image plot illustrates the corresponding ERP average of the single trials. Finally, below each ERP waveform is the mean event-related ERSP image for each component which provides a colour coded plot demonstrating how mean event-related power changes (i.e., increases or decreases) across various frequencies, relative to the pre-stimulus baseline period.

Figure A-1



The ERP waveform for component 8 shows a burst in amplitude immediately following stimulus onset. An increase in ERP voltage is usually assumed to represent an increase in power of underlying neural oscillations in response to some event (i.e., in this case, the onset of the stimulus). Investigation of both the ERP image plot and ERSP image indicates that this spike in the ERP waveform is a result of an increase in power (see the ERSP image) and a lining up of the oscillation phase angles (see ERP image). Thus, for component 8 the ERP itself appears to be a good representation of the single trial data.

The story, however, is not the same for component 1. As was the case with component 8, the ERP waveform for component 1 shows a large spike in amplitude following the onset of the stimulus. However, what is critical to notice about component 1 is that the ERSP plot indicates that there is no increase in power at the time of the ERP spike. In fact, there is actually a *decrease* in power following stimulus onset. However, the ERP image plot indicates that the phase angles align at this time. Thus, from these plots it is clear that the spike in the ERP for component 1 is not due to an increase in power but rather a lining up of the oscillation phase angles. Thus, in contrast with component 8, the ERP waveform for component 1 has the potential to be misleading because it could lead one to incorrectly assume that the burst in the ERP is due to an increase in power rather than simply a lining up of the oscillation phase angles.

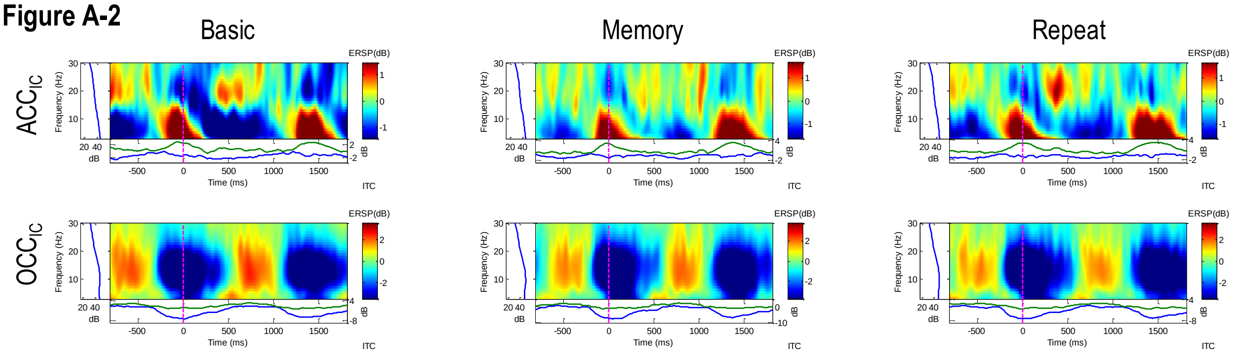
The above example demonstrates the importance of moving beyond the traditional ERP perspective, which provides an important but somewhat static view of the data, and embracing a more detailed approach that takes into account the underlying neural oscillatory activity from which ERPs are derived. Researchers are increasingly recognizing that the ongoing electrical oscillations present in EEG are not simply “background noise,” but rather, a window into the underlying neural dynamics that support complex information processing (Makeig & Onton, 2009). In order to ensure that this type of information is not overlooked, we can transition from ERP averaging to spectral decomposition of the EEG via time/frequency analysis.

Time/Frequency Analysis

Time/frequency analysis is a method that combines temporal and spectral EEG analysis techniques (Roach & Mathalon, 2008). Specifically, time/frequency analysis provides a measure of how the power at different frequencies changes across time relative to some baseline. A benefit of EEG time/frequency analysis is that it can reveal event-related dynamics that are not present in the scalp ERP (Makeig & Onton, 2009). This is because time/frequency analysis allows one to capture mean event-related dynamics of oscillatory activity that are time-locked but not necessarily phase-locked. However, the most important benefit of time/frequency analysis over the traditional ERP approach, in general and with respect to the current data set, is its potential to reveal important information about the complex processing that occurs in the brain as a network (Makeig & Onton, 2009). By examining neural oscillations at various frequencies, researchers can gain a richer understanding of the elegant interneuronal communication that occurs within the brain and supports adaptive information processing (Lisman & Buzsáki, 2008; Makeig & Onton, 2009). Furthermore, by applying time/frequency analysis to individual ICs, we can model the event-related dynamics of individual source components or independent cell assemblies (Makeig & Onton, 2009). This offers a significant advantage for the current data set since we are interested in exploring the association between ACC_{IC} and OCC_{IC}.

We applied time/frequency analysis to the activity time courses of the ACC_{IC} and OCC_{IC} to examine how spectral power at different frequencies changed relative to the onset of response. For this analysis, we examined the response-locked correct data for the Basic, Memory, and Repeat Stroop tasks. Although we could have examined errors, we chose to examine correct responses because we were interested in examining the neural dynamics underlying successful task performance. Figure A-2 shows ERSP time/frequency images for the ACC_{IC} and OCC_{IC} time-locked to correct responses for one participant across the 3 Stroop tasks. These images demonstrate that around the time of the response there is an increase in ACC_{IC} power and a decrease in OCC_{IC} power.

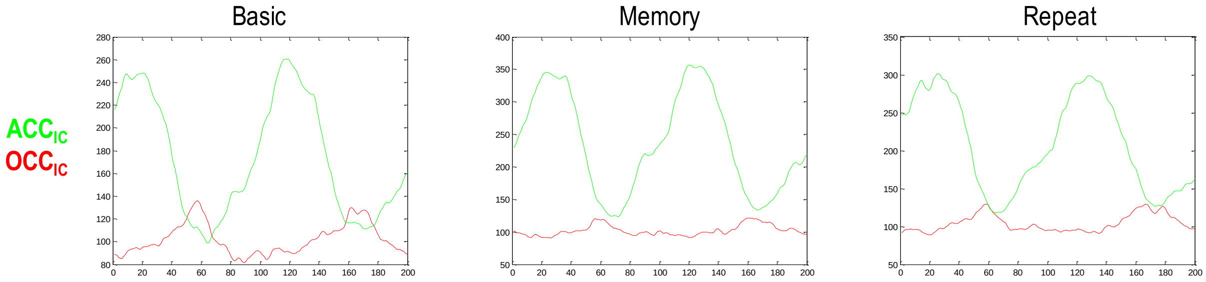
Figure A-2



In addition to the separate ERSP images we have generated for each IC, another way to examine the relationship between these two components is by taking the mean power of each component across a particular frequency and plotting it as a waveform. We focused on alpha which refers to rhythmic oscillations between 8 and 13 Hz. Interestingly, power in this frequency band is considered an inverse index of cortical activation (Carp & Compton, 2009; Davidson et al., 2000). In other words, increased alpha power is associated with reduced cortical activation.

Figure A-3 demonstrates the mean change in alpha power across time for both the ACC_{IC} and OCC_{IC} (Note: these plots represent data from the same individual whose ERSP images are depicted in Figure A-2). Taken together, Figures A-2 and A-3 seem to demonstrate a pattern of ongoing occipital alpha that changes over time as a function of the task. Specifically, the onset of the response seems to lead to a burst in ACC power and a simultaneous attenuation of the ongoing occipital alpha.

Figure A-3



This inverse association between ACC power and occipital alpha emerged in several of the participants to varying degrees. This pattern is particularly interesting in light of other research surrounding alpha and its role in cortical arousal. For instance, Carp and Compton (2009) demonstrated an association between alpha power and performance monitoring in the context of a six-choice Stroop task. Specifically, they found that alpha power was significantly reduced during the intertrial interval that followed error compared to correct responses. This pattern of results suggests that while correct responses are followed by a period of transient mental disengagement, error responses are followed by a state of increased alertness.

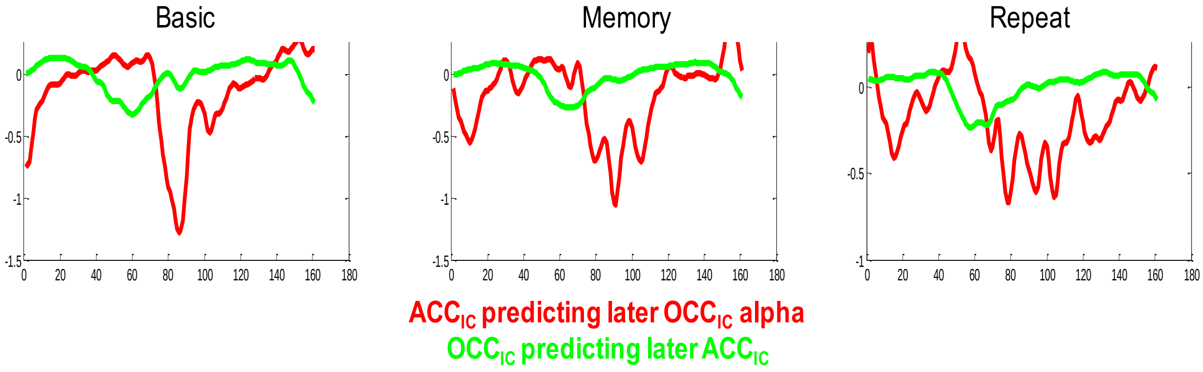
Carp and Compton’s (2009) results are particularly interesting in light of the time/frequency analysis we described above. Again, Carp and Compton demonstrated that alpha power is inversely related to mental engagement. This pattern is especially apparent on error trials, where individuals are likely to experience increases in emotional arousal and cortical activity and where the ACC is known to play a prominent role (Dehaene et al., 1994; Gehring et al., 1993). Carp and Compton’s (2009) findings, coupled with our current time/frequency results, suggest that there might be an important inverse relationship between ongoing occipital alpha and ACC activation. Moreover, the possibility exists that there could be a negative predictive influence between these two signals, such that an increase in ACC power may predict a decrease in ongoing occipital alpha.

Granger Causality

In order to investigate the potential predictive relationship between these two signals, we utilized Granger Causality (Granger, 1969). While coherence and bivariate correlations can identify underlying connections and interactions between signals, they reveal nothing about the directionality of these relationships (Gourévitch, Bouquin-Jeannès, & Faucon, 2006). Granger Causality, however, is a unique statistical technique that provides information about the direction of information flow, and therefore, can help identify causal relationships between neural signals (Granger, 1969; Kaminski, Ding, Truccolo, & Bressler, 2001). Granger Causality is based on the following premise: If the addition of variable x to variable y accounts for variance in y above and beyond the prior history of y alone, x can be said to Granger-cause y. The question for the current study, therefore, is whether the ACC transiently predicts occipital alpha. In other words, does ACC power at time 1 predict later occipital alpha power?

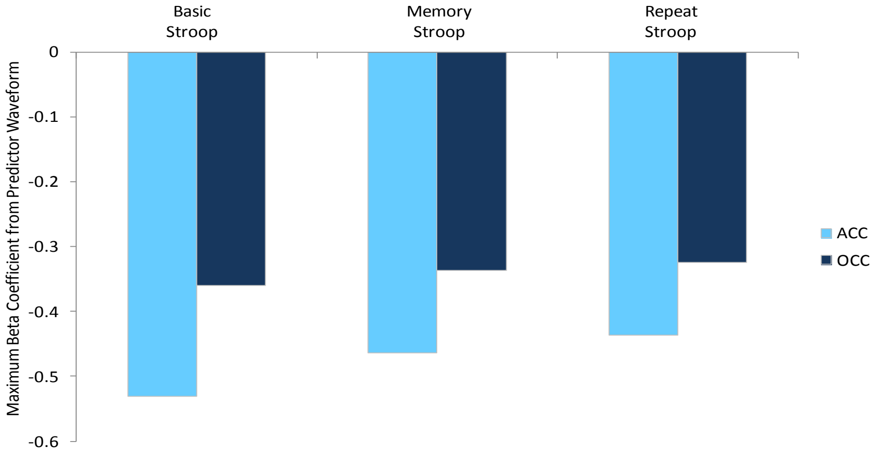
In general, we examined the correlation of signal 1 (S1) at time 1 with signal 2 (S2) at time x, partialling out the instantaneous relationship of the two signals (i.e., relation between the two signals at the same point in time) and the signal itself over time (i.e., S2 at time 1 and time x). We performed this computation twice so that we could examine the ACC's Granger causality on occipital alpha and vice versa. The correlation coefficients were calculated across time using a sliding lag. These lagged correlation coefficients were then transformed into waveforms representing the ACC's Granger causality on occipital alpha and occipital alpha's Granger causality on the ACC. Figure A-4 provides a visualization of these Granger causality waveforms for one participant across the 3 Stroop tasks (Note: Waveforms are from the same individual whose data are depicted in Figures A-2 and A-3).

Figure A-4



For each participant, we then exported the latency and amplitude from each waveform's maximum beta coefficient for statistical analysis. The bar graph in Figure A-5 depicts the maximum beta coefficient values for the ACC predictor waveform and the occipital alpha's predictor waveform for the 3 Stroop tasks. A 2 (region: ACC, OCC) by 3 (Stroop type: Basic, Memory, Repeat) repeated measures ANOVA was run using the maximum beta coefficients from the waveforms to determine whether there was a difference in ACC Granger causality on occipital alpha or vice versa. There were no main effects of region or Stroop type (all *p*s > .11) and no region by Stroop type interaction (*p* > .51).

Figure A-5



Exploring Individual Differences

Even though there was no difference in the magnitude of either region's Granger causality on the other region, we were still interested in examining whether either region's Granger causality related to any meaningful measures of individual differences. We started by examining individual differences in accuracy on the Basic, Memory, and Repeat Stroop tasks. We examined whether the magnitude and/or latency of either region's Granger causality related to accuracy. Results indicated that neither magnitude of ACC Granger causality on occipital alpha, nor magnitude of occipital alpha Granger causality on ACC, related to accuracy on any of the Stroop tasks (all *p*s > .48). Additionally, neither the latency of ACC Granger causality on occipital alpha, nor the latency of occipital alpha Granger causality on ACC, related to accuracy on any of the Stroop tasks (all *p*s > .12).

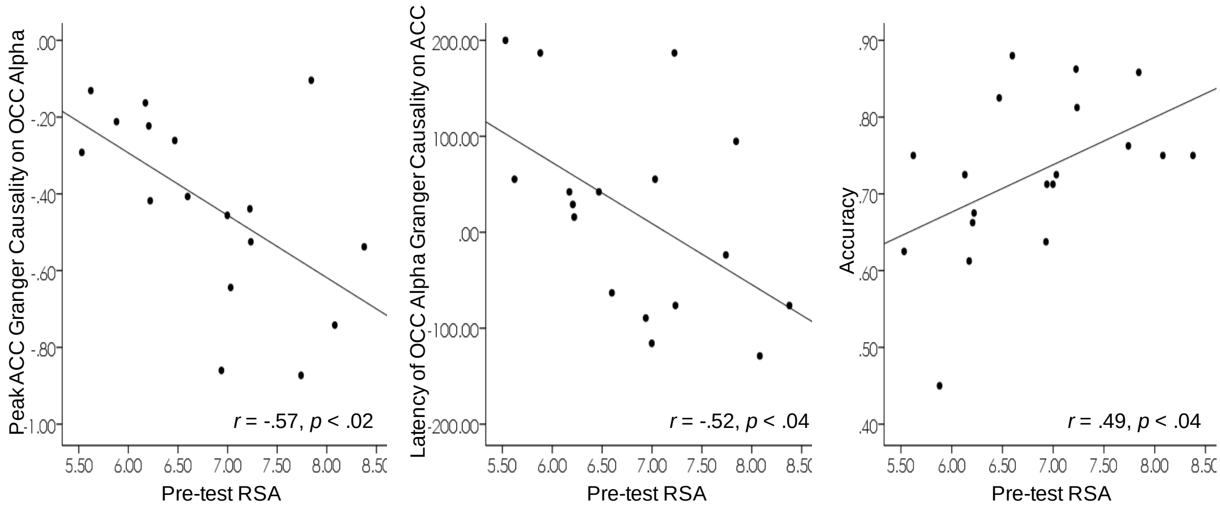
Next, we decided to examine individual differences in pre-task respiratory sinus arrhythmia (RSA). RSA is a particularly interesting individual differences measure because higher levels are thought to reflect a system that can respond flexibly and adaptively to situational demands (Thayer & Lane, 2009; Thayer, Sollers, et al., 2009). Therefore, we examined whether pre-task RSA related to the magnitude of ACC Granger causality on occipital alpha or the magnitude of occipital alpha Granger causality on the ACC. No relations emerged in the context of the Basic or Repeat Stroop (all *p*s > .11); however, an association between RSA and the magnitude of ACC Granger causality on occipital alpha emerged in the context of the Memory Stroop ($r = -.57$, $p < .02$). Figure A-6 (left) demonstrates that when individuals had higher RSA, the magnitude of the ACC's negative prediction on later occipital alpha was greater.

We also examined whether pre-task RSA related the timing of the peak Granger causality of either region on the other. We found that pre-task RSA was related to the latency of the occipital alpha peak Granger causality on the ACC in the context of the Basic ($r = -.48$, $p = .05$) and Memory Stroop ($r = -.52$, $p < .04$; all other *p*s > .06). Figure A-6 (middle) depicts the association that occurred in the Memory Stroop, specifically. It demonstrates that the time at which occipital alpha Granger causality peaked (i.e., the time when occipital alpha most strongly predicted later ACC) occurred earlier in those individuals with higher RSA.

The present results indicate that the most consistent relations between pre-task RSA and measures of Granger causality (i.e., magnitude of ACC Granger causality on occipital alpha; latency of peak occipital alpha Granger causality on ACC) occurred in the context of the Memory Stroop. This is particularly interesting because previous analysis with this same data set indicated that pre-task RSA related to behavioural performance but only in the context of the Memory Stroop (all other *p*s > .22). Specifically, higher pre-task RSA was associated with increased accuracy on the Memory Stroop (*r* = .49, *p* < .04) (Figure A-6, right).

Figure A-6

Memory Stroop Relationships

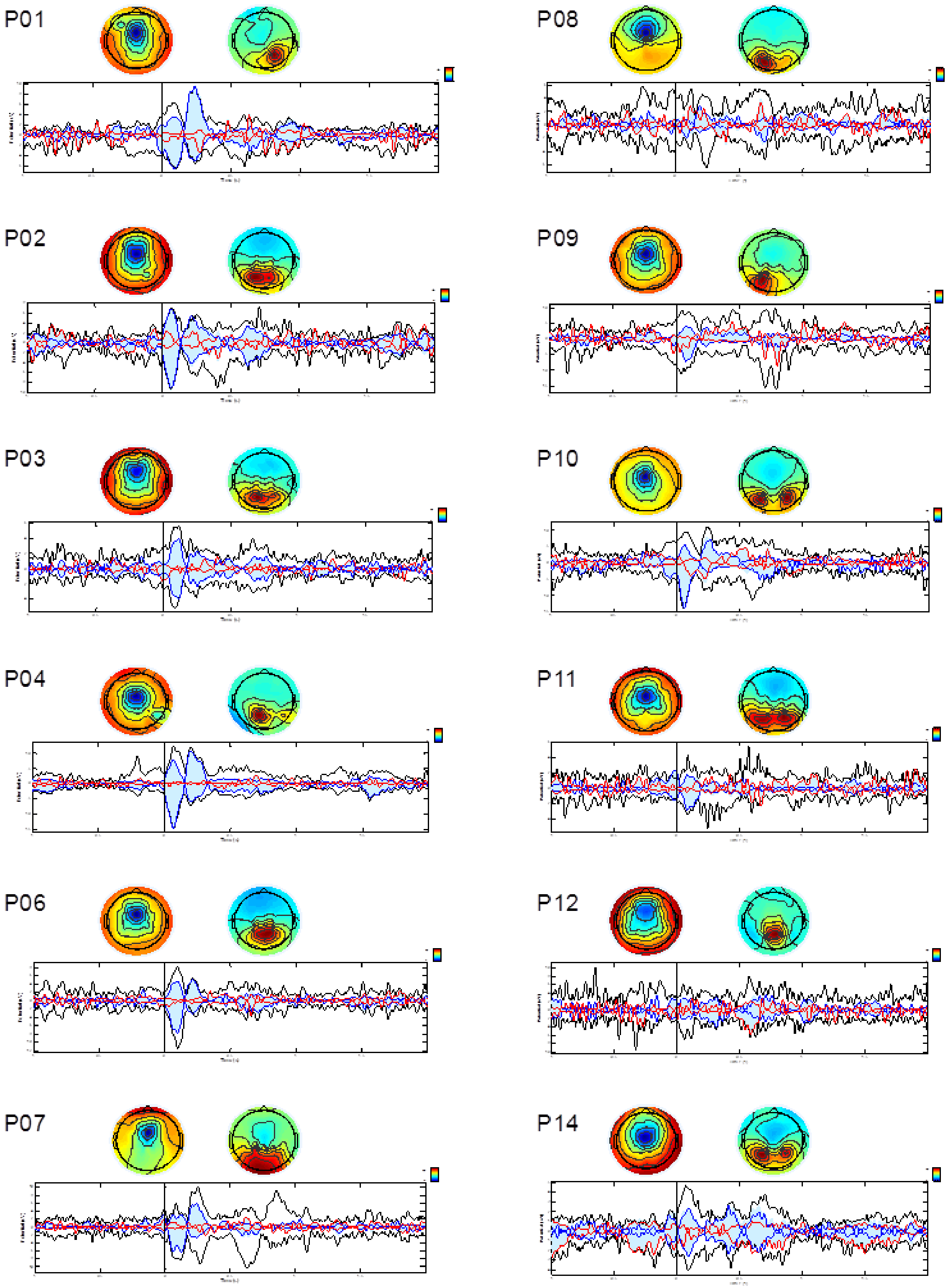


The present results indicate that there is clearly something special about the Memory Stroop task in that various relations with RSA, a measure of flexibility and adaptability, emerge in this context. When pre-task RSA is higher, the magnitude of the ACC's prediction on later occipital alpha is greater, the drop in occipital alpha power that is predicative of the later increase in ACC power occurs earlier, and accuracy on the Memory Stroop itself is enhanced.

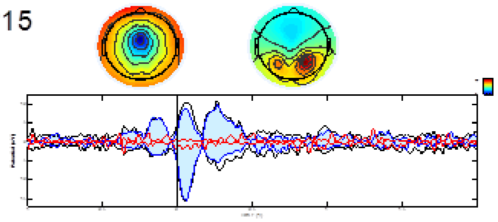
Future Directions

In terms of future directions, it will be important to examine whether ACC power relates to RSA. This will allow us to determine whether it is specifically the ACC's outflow to the occipital region that relates to RSA or whether it is simply ACC activation itself. It would also be beneficial to use EEGLab's source information flow toolbox (SIFT) to examine connectivity between multiple cortical areas. The current study simply looked at the predictive relationship between two ICs, the ACC_{IC} and OCC_{IC}. However, it is important to not only say that one component predicts another component above and beyond their instantaneous relationship and the second component's own past, but that this predictive relationship exists *over and above* all other possible predictors (i.e., brain regions). SIFT will allow us to tackle this issue by examining the connectivity of multiple ICs within each person.

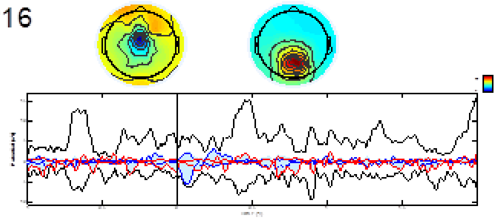
Figure A-7



P15



P16



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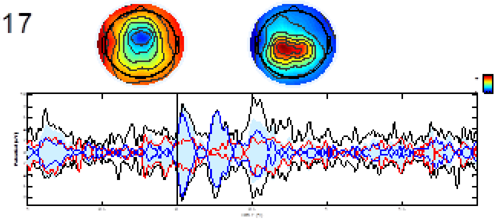
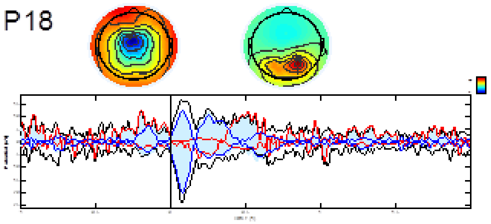
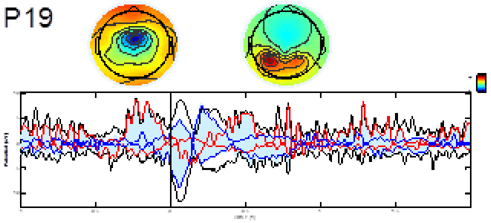


P18



P19



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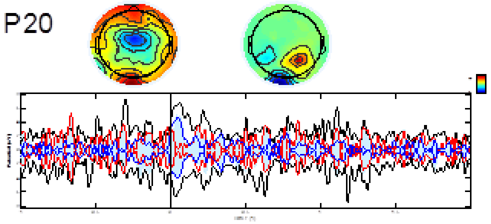

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Appendix B

Processing Details of Study 3 EEG Data

The following section provides the details that were involved in the processing of EEG data from Study 3 (Chapter 4). All pre-processing was performed in MATLAB using functions from the open source toolbox EEGLAB (Delorme & Makeig, 2004) as well as in-house functions developed for automatic artifact removal on the Shared Hierarchical Academic Research Computing Network (SHARCNet).

First, all three of the Stroop task recordings from Study 3 (Basic, Memory, Super Memory) were appended together in EEGLab, and all break periods were then manually removed from each file. Each participant's EEG file was then submitted for automated preprocessing. A bandpass filter from 2 to 30 Hz was used, and all electrodes were re-referenced to a common average reference. The continuous data was then segmented into 50% overlapping windows, each 600 milliseconds (ms) in length.

In order to identify noisy channels, for each time window the maximum correlation coefficient R was calculated for each channel and its three nearest neighbours. The 99% confidence interval of R values for each window was then determined. Following this, every time window was scanned and those channels with R values that fell outside of the 99% confidence interval were flagged. Those channels that were flagged in more than 10% of the time windows were considered noisy and were subsequently rejected.

The next step was to identify linked or bridged channels. In order to do this, the mean and standard deviation R values for each channel were calculated across all of the time windows. Each channel's mean R value was subsequently divided by its standard deviation. This calculation produced a composite score that, in the case of a linked electrode, indicated a high, relatively invariable correlation with its bridged neighbour. If a channel's composite score turned out to be more than 8 standard deviations away from the 25% trimmed mean of all channel composite scores, that channel was considered linked and was therefore rejected.

Following removal of noisy and linked channels, the time windows were investigated. The maximum nearest neighbour coefficient was recalculated for each window. The 99% confidence interval was then calculated across time windows for each channel. Each time window was then inspected, and if a channel's R value fell outside of the 99% confidence interval, that cell was flagged. Each of the time windows were then scanned and if 10% or more of the channels in a given window were flagged, the window was automatically rejected.

Once the necessary time windows were removed, the data was put back together and areas with discontinuities were marked as boundaries. In addition, continuous periods of data that were less than 2 seconds in length were automatically removed. At this point, the remaining continuous time intervals were detrended and the data was submitted to the extended Infomax ICA with an N channels – 1 PCA reduction.

Following the initial ICA decomposition, the ICA time course activations were used to identify additional windows of time that needed to be rejected. The ICA weights were projected back to the continuous data, and the data was again segmented into 50% overlapping windows, each 600 ms in length. For each time window the standard deviation of activation for each IC was computed. The 99% confidence interval of standard deviation scores was then computed for each IC across all time windows. For each time window, if an IC's standard deviation of activation fell above the confidence interval, this cell was flagged. If 10% or more of the ICs in a particular time window were flagged, the window was subsequently removed. Following removal of necessary time windows, the data was reassembled and areas of discontinuity were marked as boundaries. In addition, continuous periods of data that were not at least 2 seconds in length were removed. The remaining time intervals were then detrended and submitted to a second extended Infomax ICA with an N channels – 1 PCA reduction.

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Appendix C

Relations between Cardiac Workload and Performance

The present thesis provided evidence for the role of cardiac workload, measured via pre-task RPP, on performance accuracy, but the pattern of relationships observed across studies was inconsistent. In Study 1 (Chapter 2), we found, as expected, that higher pre-task RPP among older adults, indicating higher cardiac workload, was associated with reduced NoGo accuracy on the WMIC task. In Study 2 (Chapter 3), we found a similar relationship in a younger adult sample. Higher pre-task RPP among younger adults was associated with a reduction in total rejection accuracy in the context of the Memory task during both standard and incentive phases. Although the relations in Study 2 were highly dependent on one younger adult with atypically high RPP, we note that the direction of the association between pre-task RPP and accuracy was the same as that in Study 1 and consistent with a theoretical perspective that suggests well-modulated arousal facilitates the ability to perform high-level cognitive tasks that require the control of attention. Study 3 was similar to Study 1 in that RPP was again not related to accuracy in the younger group; however, Study 3 (Chapter 4) differed from Studies 1 and 2 in that that higher pre-task RPP in older adults related to *better* incongruent rejection accuracy in the context of the Memory task during both standard and incentive phases. To better understand this anomalous pattern of associations, we have enquired further into the nature of the relationships reported here by examining the range and distribution of pre-task RPP levels across the three studies.

From Figures C-1a and C-1b, it is clear that those individuals who were on the upper end of the pre-task RPP range (between 110 and 120) were the ones whose accuracy suffered most in Studies 1 and 2. We note, however, that in Study 3, none of our participants, not even the older adults, reached this upper range of RPP (Figure C-1c). In fact, the highest pre-task

RPP value that an older adult demonstrated in Study 3 was 100, compared to a maximum of 117 in Study 1 and 112 in Study 2. The presence of such low pre-task RPP levels among the older adults from Study 3 may reflect the fact that these older participants were younger (60-78 years, *M* = 68.8) than the older adults from Study 1(65-83 years, *M* = 72.3). They were also selected more carefully with respect to general health because we were asking them to complete the Canadian Step Test in order to examine the role of fitness in our study. As well, individuals from Study 3 came in on two separate occasions, and RPP was measured during their second visit to the lab. Thus, the older adults from Study 3 may have been more relaxed than those from Study 1, who came to the lab on only one occasion.

These differences in the health and age of the older adults included in Studies 1 and 3, as well as differences in study design, may have resulted in the RPP level differences apparent among the older participants from these two studies. Still, this does not explain why the direction of the relationship between RPP and accuracy that emerged in Study 3's older adults was reversed from that observed in Study 1's older adults and the young adults in Study 2. To understand this discrepancy, we return to earlier unpublished data from Study 1.

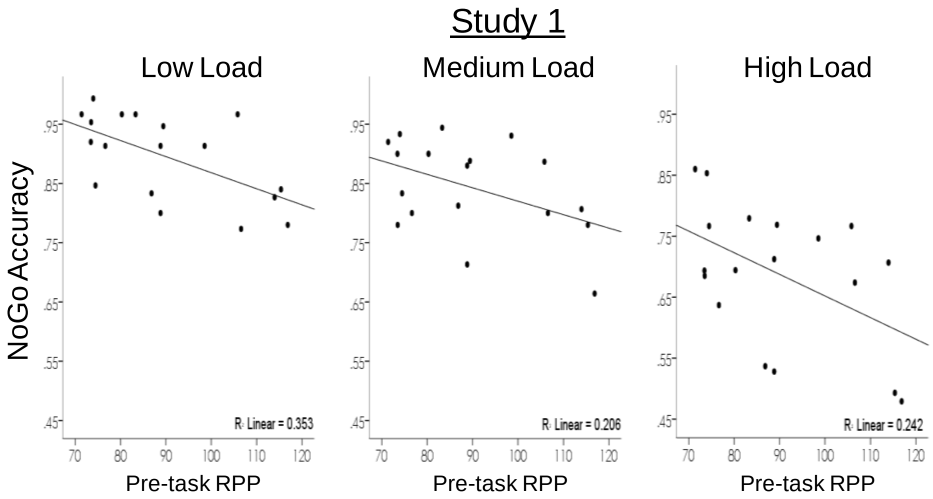

Figure C-1a. Relations between pre-task RPP and NoGo accuracy observed during Study 1 for older adults across the three levels of the WMIC task.

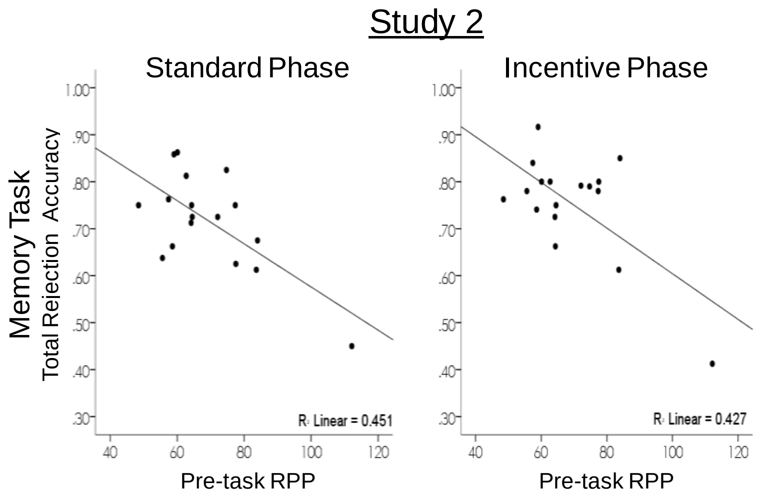

Figure C-1b. Relations between pre-task RPP and total rejection accuracy observed during Study 2 for younger adults during standard and incentive phases of the Memory task.

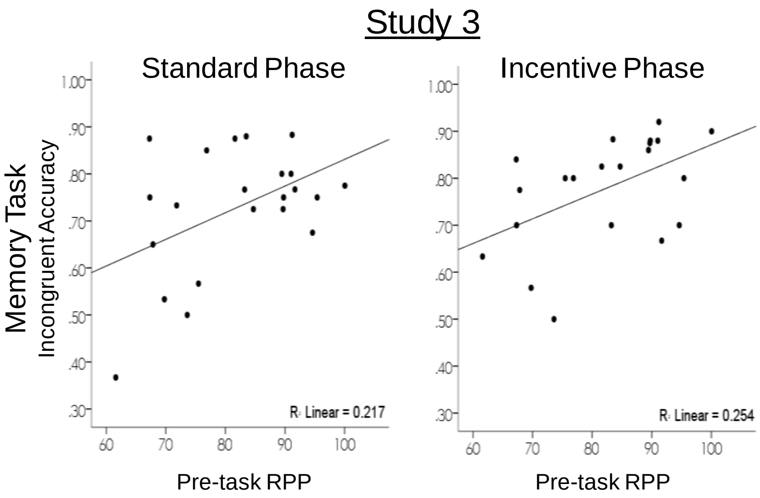

Figure C-1c. Relations between pre-task RPP and incongruent rejection accuracy observed during Study 3 for older adults during standard and incentive phases of the Memory task.

Initially, we ran 17 younger adults for Study 1 and were surprised to find that higher pre-task RPP was associated with an *increase* in NoGo accuracy, a pattern opposite to that observed in our older adults. However, upon further inspection, we noticed an important difference in the range of RPP within each group. Specifically, we realized that those younger adults who were at the upper range of RPP within their age group demonstrated RPP levels similar to those of older adults who were at the lower range of RPP within their age group (Figure C-2). Subsequently, we decided to combine both groups and examine the association between pre-task RPP and total NoGo accuracy. Results of our analysis revealed a curvilinear relationship between pre-task RPP and NoGo accuracy ($r^2 = .36$, $p < .01$, see Figure C-3). Thus, across both age groups, those individuals who demonstrated moderate levels of pre-task RPP (i.e., between 70 and 100) were the ones who demonstrated the best NoGo accuracy on the WMIC task.

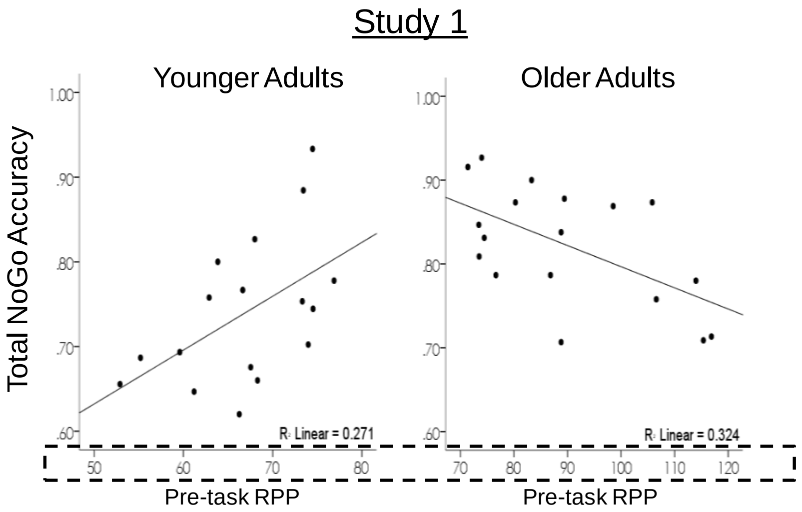

Figure C-2. Relations observed during Study 1 between pre-task RPP and total NoGo accuracy on the WMIC task in older and younger adults. *Note: The figure for the younger group is based on data from the initial sample of 17 younger adults.

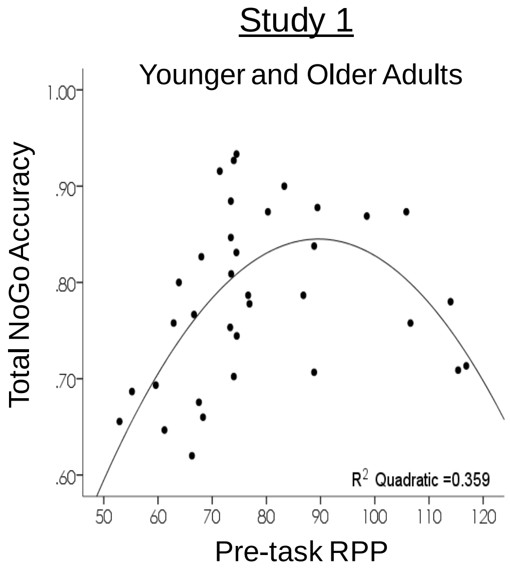

Figure C-3. Curvilinear relationship observed during Study 1 between pre-task RPP and total NoGo accuracy on the WMIC task for the combined sample of older and younger adults. *Note: This figure is based on data from the initial sample of 17 younger adults.

The curvilinear relationship described above was based on data from the first 17 younger adults we ran for Study 1. Six months later, we ran an additional 5 younger adults to increase our sample size. We were hoping these new young subjects would include a few more at the higher end of the RPP range to further test the view that a high score in young adults would lead to better, as opposed to worse, performance. However, all new participants were in the low to mid-range on pre-task RPP and, thus, the association between RPP and total NoGo accuracy no longer reached significance (*p* > .69, see Figure C-4). Furthermore, the curvilinear relationship between RPP and NoGo accuracy in the combined sample was also no longer present (*p* > .38). Thus, because the positive association between pre-task RPP and accuracy seemed less stable in the younger group, we focused on the negative association observed in the older group when discussing the results of Study 1 (Chapter 2). Nonetheless, the initial curvilinear relationship we observed may shed light on the seemingly anomalous association that emerged between RPP and accuracy in Study 3 (Chapter 4).

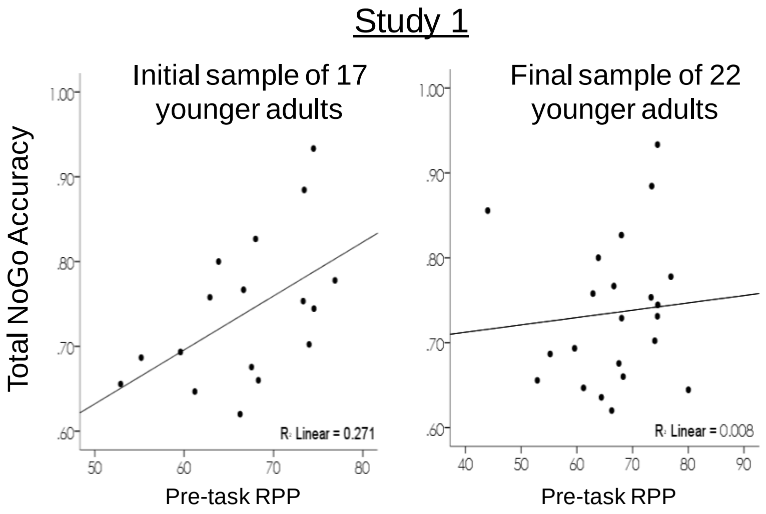

Figure C-4. Relations observed during Study 1 between pre-task RPP and total NoGo accuracy on the WMIC task for the initial sample of 17 younger adults and the final sample of 22 younger adults. The positive association between RPP and accuracy was no longer present in the final sample of 23. *Note: Even when the individual who is furthest to left in the final sample graph is removed, the relationship between RPP and accuracy still does not reach significance.

As explained above, the older adults from Study 3 (Chapter 4) did not demonstrate RPP levels that were as high as those observed in the older adults from Study 1 (Chapter 2). In fact, the older adults from Study 3, in general, fell within an RPP range that was comparable to that observed in the younger adults in Study 1, where RPP was positively associated with accuracy. Thus, it may be that a moderate level of RPP is beneficial to subsequent performance on cognitive tasks (as suggested by the results of Study 3), but once a certain threshold is crossed, this level of cardiac workload becomes detrimental to task performance (as suggested by Study 1).