

Explaining the Many Varieties of Working Memory Variation:
Dual Mechanisms of Cognitive Control

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To appear in *Variation in Working Memory*, A. Conway, C. Jarrold, M. Kane, A.
Miyake, J. Towse (Eds.), Oxford University Press.

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Overview

Virtually all working memory (WM) theorists agree that control processes are a critical component of WM function. Some set of internal mechanisms must be responsible for: 1) selecting information for active maintenance in WM; 2) ensuring that it can be stored for an appropriate length of time; 3) protecting it against sources of interference; 4) updating it at appropriate junctures; and 5) utilizing it to influence other cognitive systems (i.e., perception, attention, memory and action). Yet, equally clear to most theorists is the observation that the ability to exert control over WM varies substantially, both within individuals (across time and task situations) and across individuals. In some sense, this observation poses perhaps the core paradox regarding cognitive control: Why is cognitive control so important, yet simultaneously so fragile and vulnerable to disruption? Why does it appear that our ability to exert control is so strong in some cases, but so weak in others? If exerting cognitive control seems to be the optimal response in many situations, why does it seem as if behavior is sub-optimally controlled much of the time in many individuals, and at least some of the time in all individuals?

In this chapter, we put forth a theory of cognitive control in WM that attempts to explain this variability. Our central hypothesis is that cognitive control operates via two distinct operating modes – **proactive control** and **reactive control**. We will present arguments suggesting that these two modes are dissociable on a number of dimensions, such as computational properties, neural substrates, temporal dynamics, and consequences for information processing. We will suggest that although most formulations of cognitive control in WM only consider proactive control, reactive control

mechanisms may be more dominant. We will further suggest that by distinguishing between these two modes we will be able to: 1) resolve some of the apparent inconsistencies in the existing WM literature; 2) understand how and why the impact of cognitive control processes in WM can vary so strongly within individuals across time and task situations; 3) gain insight into the nature of cognitive control impairments found in healthy aging (and possibly in other populations suffering from neuropsychiatric disorders); 4) understand some of the critical underlying mechanisms related to individual differences in WM function; and 5) account for potentially surprising data indicating that putatively “non-cognitive” variables such as mood states and personality traits (e.g., extraversion, neuroticism) may also influence WM function.

The general theoretical framework that we advance here for understanding the sources of variation that affect WM and cognitive control is termed the **Dual Mechanisms of Control**, or **DMC** account. It is worth noting that, although we have been developing this framework for several years now, this chapter marks the first comprehensive treatment of the theory and its empirical support. As such, we combine discussion of both published and not-yet-published experimental data in the sections below, to better make the case for how the DMC theory provides a fully integrated account of a variety of cognitive control phenomena. Moreover, before turning to experimental findings, we first provide important theoretical background that motivated the development of this new theory.

A general theoretical model of working memory

In this section, we describe the overarching theoretical framework that guides our work (i.e., **Question #1**). Our theoretical model attempts to specify critical WM

components in terms of underlying neurobiologically-based computational mechanisms (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver & Cohen, 2000; O'Reilly, Braver, & Cohen, 1999) (see **Figure 1** for schematic of model). The central hypothesis is that the core of WM is controlled processing: the ability to flexibly adapt behavior to particular task demands, favoring the processing of task-relevant information over competing sources of information and emphasizing goal-compatible behavior over habitual or otherwise dominant responses. This definition is fairly similar to others that have been put forth in the literature (e.g., Duncan, Emslie, Williams, Johnson, & Freer, 1996; Norman & Shallice, 1986), and in this volume (e.g., Kane et al., Munakata et al.). We suggest that controlled processing is an emergent phenomenon, arising from dynamic interactions between specialized processing subsystems in the brain. Considering each subsystem in isolation cannot fully account for any of the mechanistic properties of WM functionality. Nevertheless, we argue that a number of core brain systems play critical roles in WM function due to their specialized computational properties. A central feature of our theoretical framework is that these specializations arise in neural tissue as a means of optimizing a fundamental computational tradeoff. The interaction between these specialized systems enables a kind of global constraint satisfaction process to occur, whereby maximal flexibility is ensured across the entire range of information processing situations.

Insert Figure 1

In particular, we suggest that the prefrontal cortex (PFC) is an especially influential structure in WM due to its extensive connectivity with other brain regions and

specialized processing capabilities. As discussed in much greater detail below, the PFC is hypothesized to play a central role in the *active maintenance* of internally represented context information, allowing it to *bias* processing in other neural systems in accordance with this maintained information (e.g., goals, instructions, intermediate products of mental computation). The PFC is aided in this function by its interactive connectivity with the hippocampus/medial temporal lobe complex (MTL), the midbrain dopamine (DA) system and the anterior cingulate cortex (ACC). The MTL complex augments PFC functions through rapid, associative *binding* of active representations throughout the brain, which can then serve as an auxiliary form of storage in WM tasks (O'Reilly et al., 1999; a similar type of mechanism is described in the Oberauer et al. chapter). The DA system is postulated to regulate the contents of PFC via a *dynamic updating* mechanism sensitive to reinforcement contingencies (Braver & Cohen, 2000). The ACC is postulated to modulate the general responsiveness of PFC through a *performance monitoring* mechanism that continuously indexes the need for top-down control via a computation of on-going processing conflict (Botvinick et al., 2001). The PFC also interacts extensively with posterior brain systems, which store domain-specific content knowledge. The content-specific computational specializations within posterior cortex may contribute to domain-specific components of WM, such as the storage of sequential order information associated with verbal WM, and the storage of configural and/or movement-based representations associated with visuo-spatial WM.

The prefrontal cortex and proactive cognitive control

Our research has primarily focused on understanding the role of the prefrontal cortex (PFC) in cognitive control and WM. There is general agreement that PFC plays a

critical role in control functions, but much less agreement concerning the particular computational and neural mechanisms that enable it to play such a role. A great deal of data regarding PFC function has come from single-cell recording studies in non-human primates during simple WM tasks, such as the delayed-response paradigm. In these studies, a highly reliable finding is that PFC neurons (particularly in dorsolateral regions of PFC) show elevated and sustained activity during the retention interval (Fuster, 1997). This pattern of activity, along with related results, has been taken as evidence that PFC subserves storage functions in WM. Human neuroimaging data has provided some support for this notion, showing sustained lateral PFC responses during WM maintenance periods (Cohen et al., 1997). However, a growing trend within the neuroimaging literature has been to emphasize PFC involvement in cognitive control rather than WM *per se* (E. E. Smith & Jonides, 1999). Indeed, a number of imaging studies have suggested that WM tasks involving simple storage may not engage PFC at all, or at least not the dorsolateral regions targeted in primate neurophysiology studies (e.g., Postle, Berger, & D'Esposito, 1999). Yet at the same time, there is no clear consensus as to what are the specific control functions that engage PFC.

Our own work has been guided by the hypothesis that PFC is central to cognitive control and WM because it is specialized to enable the representation and active maintenance of *context* information. Context is defined as task-relevant information that is internally represented in such a form that it can bias processing in the pathways responsible for task performance. Representations of context are similar to the goal representations of other theoretical formulations (e.g., Norman & Shallice, 1986), but are

flexible enough to influence not only action systems but also perception, attention, memory, and emotion. Likewise, some context representations should be considered micro-goals, in that they operate over short time-scales or act to bias a narrow range of target representations.

Representations of context are particularly important in situations when there is strong competition for response selection. These situations may arise when the appropriate response is relatively infrequent (such as the color name in the Stroop task). Because context representations are maintained on-line, in an active state, they are continually available to influence processing. Consequently, context can be thought of as one component of WM. Specifically, context can be viewed as the subset of representations within WM that govern how other representations are used. In this manner, context representations simultaneously subserve both mnemonic and control functions. This aspect of the model differentiates it from standard models of WM (e.g., Baddeley, 1986), which postulate a strict separation of representations for storage versus control.

An important component of our account of PFC function concerns the interaction between PFC and the DA neurotransmitter system, which projects strongly to this region of the brain. We suggest that active maintenance of context within PFC occurs via local recurrent connectivity, resulting in a stable, self-sustaining pattern of neural activity (i.e., an attractor, in computational terms). The DA system is postulated to regulate active maintenance within PFC, by gating the entrance of information into PFC, such that only task-relevant context will be actively maintained. We claim that this regulatory action occurs in response to phasic bursts of DA release within PFC, which produce a

neuromodulatory effect on PFC neurons, enabling them to update and actively maintain afferent inputs arriving from other brain regions. Without such a synchronous burst of DA activity at the time of external inputs, they will only be transiently represented within PFC, decaying shortly after the external input stops. For this reason, actively maintained representations of task-relevant context in PFC will be relatively robust to interference from task-irrelevant inputs.

Importantly, the DA system is postulated to also play a critical role in learning based on predictions of expected reward (i.e., reinforcement-based learning; Schultz, Dayan, & Montague, 1997). Because of this learning role, the DA system can self-organize to develop the appropriate timing of gating signals to enable the appropriate updating and maintenance of relevant context. As such, the system is not a “homunculus”, in that it uses simple principles of learning to dynamically configure and adaptively regulate its own behavior. Moreover, our hypotheses regarding the functional roles of PFC and DA and their interaction have been studied within implemented computational models (e.g., Braver & Cohen, 2000).

For example, we have developed a model of PFC function in a simple delayed response paradigm known as the AX-CPT, in which contextual cues must be actively maintained over a retention interval to bias processing to a subsequent probe item. A key aspect of the task is that in some trial conditions (termed “BX”), the contextual information must be used to inhibit a dominant response tendency, whereas in other trials (termed “AY”) context serves an attentional biasing function. In our computational model of the AX-CPT, the representation and maintenance of the context provided by the cue is postulated to occur within PFC. The DA system regulates the

access of this context information to PFC, such that context can be appropriately updated on a trial-by-trial basis and sustained over the delay without interference. In a systematic series of simulation and empirical studies (Braver, Cohen, & Barch, 2002), we demonstrated that the model can account for a wide range of behavioral and brain imaging data in both healthy young adults and different WM-impaired populations (aging and schizophrenia). Thus, the model appears to provide a good description of the control and WM mechanisms that might underlie AX-CPT performance, their relationship to PFC and DA function, and the consequences of their breakdown.

The simulation studies with the AX-CPT suggest some of the specific mechanistic properties of cognitive control. In particular, the simulations suggest that successful WM performance is achieved via a proactive strategy of actively maintaining contextual information provided by the cue within PFC regions, such that this information can appropriately prepare the system to respond most effectively to subsequent events. Thus, context-maintenance can drive attentional expectancies for perceptual inputs and prime predicted responses. More generally, our model has implications for how control can be effectively achieved in many cognitive tasks: by actively maintaining representations in PFC that can serve as a source of top-down bias on pathways that are directly involved in task performance. We suggest that this bias influences a number of dimensions of information processing: enhancing perceptual fluency, orienting attention, configuring response selection parameters, structuring action sequencing systems, and coordinating the operation of domain-specific storage buffers. Critically, in situations where the upcoming need for cognitive control is signaled by a pre-occurring contextual cue, the suggestion is that this contextual information must be

successfully encoded into PFC, and actively sustained over the intervening delay for control to be achieved. Based on our model of DA-PFC interactions, we further hypothesize that such encoding and sustained maintenance depends on a specific pattern of DA system activity. Specifically, at the time of cue presentation there must be a strong phasic burst of DA activity to enable this information to appropriately engage PFC. In contrast, during the delay interval, tonic DA activity levels must be relatively low, to ensure that this information is appropriately sustained without interference or decay.

The DMC account

Our previous theory and modeling work focused exclusively on how proactive cognitive control might be implemented, and the benefits accrued by such a control mechanism. Our current account of cognitive control substantially refines this earlier view, by suggesting a dual-process framework, that we term the DMC account. Specifically, the DMC account suggests that cognitive control may not only be achieved by proactive mechanisms but also through *reactive* mechanisms. Importantly, we believe that the DMC account provides important new insight into WM and cognitive control by elucidating the intrinsic variability that is at the core of this domain. In other words, the DMC account is primarily an account of why there is variation within WM and cognitive control (i.e., **Question #2**). Moreover, as we develop further below, the DMC account provides a coherent explanation as to how many types of empirically observed sources of variation in WM function – task or situational factors, neural dysfunction, cognitive individual differences or even non-cognitive (i.e., affective and personality) variables – might relate to the distinction between proactive and reactive control. In this section, we describe the DMC account in detail, focusing on how reactive control can be

distinguished from proactive control and the relationship between these two mechanisms. The critical distinctions between proactive and reactive control are summarized in Table 1.

Insert Table 1

What is reactive control? As the name suggests, reactive control is engaged after, rather than before the occurrence of some imperative event. Prior to this event, the system remains relatively unbiased, and so is therefore more influenced by bottom-up inputs. Furthermore, reactive control mechanisms are engaged only as needed, on a "just-in-time" basis rather than consistently and in advance of critical events. Finally, when control depends upon the use of context information, the activation of such information by reactive mechanisms occurs transiently rather than in a sustained fashion, and thus decays away quickly. As a consequence, in situations when the same context must be repeatedly accessed, this must occur through full re-activation of the information each time it is needed.

The distinction between proactive and reactive control can be thought of as a distinction between early selection and late correction (Jacoby, Kelley, & McElree, 1999). Concrete examples can help illustrate the proactive-reactive distinction. A real-world example might be the typical prospective memory situation in which an intention is formed about a behavioral goal to be completed at some later point, such as stopping at the dry cleaners after work. A proactive control strategy would require the goal information to be actively sustained from the time the intention is formed until the goal is

satisfied (e.g., the end of the day). The usefulness of such a proactive strategy is that plans and behaviors can be continually adjusted to facilitate optimal completion of the goal (e.g., not scheduling a late meeting). In contrast, with a reactive control strategy the goal would only be transiently activated at the time of intention, and then need to be re-activated again by an appropriate trigger event (e.g., opening the car door). Because of this need for repeated re-activation, there is greater dependence on the trigger events themselves, since if these are insufficiently salient or discriminative they will not drive re-activation (e.g., the dry cleaning errand might only be remembered because of cleaning ticket left on the car seat).

The AX-CPT task, described above, provides another example. A proactive control strategy would result in a context representation being activated by the cue stimulus, and maintained at full strength over the intervening delay prior to the probe. During this delay, cognitive control would be achieved by priming the perceptual and response systems in accordance with cue-driven attentional expectancies. In contrast, a reactive control strategy would result in context information being only transiently represented following the cue. During the delay between cue and probe, context activation, and as a result, response-related priming, would be minimal. Upon presentation of the probe, context would need to be re-activated via retrieval. Once contextual representations reached full activation strength they could be used to overcome interference that had occurred in the interim, due to probe-related biases. Thus, in the AX-CPT, proactive control means control engaged by the cue, whereas reactive control means control driven by the probe.

The hypothesized distinction between proactive and reactive control extends to

neural mechanisms. In particular, we have suggested above that proactive control requires context representations to be sustained over extended periods, whereas in reactive control the representation of context occurs only transiently, as needed. Our theory assumes that the representation and active maintenance of context occurs in PFC, and most specifically in lateral (rather than medial) PFC regions. Thus, when proactive control is engaged, sustained activity should be found in these PFC regions during the interval between the initial presentation of context and the point at which it is used. Under proactive control conditions, PFC activity should be present reliably across events, and not just on those in which it is most needed. In contrast, under conditions of reactive control, PFC activity will be: 1) transient rather than sustained; 2) present only for those events that directly require the reactivation of context to mediate appropriate performance; and 3) activated after rather than before the onset of an imperative stimulus. Additionally, the two control mechanisms should differ in terms of the involvement of the DA system. We have suggested that the ability to sustain inputs in PFC requires a phasic DA-mediated gating signal occurring at the time of context presentation. Without such a gating signal, PFC can only be transiently activated. Thus, our hypothesis is that under conditions of proactive control, presentation of contextual input is accompanied by a phasic change in DA, whereas under reactive conditions there is no DA-mediated gating signal. In the absence of DA gating, PFC can only be transiently activated, and only in situations where there is a strong enough association between the context representation and the triggering stimulus to produce spreading activation.

Under reactive conditions, we would also expect that other brain systems in addition to PFC would be more strongly involved in mediating performance. For

example, if reactive control can be achieved through the activation of long-term memory traces or through retrieval of episodic information, then we would expect to see engagement of either posterior cortical regions or the hippocampal / medial temporal lobe complex. Another brain system that might be critical for reactive control is the ACC. A currently influential account of ACC function postulates that this brain region indexes the demand for cognitive control by detecting the presence of response conflict due to either interference, weak response strength, or the activation of an erroneous response (Botvinick et al., 2001). Critically, conflict-related ACC signals are postulated to modulate activation in lateral PFC regions which can implement an increase in top-down control to resolve such conflict. Thus, the conflict signal in ACC might be used to increase the tendency to use proactive control on subsequent trials, as has been postulated by current theory (Botvinick et al., 2001). However, it might also be the case that the ACC serves as a core component of reactive control processing, by rapidly signaling the need for increased control on the current trial, to resolve interference, increase response strength, or correct an impending error. In preliminary computational modelling work, we have been exploring the hypothesis that the ACC may serve a dual role in proactive and reactive control through outputs to different PFC systems (DePisapia & Braver, 2004).

Costs and benefits of proactive and reactive control

We have just described some of the functional and neural characteristics that distinguish reactive from proactive control. Yet an obvious question is why postulate such a dual-process account at all, given the virtues of parsimony and the wisdom of Occam's Razor? This question can best be answered by considering that there may be

both costs and benefits associated with proactive and reactive control, such that a computational tradeoff exists. By utilizing both mechanisms to varying degrees through a dual-process control architecture, the cognitive system is best able to overcome these tradeoffs, and in so doing optimize behavioral performance across a wide range of environments and task demands. Indeed, this type of dual-process architecture, involving a mixture of proactive and reactive control mechanisms, is one that tends to be present in many existing computer systems. Specifically, most computer operating systems tend to operate with a standard top-down flow of control driven by a stored program (i.e., proactive control), but with a separate built-in mechanism to deal with interrupts (i.e., reactive control). Likewise, general purpose symbolic computational cognitive architectures, like SOAR (Newell, 1990), frequently operate in two distinct control modes --- one in which problem spaces are traversed according to the dictates of a pre-existing goal stack (similar to proactive control), and a second mode that initiates to resolve unexpected impasses or conflicts (similar to reactive control). Thus, on purely computational grounds it is sensible to argue that a dual-process or mixture model mechanism of control is one that serves to optimize information processing. Nevertheless, it is important to consider these computational tradeoffs between proactive and reactive control more explicitly, since they provide insights into the factors that should affect which control mode is dominant in specific situations and for specific individuals.

Below, we list some of the limitations and disadvantages of proactive control, followed by the negative consequences of reactive control:

- *Proactive control requires the presence of predictive contextual cues.*

Many times predictive contextual information is not present in the environment, and as such, control can not be prepared in advance. In these circumstances, the only possible control strategy is a reactive one.

- *Proactive control requires predictive contextual cues to be highly reliable.*

In situations where predictive cues turn out to be invalid, there can be a strong cost if the cue-based contextual information is used as a basis for proactive control. Such cue invalidity costs can be seen in a range of cognitive situations (e.g., the Posner spatial cued reaction time task, Posner, Snyder, & Davidson, 1980). Thus, adoption of a proactive control strategy is only likely in situations where contextual cues serve as highly reliable predictors of upcoming events or required actions.

- *Proactive control is metabolically costly.*

According to our theoretical model, the active maintenance of goal-relevant information requires a high and sustained level of neuronal activity in lateral PFC during the entire retention interval. Such extended periods of high firing are likely to require additional metabolic resources (e.g., for glucose consumption, waste removal, neurotransmitter recycling, etc.) that may not always be available, or at the minimum, reduce the amount available for other purposes. Even without considering metabolic requirements directly, it seems clear that proactive control is capacity demanding, since only a small number of goals can be actively maintained in the focus of attention (Cowan, 2001). Thus, proactive control draws away resources from other active maintenance demands. Consequently, it is likely to only be used if sufficient capacity is

available (i.e., other WM demands are low, general cognitive resources are high, and cortical arousal is optimal).

- *Proactive control is prohibitive with very long retention intervals.*

Because the sustained, active context maintenance associated with proactive control is so resource-demanding, the longer the interval between the maintenance initiation and context utilization, the less feasible this strategy becomes. Thus, proactive control is unlikely with retention intervals longer than a few minutes. Certain prospective memory tasks are the best example of situations in which the interval between goal formation and goal realization can be hours or days. In such situations, actions are accomplished through reactive control – that is, by transiently re-activating the goal (via episodic retrieval) at the appearance of an appropriate trigger stimulus such that it can bias the goal-relevant behavior. This idea is consistent with the bulk of the prospective memory literature, which has suggested that retrospective processes are the primary mechanisms guiding delayed-intention behavior (Einstein & McDaniel, 1996). Nevertheless, recent studies have begun to suggest that in certain experimental prospective memory paradigms, preparatory control may be occurring, even across longer time-scales of retention (R. E. Smith, 2003). It will be important to determine more conclusively whether, and under what constraints, active maintenance processes are being used in such paradigms.

- *Proactive control is less sensitive to changes in reward/punishment contingencies.*

Because environments are typically non-stationary, contingencies can often change without warning. The active representation of goals during proactive

control modes causes the system to be biased to attend primarily to goal-relevant features of the environment, and to be predisposed to interact with these features in a goal-driven manner. This leads to a reduction in incidental encoding of goal-irrelevant or goal-incongruent features, which may, in fact, serve as cues that the environment is changing. Theorists have suggested that continuous monitoring of environmental (or internal) background information is a critical function of motivationally-oriented neural systems. For example, such mechanisms can lead to optimal detection of low-probability but potential threats (Goschke, 2003). Thus, high-demands or a pre-existing bias for background monitoring (such as when vigilance towards potential threats is required) will make the utilization of proactive control less likely.

- *Proactive control impedes the natural progression towards automatization.*

There is a fundamental tension between the exertion of cognitive control and the development of automaticity, which has been termed the “control dilemma” (Goschke, 2003). Because automatic processes are robust, fast and efficient, it is likely that there is an inherent computational pressure or bias on the cognitive system to automatize processing wherever possible, via strengthening of internal associations and stimulus-response bindings. Proactive control processes oppose such mechanisms by providing a sustained top-down flow of information that enables contextual goals to override default processing. Indeed, it is reactive rather proactive control that allows for the best optimization of the control dilemma, by introducing a highly transient and minimalist (i.e., only-as-needed) form of intervention, that allows habits,

skills, and procedures to be learned while still enabling the system to override these forces if necessary.

- *Reactive control is more susceptible to proactive interference (PI)*

Control mechanisms are necessary because many times the effects of past experience conflict with current goals. However, such sources of proactive interference (PI) cannot be completely counteracted by a reactive control strategy. This is because reactive control is initiated by post-stimulus processing, such that potentially interfering stimulus-based associations will already be activated by the time control mechanisms are engaged. In contrast, proactive control may lead to complete suppression of PI, via optimal attentional configuration. Thus, in conditions where PI effects are very strong and the costs of interference are high, the disadvantages of reactive control will be most apparent.

- *Reactive control is sub-optimal when stimulus-driven processing is insufficient.*

Because reactive control is stimulus-driven rather than preparatory, it is always a sub-optimal control strategy. However, the limitations of reactive control are most prominent in conditions where perceptual information is weak, response selection parameters are underdetermined, and/or when there is a premium on optimal performance (i.e., high speed and accuracy constraints).

- *Reactive control does not maximize rewards*

Maximizing reward often depends upon the ability to predict its occurrence and magnitude. Proactive control aids in maximizing rewards through the utilization of predictive contextual cues that can bias action selection. The

strong link between proactive control and reward prediction can be seen in the phasic DA signals that are postulated to engage proactive control processes in PFC, according to the DMC account, and also appear to signal reward-related salience of predictive cues, according to influential reinforcement learning models (Schultz et al., 1997). In contrast, reactive control is not geared toward maximization of rewards but rather towards resolving interference and facilitating the transition to automaticity. Thus, in conditions where processing is oriented towards reward maximization, and where reward attainment depends on precise focusing of attention or optimal response preparation, a reactive control strategy will be highly disadvantageous.

As the foregoing indicates, there are a number of advantages and limitations associated with both reactive and proactive control. This suggests that successful cognition depends upon some mixture of both proactive and reactive control strategies. Indeed, it may be the case that the two systems are fully independent, and thus may be both engaged simultaneously. Nevertheless, there is likely to be some bias favoring one type of control strategy over the other. It is our hypothesis that a default mode for the cognitive system is one favoring reactive control, given its greater applicability (i.e., utilization in more situations), lower demands on metabolic resources, and maximal compatibility with the development of automatization. However, other factors may be present that exert pressures on the system to engage in proactive control. These factors can be characteristics of the task situation, but may also be characteristics of the individual. Indeed, we believe that the DMC account provides a unifying

framework for understanding both intra-individual and inter-individual variability in normal WM function in terms of shifting biases toward proactive vs. reactive control. Likewise, because of the putative dependence of proactive control on specific neural mechanisms (e.g., DA interactions in lateral PFC), the DMC framework also provides a coherent explanation as to why specific populations suffering from breakdown or dysfunction in these neural systems might also lead to specific changes in WM and cognitive control function. Finally, the DMC account suggests that there should be an important role for “non-cognitive” factors in producing WM variation. This is due to the role played by constructs such as reward prediction and background threat monitoring in altering the balance between proactive and reactive control. These constructs are likely to be impacted by related state (e.g., mood) and trait (e.g., personality) variables.

In the sections that follow, we elaborate each of these points in turn, discussing how the DMC account makes specific predictions regarding different sources of variability on WM and cognitive control function: a) within-individual variation; b) cognitive individual differences; c) neural dysfunction; and d) non-cognitive factors. Moreover, we describe results of recent studies designed to provide empirical support for each of these components of the DMC account.

Within-individual variation

A central assumption of the DMC framework is that a change in situational factors will result in alteration of the weighting between proactive and reactive control strategies. These situational factors include: 1) the availability and reliability of predictive

information; 2) length of time to engage in preparation; 3) demands on speed/accuracy; 4) length of retention interval; 5) strength of habit or response biases; 6) expectation of proactive interference; 7) arousal level; 8) motivational focus (reward vs. punishment); 9) expected WM load and 10) available capacity. Changes in any or all of these factors are thus predicted to produce a change in cognitive control strategy. Thus, the DMC account naturally leads to the idea that there will be considerable variability in the control strategies employed by healthy individuals across different task situations. Indeed, it is possible that potentially subtle differences between otherwise similar tasks might lead to large changes in an individual's preferred cognitive control strategy. These control mode differences would be expected to result in shifts in both behavioral performance characteristics and in brain activation profiles. In recent work, we have examined this aspect of the DMC account, by directly manipulating factors expected to influence cognitive control strategy during the performance of WM (and other cognitive) tasks. These experiments were all conducted using a within-participants design, to determine whether we could observe intra-individual variation in cognitive control processes.

In one such study (Speer, Jacoby, & Braver, 2003), we examined whether WM load – in terms of number of items to be simultaneously maintained over a delay – would impact the utilization of proactive vs. reactive control during performance of a classic WM task: Sternberg item recognition (Sternberg, 1966). The key aspect of this study was that we were interested not in the direct effect of memory load manipulations, which has well established effects on performance (Sternberg, 1966) and brain activity (Grasby et al., 1994), but rather in the effect of *expected* memory load. Thus, we investigated

whether participants' expectations regarding how many items they would have to maintain influenced the control processes they used to perform the task, irrespective of the actual number of items they were to maintain on a given trial. This manipulation of expectancy was achieved by having participants perform task blocks in which memory set size varied randomly from trial-to-trial. However, in one block of trials the average memory load was low (~3 items), while in another the average load was high (~8 items). Critically, however, there was a subset of trials (25%) in each block that were exactly equivalent in memory load (6 items). The analysis focused exclusively on comparing performance and brain activity dynamics (through the use of event-related fMRI) on these load-matched trials.

The reason for examining load expectancy rather than the load effect itself is that the DMC account suggests that a critical source of variation in WM tasks is not the representations used for short-term storage per se (which involve domain-specific mechanisms such as the phonological loop, and which should be affected directly by WM load), but rather how such representations are utilized and controlled to bias response selection. Specifically, we hypothesize that proactive control in a task such as the Sternberg translates into whether, *during the delay period*, items stored in short-term memory get represented in a form that is useful for rapid target decisions -- i.e., a goal-based representational code that might take something of the form: "if probe is X (or Y or Z) make target response, otherwise make nontarget response". Such goal-based proactive representations are postulated to be present within lateral PFC. Conversely, reactive control processes would ensure that probe information, *once presented*, could be represented in a form that could drive a successful matching (e.g., familiarity evaluation)

or retrieval operation (e.g., episodic search) with memory set items. Importantly, such reactive control processes would also be facilitated by having memory set items stored in a highly activated and accessible trace. Thus, the proactive-reactive distinction reflects both a distinction in the types of control processes that engage with short-term memory representations to bias response decisions, and also a distinction in the timecourse of activation for these control processes.

Our specific hypothesis was that the utilization of a proactive control strategy in the Sternberg task would be most likely under conditions of low WM load. With only a few items to be maintained, it should be easier to activate a goal-based representation of memory set items during the delay period and begin to use such a representation to bias target detection processes. Conversely, under high load conditions, this type of control strategy would be more difficult and thus less likely activated. Thus, a reactive control strategy would likely be preferred. However, our key prediction was that the preferential engagement of proactive vs. reactive control would be truly strategic, and thus, tied primarily to expectations of what would be most successful, rather than directly constrained by specific task conditions. Of course, it is important to note that the term “strategic” should not be taken to imply that such processes are necessarily consciously engaged by participants, since we are not at all convinced that consciousness has anything to do with the process. Instead, we use the term strategic to imply that the preferential engagement of one control process or the other is somewhat optional (i.e., variable), rather than fully constrained, but is likely tied to a (potentially implicit) evaluative process that attempts to optimize performance given the expected task conditions. Thus, the DMC account predicts that load-expectancy effects will impact

the engagement of control even on the 6-item trials with matched load.

The results of the study were just as predicted. Probe decisions on 6-item trials were both faster and more accurate in the low-load expectancy condition. This is consistent with the hypothesis that in the low-load condition probe decisions were based on a rapid target detection process associated with proactive control. However, in the high-load condition, it appeared as if probes were more deeply encoded (as assessed by a surprise delayed recognition test for nontarget probes), consistent with the hypothesis that the probes were used as retrospective retrieval or matching cues to achieve reactive control. More importantly, we observed a strong double dissociation in the pattern of activity dynamics within PFC (see **Figure 2**). First, in a number of medial and mid-lateral PFC regions, we observed that activity in the low-load condition tended to progressively increase throughout the memory set encoding and delay period of the 6-item trials. However, in the high-load condition the same 6-item trials, evoked an activity pattern of rapid increase at the beginning of the memory set encoding period, but no further increase (and, in fact, a tendency towards decreased activity) during the delay. In contrast, within a more anterior PFC region (an area that has previously been associated with episodic retrieval processes, e.g. Lepage, Ghaffar, Nyberg, & Tulving, 2000), activation was found to increase only during the period of probe judgment, and was significantly greater for 6-item trials in the high-load condition. These observed activity patterns are consistent with the hypothesis that the mid-lateral PFC regions reflect the engagement of proactive control processes that are increased in the low-load condition, while the anterior PFC is associated with a reactive control process that is preferentially engaged in the high-load condition.

Insert Figure 2

The central message of the Sternberg study is that a subtle task factor, such as the expected memory load, can dramatically influence both performance and brain activation during the performance of WM tasks. Indeed, the subtlety of the manipulation demonstrates that the cognitive control processes engaged to achieve successful performance might be highly variable even across very similar WM conditions. In particular, some WM conditions might be associated with a preferential engagement of proactive control, which would be reflected in sustained (or increasing) lateral PFC activity during retention periods, while other conditions might be associated with a stronger bias towards reactive control, which would be reflected in reduced retention-period activity in PFC, but potentially a greater probe-driven response in different brain regions (including other areas of PFC).

Significantly, these results have important implications for resolving some of the apparent inconsistencies and controversies in the recent neuroimaging literature investigating the role of PFC in WM task performance. The current controversy surrounds whether PFC, and specifically dorsolateral PFC, actually subserves active maintenance functions in WM, or whether it instead performs "executive" operations (i.e., manipulation, selection) on maintained items, but does not subservice maintenance itself (e.g., D'Esposito et al., 1998). Although there is quite a bit of evidence for the active maintenance view from both primate neurophysiological studies (Fuster, 1997), and human neuroimaging (Cohen et al., 1997), findings from some more recent studies have directly called into question the maintenance account. The strongest evidence comes

from fMRI studies using event-related designs that isolate PFC activity to different periods of a trial, in which the activation of PFC has been observed to be transient rather than sustained and most prominent during the encoding or response period rather than the maintenance interval (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000).

Our results suggest such cross-study differences in the dynamics of PFC activity might actually be due to cross-study differences in whether proactive vs. reactive control processes were preferred for task performance. Thus, the lack of sustained delay period activity in lateral PFC might reflect the presence of tasks or subtle task factors that encourage reactive rather than proactive control strategies on the part of participants. Indeed, undetected cross-study differences in the utilization of proactive vs. reactive control may constitute an uncontrolled source of variability that can confound clear interpretations of the results of WM studies.

Critically, the DMC account suggests that there are a number of task factors, in addition to expected WM load, that could lead to variability in the type of cognitive control strategy preferred across different task situations. Furthermore, we postulate that such condition-related variability in cognitive control may not only impact WM tasks, but also other cognitive domains that place a high demand on control processes. Indeed in other studies that we are currently conducting, we have observed substantial within-individual variation in proactive vs. reactive control associated with: interference expectancy in the Stroop task (T. S. Braver & Hoyer, submitted); trial-by-trial fluctuations during task-switching (T. S. Braver, Reynolds, & Donaldson, 2003); and motivational incentives in the AX-CPT (Locke & Braver, 2005). Such work will help to

provide a better foundation in which to design and interpret WM studies by taking into account potential sources of cognitive control variation.

Cognitive Individual Differences

An important factor that likely has an influence on the selection of control strategy is individual differences in cognitive abilities. We make this claim because many of the psychological factors that should influence cognitive control strategies are likely to vary in a stable manner across individuals. These include: available cognitive resources, arousal level, and motivational orientation. In terms of the effects of cognitive resources, we have suggested that engaging in proactive control is more resource-demanding than engaging in reactive control. Thus it is likely that individuals possessing greater cognitive resources will be the ones most willing and able to adopt a proactive mode. Indeed, there has now been a great deal of research suggesting that the construct of cognitive resources may index the same underlying mechanism indexed by the constructs of WM capacity and fluid intelligence (Kane & Engle, 2002). Individual differences in these constructs have been shown to have high validity in predicting performance on tasks that place a strong demand on proactive cognitive control (Duncan et al., 1996).

It is not yet clear how to directly translate these constructs into their underlying computational and neural mechanisms. Nevertheless, there is growing evidence that these constructs are closely linked to PFC function, which provides support for the idea that they have a relationship to proactive cognitive control (Duncan et al., 1996). In particular, we are highly influenced by the work of Kane, Engle and colleagues, who have suggested that the constructs of WM capacity and general fluid intelligence (gF)

jointly index the efficacy of PFC function, and in particular the ability to actively maintain goal-relevant information in the face of interference (Kane & Engle, 2002; see also Kane et al chapter). In our framework, high WM-span / high gF individuals should thus show an increased tendency to use proactive control strategies, but only in the task demands that most require, and benefit from, such strategies.

In a first test of this hypothesis, we examined the role of gF in predicting performance and brain activity in the well-known n-back WM paradigm (J. R. Gray, Chabris, & Braver, 2003). We found that gF was positively correlated with increased activation in lateral PFC and parietal cortex regions. Moreover, we found that this relationship was selective to trial conditions having the highest levels of interference (so-called “lure” nontargets, in which the current item is a repeat of a recent trial, but not the critical n-back trial). Most strikingly, we found that the increased PFC and parietal activation on high-interference trials statistically explained the facilitated performance that high gF individuals exhibited on these trials. Together these findings provide important new evidence that individual differences in gF are associated with individual differences in the ability to activate control processes in lateral PFC and parietal cortex that enable the successful management of interference. However, the Gray et al. (2003) n-back study provides only an indirect test of the DMC account. The DMC account predicts that gF-related individual differences should primarily reside in the ability to utilize proactive control processes. In particular, evidence of increased proactive control in high gF individuals should be reflected in increased and sustained lateral PFC activity prior to onset of a target event. It is difficult to test such a hypothesis within the context of the n-back task, since the task design involves a continuous WM load (i.e., active

maintenance is continuously required across each trial and inter-trial interval) . Thus, there is no clear way to distinguish between pre-target maintenance and preparation vs. post-target interference resolution.

To more directly test hypotheses based on the DMC account regarding individual differences in gF, we recently conducted a second study using the Sternberg paradigm instead of the n-back (Burgess & Braver, 2004). The Sternberg paradigm enjoys a conceptual advantage over the n-back, in that it enables the temporal decomposition of cognitive effects occurring at the time of the retrieval probe from those occurring during encoding or delay periods. We were interested in examining whether high gF individuals would show an increased tendency to utilize proactive control during Sternberg performance. Our specific hypothesis was that high gF individuals would preferentially engage proactive rather than reactive control mechanisms during WM performance under high interference conditions. To examine this hypothesis within the context of the Sternberg task, we utilized a version that has been recently popularized by Jonides and colleagues (Jonides, Badre, Curtis, Thompson-Schill, & Smith, 2002). In this “recent negative” Sternberg task, probes on some trials were “negative”, in that they were not present in the current trial memory set, but they were also “recent”, in that they were present in the memory set from the *previous* trial. These recent negative probes produce increased interference, since their high familiarity induces a bias to make an erroneous target response. As such, recent negative trials in the Sternberg task can be thought of as being formally similar to the high-interference lure trials in the n-back task. This is supported by a series of neuroimaging studies suggesting that recent negative trials are associated with increased activity in left lateral PFC (Jonides et al., 2002). Consequently,

a straight-forward prediction, based on the Gray et al. (2003) results and the general framework of Kane, Engle and colleagues (Kane & Engle, 2002), is that high gF individuals would show an increased ability to manage recent negative interference. Moreover, these gF effects in performance should be associated with increased activation in lateral PFC. However, a more specific prediction of the DMC account is that individual differences in gF would be selectively associated with an increased ability to utilize proactive control mechanisms to prevent the adverse effects of interference.

An additional critical aspect of the DMC account is that the tendency to use proactive control will primarily emerge under conditions in which interference effects are not only large and costly (in terms of performance), but also when they can be reasonably anticipated. Thus, a second prediction of the theory that we tested is that the relationship between gF and proactive control would be most apparent under conditions where interference effects are frequent and expected. To test these predictions of the DMC theory, we had participants perform two different conditions of the recent negative Sternberg task. In the *low interference expectancy* condition, recent negative trials occurred infrequently (20% of negative probe trials), resulting in a lower occurrence of interference. In addition, 80% of “positive” probes (i.e., probes that were present in the current trial memory set) were also “recent” (part of the memory set during the previous trial). For positive probes, the increased familiarity due to recency of previous exposure can be used to facilitate correct responding. We expected that these two factors together would lead to an increased tendency to use reactive rather than proactive control mechanisms to manage interference. Alternatively, in the *high interference expectancy* condition, the context was changed, so that recent negative trials occurred frequently

(80% of negative probes), while recent positive trials occurred infrequently (20% of positive probes). In this condition, the tendency for familiarity (due to recency) to be incompatible with the correct response should encourage a proactive strategy aimed to resist the impact of recency. In both conditions, the positive and negative probes that were not “recent” were instead “novel”, in that they had not been present in any memory sets from previous trials.

We conducted both a behavioral (N=41) and neuroimaging study (N=19) of the recent negative Sternberg task (memory sets in both studies were 5 English words, presented simultaneously on a visual display) with both high and low gF individuals (as measured by performance on the Ravens Advanced Progressive Matrices test, a standard experimental test of gF). Across both studies we found that high gF individuals showed a reduced interference effect compared to the low gF individuals (in terms of accuracy and/or RT), but that the reduction occurred selectively on the high interference expectancy condition (behavioral study: high expectancy gF – RT correlation, $r(39) = -.36$, $p < .05$, low expectancy gF-RT correlation, $r(39) = .18$, $p > .1$; neuroimaging study: accuracy gF x condition interaction, $F(1,17) = 6.9$, $p < .05$). In the neuroimaging study, we further were able to analyze the temporal dynamics of brain activity within PFC and other regions using event-related fMRI. These analyses suggested that in the left lateral PFC, significantly increased activation in high gF individuals (relative to low gF individuals) was observed during the memory retention interval, but only in the high interference expectancy condition, and not in the low interference expectancy condition (see **Figure 3**). Thus, we observed a significant gF x task condition interaction $F(1,17) = 7.2$, $p < .05$. This elevated activity for high gF individuals was found across all task

trials in the high interference expectancy condition (i.e., recent and novel negatives, and recent and novel positives). These findings support the increased utilization of proactive control mechanisms by high gF individuals in the high expectancy condition, since this type of mechanism would be engaged across all trials in advance of the probe. In other words, the utilization of proactive control mechanisms should not depend upon whether interference is *present* on any individual trial, but instead should depend upon whether *interference is likely* across trials.

Insert Figure 3

In addition, however, we also examined activation that occurred at the time of the probe and showed direct sensitivity to recent negative trials. Our motivation for examining this aspect of the data stemmed from the prior neuroimaging literature. In previous studies, Jonides and colleagues found that left ventrolateral PFC (VLPFC) regions are selectively activated by recent negative trials in the Sternberg task, suggesting that this region is recruited to successfully resolve interference. Moreover, using event-related fMRI, D'Esposito and colleagues determined that the increased recent-negative activity in left VLPFC occurred at the time of probe onset (D'Esposito, Postle, Jonides, & Smith, 1999). Such an effect suggests that the left VLPFC activity indicates the presence of a reactive control process that is mobilized following the detection of interference to help resolve potential processing conflict. This is supported by the finding that older adults show increased behavioral interference on recent negative trials, accompanied by decreased left VLPFC activity (Jonides et al., 2002)

Based on the results of this previous literature, one might expect that it would be effective reactive control rather than proactive control that should be most strongly associated with successful interference management on recent negative trials. However, our results did not provide strong support for that hypothesis. When collapsing across conditions and gF, we did find increased activation in left VLPFC on recent negative trials (relative to novel negatives) at the time of the probe ($F(1,17) = 8.2, p < .05$). However, we did not observe the recent negative activation to be reliably greater for high gF individuals. In fact, in a left VLPFC region very near to that observed show control effects, recent negative activity actually tended to be lower in high gF individuals during the high expectancy condition (albeit non-significantly; gF x recency: $F(1,17) = 1.65, p > .1$; see **Figure 3**). At first blush, this finding is somewhat surprising, since the high interference expectancy condition is associated with reduced interference effects in the high gF individuals. However, the results are consistent with the DMC account, which suggests that high gF individuals shifted from a primarily reactive to a primarily proactive control strategy in the high interference expectancy condition. Since proactive control is thought to be a more effective strategy for preventing interference, a switch towards such mechanisms would improve performance selectively in the high gF group, while simultaneously reducing the need to engage reactive control mechanisms. Thus, the results of this study, like our other work, provide a clear and coherent interpretation of what might otherwise be counter-intuitive results regarding the role of PFC and individual differences in mediating performance on tasks placing high demands on cognitive control processes. In future studies, it would be useful to determine whether

the DMC account could also explain the effects of related individual difference constructs on WM and cognitive control (e.g., WM span).

Neural Dysfunction

The previous section discussed situational factors that are likely to influence control biases in healthy young adults. However, another important factor that will affect control strategy is the structural integrity of the neural systems supporting each mechanism. If one system is dysfunctional, there will be a strong bias towards adopting the other, intact control mode. Our theoretical framework suggests that the proactive control system will be most vulnerable to disruption, given its dependence on precise dynamics (i.e., sustained activation of PFC representations, strong phasic DA response to contextual cues, moderate tonic DA activity). In fact, the available evidence suggests that many neuropsychiatric disorders involving cognitive control impairment – such as schizophrenia, Parkinson’s Disease, and ADHD – are also associated with dysfunction in PFC and/or DA systems (Arnsten & Robbins, 2002). Consequently, our theory predicts that these populations will show primary impairments in the use of proactive strategies. Importantly, in some cases, it may be that the control impairment is completely selective, such that the reactive control system is intact. A population that likely fits this scenario is healthy older adults. The evidence is accumulating that healthy aging is associated with declines in both PFC and DA function and with impairments in cognitive control (T. S. Braver et al., 2001). However, given that healthy aging is by definition non-pathological, it is likely the case that these biological changes are relatively mild (at least in relation to clinical populations suffering dysfunction in the same systems).

From a theory-testing and validation perspective it would be ideal if there were

evidence that other clinical populations showed evidence of the reverse form of impairment – intact proactive control, but impaired reactive control. However, this pure double dissociation may be unlikely given the argument that proactive control processes are the ones most vulnerable to disruption by brain dysfunction. Nevertheless, it may be the case that there are certain populations that show an over-reliance on proactive control, even under conditions that should normally favor reactive strategies. Although purely speculative at this point, one population that may fit this description is patients suffering from obsessive-compulsive disorder, or OCD. In particular, some theorists have suggested that OCD can be characterized as “hyper-activation” of the executive control system (Tallis, 1995). Further work will be needed to investigate this idea more directly.

In our own prior work, we have examined changes in cognitive control strategy in healthy older adults. This work has demonstrated that older adults show a reduced tendency to engage in proactive control, but still show the ability to effectively engage reactive control mechanisms. Specifically, in two studies with the AX-CPT task, older adults displayed a relative impairment on inhibitory (BX) trials, in terms of disproportionately slowed responding, yet nevertheless showed only a slight increase in error rate in this condition (T. S. Braver et al., 2001). The fact that older adults did not make many inhibitory errors suggests that they are able to appropriately represent context. However, the greatly increased reaction time interference on these trials suggests that context representation occurred in a reactive rather than a proactive fashion. That is, we hypothesize that under conditions where control is engaged reactively, context information is not represented prior to probe onset, and instead must be re-activated

following the appearance of the probe. The context activation process must happen quickly when it occurs reactively, so that it can suppress the priming effect of the probe before an error is committed. However, even in this case it is still likely that slowing of performance will occur, since during the time of context re-activation the probe has an opportunity to prime inappropriate response pathways. The low error rates but high interference in older adults indicates that they were able to achieve control, but that such control may have necessitated a more intense engagement of reactive control mechanisms on inhibitory trials (relative to the intensity needed for proactive control). In other words, it is likely that, due to their increased dependence on reactive control mechanisms, older adults had to exert compensatory effort in order to achieve successful inhibition.

This suggestion is consistent with recent observations from neuroimaging studies. In these studies, older adults have been found to show increases as well as decreases in brain activation during performance of difficult cognitive control tasks (Cabeza, 2001). Our hypothesis suggests that a shift from proactive to reactive control would result in both the activation of brain regions that are not typically activated in young adults (i.e., those subserving reactive control) and in a different pattern of activity dynamics in regions that were activated by young adults (i.e., greater activation in conditions most dependent on control, reduced activity in conditions with lower control demands).

In a recently completed neuroimaging study with the AX-CPT, we found evidence supporting the hypothesis that older adults showed increased neural activity in conditions low in control demands, but decreased activity in the conditions associated with proactive control (Barch, Racine, & Braver, submitted). In this study, 20 older

(range: 66-83; mean age= 73) and 21 younger adults (range: 18-31; mean age=23), performed the AX-CPT under both short (1s) and long (7.5s) delay conditions (with total trial duration held constant across conditions at 10s). The delay manipulation (which was blocked) enabled the isolation of brain regions involved in actively maintaining cue information, since the only variable manipulated was the proportion of the trial in which the delay occurred. In addition, task blocks alternated with control (fixation) blocks, which allowed the identification of regions generically (i.e., non-specifically) activated by task performance. We predicted that older adults would show decreased delay-related activity in dorsolateral PFC, indicating a reduction in proactive control, while at the same time showing generalized (i.e., brain-wide) increases in task-related activation, indicating greater activation of reactive control processes.

The results confirmed the predictions (see **Figure 4**). Younger adults showed a significant delay-related increase in left dorsolateral PFC activity ($F(1,20) = 27.3$, $p < .001$) located in area that exactly replicated previous studies (Braver et al., 2002). In contrast, older adults actually showed a delay-related *decrease* in the activity of this region, producing a significant age x delay interaction ($F(1,39)=5.4$, $p < .05$). Interestingly, the interaction was of the cross-over form, such that older adults showed greater activity than young adults in the short delay condition, but less activity in the long delay. Moreover, in terms of general task-related activation, older adults showed a strong trend towards greater activation in a number of brain regions, including other regions of PFC.

Insert Figure 4

Taken together, these results provide initial support for the hypothesis that healthy aging produces a shift from proactive to reactive control that is observable in terms of a changing pattern of activity in PFC and other brain regions. Under conditions of high demand for proactive control (long delay), older adults showed reduced activation, while more generally showing increased activity, consistent with a greater reliance on less effective reactive control processes. Yet more direct investigation of this hypothesis is required. Specifically, these results were observed with a block design study, that provided no information regarding the temporal dynamics of activity. The use of event-related fMRI would enable a test of the DMC hypothesis that older adults would show reduced activity during the cue and delay period but increased activation during the probe (specifically on inhibitory BX trials). This exact study is currently on-going in our lab.

Non-cognitive Factors

A unique aspect of the DMC account is that it provides a potential means for understanding how non-cognitive factors might influence cognitive control. As described earlier, we believe that there is a close linkage between proactive control and reward prediction. Conversely, a relationship might exist between reactive control and background threat monitoring and detection. These constructs of reward prediction and threat detection might be primarily affective in nature. Indeed, personality theorists have suggested that constructs related to reward-sensitivity and threat-sensitivity might represent the two fundamental affective dimensions of personality. For example, the theory of J. A. Gray (J. A. Gray, 1994) has described these personality dimensions in terms of neural systems that trigger motivational and goal-directed behaviors. The Behavioral Approach System (BAS), which is roughly linked

with extraversion, is motivated by reward-associated cues, and works to achieve appetitive outcomes. On the other hand, the Behavioral Inhibition System (BIS), associated with neuroticism, is driven by threat cues to withdraw from potentially aversive outcomes. These trait variables are also linked to affective states, with high BIS individuals being more susceptible to negative mood inductions and high BAS individuals being more susceptible to positive mood inductions (Larsen & Ketelaar, 1991).

Our hypothesis is that a reward-focused motivational orientation (high BAS sensitivity) is intrinsically proactive, in that achieving complex reward goals requires anticipatory planning and attentional focusing. Conversely, a punishment-focused orientation (high BIS sensitivity) may bias a more reactive state, in which attention is diffusely vigilant and aroused, monitoring for potential threats, so that the individual can react appropriately when any threat appears. Similarly, positive moods may increase the tendency toward a reward-focused, proactive orientation, while negative moods may increase the tendency toward a punishment-focused reactive orientation. The magnitude of these effects is likely to interact with trait sensitivity (e.g., high BIS individuals will likely have a different response to situations promoting a negative mood than will low BIS individuals).

The DMC theoretical framework also suggests a possible mechanistic basis on which to integrate and explain these relationships between affect/personality and cognitive control in terms of underlying neurobiology. A recent influential theoretical analysis of the neurobiology of personality has suggested that BAS/extraversion is directly related to variability in DA function (Depue & Collins, 1999). Likewise, in an

extensive series of studies, Davidson and colleagues have persuasively argued that both BAS and BIS traits and positive and negative moods are associated with hemispheric shifts in lateral PFC activity (Davidson, 1995). These accounts are strikingly consistent with the reward prediction aspects of the DMC model. As we have described above, the phasic DA response signals the reward-related salience of environmental cues. Encoding these cues as context in PFC helps to maximize the achievement of reward. Thus, according to the DMC model, high BAS individuals should be more able to achieve the precise neural activity dynamics required for proactive control.

The DMC account does not provide as rich of a mechanistic framework for understanding the neurobiology of the BIS trait. However, if BIS/neuroticism is associated with a heightened sensitivity to threats, this should be associated with greater reactivity in a conflict monitoring system used to detect the presence of such threats. Thus, it is noteworthy that a number of studies have reported that BIS/neuroticism is associated with increased resting state activity within the ACC (e.g., Zald, Mattson, & Pardo, 2001) – the brain region most strongly associated with conflict detection. However, these prior studies were not conducted during cognitive task performance, which it makes it hard to determine whether the activity reflects increased conflict monitoring per se. Nevertheless, we speculate that high BIS may be associated with an increased bias toward reactive control strategies.

In our first preliminary studies investigating these hypothesis, we examined the role of affective states and affect-related personality traits in modulating behavioral performance and brain activity during performance of the n-back WM task (J. R. Gray & Braver, 2002b; J. R. Gray, Braver, & Raichle, 2002). Through initial behavioral

studies, we found that inductions of positive and negative mood (through viewing of emotionally evocative video clips) had a striking influence on performance that selectively interacted with the n-back task condition (J. R. Gray & Braver, 2002a). Thus, when participants were induced into a positive mood performance was facilitated when they were doing a version of the task involving verbal materials, but impaired when performing a non-verbal task variant. Conversely, when a negative mood was induced, the opposite pattern of performance modulation was observed (improved performance on the non-verbal version, impaired performance on the verbal version). This initial finding was replicated and extended in an fMRI study, where we observed that the cross-over interaction effect of mood and task was expressed within lateral PFC regions (J. R. Gray et al., 2002). In particular, PFC activity was greatest in the conditions where performance was poorest (positive mood / non-verbal condition; negative mood / verbal condition). Moreover, the participants showing the greatest modulation of PFC activity by the conjunction of mood and task also showed the least modulation in behavioral performance. These patterns strongly suggest that the PFC activity served to compensate for increases in demands on cognitive control, which appear to have arisen here from the conjunction of task and affective factors. A specific explanation of the emotion-cognition interaction effect is beyond the scope of this chapter (see J. R. Gray & Braver, 2002a), but the findings are consistent with the general point of the DMC model that affective states can impact cognitive control demands and PFC activation during WM task performance.

A second set of studies examined the role of the BIS and BAS personality traits in modulating performance and brain activity during the same n-back tasks (J. R. Gray

& Braver, 2002b). In a large behavioral sample, the BAS trait was found to show a weak but significant positive correlation with n-back performance ($r=.27$) that held across both the verbal and non-verbal conditions. This finding parallels other recent results also showing BAS or extraversion associated with facilitated WM performance (Lieberman & Rosenthal, 2001). A follow-up fMRI study, using a smaller sample size ($n=14$) demonstrated BAS was negatively associated with activity in caudal regions of ACC (typically associated with conflict monitoring), while BIS was positively associated with ACC activity. These results are consistent with the predictions of the DMC model that high BIS individuals show an increased tendency towards reactive control (high conflict monitoring), while high BAS individuals show an increased tendency towards proactive control (low conflict monitoring, superior WM performance). Increased proactive control should be associated with a reduced demand on reactive control processes, such as conflict monitoring, since proactive control serves to anticipate and prevent conflict before it occurs. Finally, we observed that the observed personality effects were also modulated by manipulations of affective state. Thus, the negative correlation of BAS and ACC activity was strongest following a negative mood induction, whereas the positive correlation of BIS and ACC activity was strongest following a positive mood induction. We interpret these results as suggesting that withdrawal states tend to increase task-related ACC activity by biasing a reactive control mode, but do so less for high BAS individuals (i.e., they will be most resistant to the ACC-increasing effects of withdrawal states). Conversely, approach states will generally decrease task-related ACC activity by biasing a proactive control mode, but do so less for high BIS individuals (i.e., they will be most resistant to the ACC-

decreasing effects of approach states).

Although these preliminary studies provide an important first step in establishing the role of affect and personality factors on cognitive control processes during WM, they provide only a fairly weak test of the DMC account. In particular, the fMRI studies were conducted using a block-design approach, which does not provide a means from dissociating tonic activation from trial-specific effects. Thus, according to the DMC account reactive control processes should be maximally engaged during high conflict trials, and thus should exhibit trial-specific activity changes. Likewise, our original fMRI studies were conducted with a small sample size ($n=14$), which makes it difficult to know how consistently reliable are the effects. In recent work we have replicated our study examining personality effects in the n-back using a much larger sample of 53 participants (J. R. Gray et al., submitted). Moreover, we utilized a “state-item” experimental design (Visscher et al., 2003), that enabled extraction of both trial-specific and tonic activity from the fMRI signal.

There are three sets of findings from this study that have implications for the DMC account. First, we replicated the finding that BAS was negatively correlated with caudal ACC activity ($r(51)=-.28$, $p<.05$), but further observed that the correlation was found on event-related responses (i.e., was trial-specific; see **Figure 5**) rather than on tonic activation levels ($r(51)=.06$, $p>.1$). This finding suggests more conclusively that ACC conflict detection responses (which should occur transiently) are reduced during n-back task performance in high BAS individuals. This is precisely what would be predicted if such individuals were more strongly biased towards a proactive control mode. Second, we also found that BAS was associated with reduced trial-

specific activity in lateral PFC ($r(51) = -.29$). Interestingly, these correlations were observed in the same lateral PFC region previously found to be associated with gF in our previous work (J. R. Gray et al., 2003). Yet a multiple regression analysis indicated that these two sources of individual difference variation (gF, BAS) were independent predictors of lateral PFC activity. Because the gF and BAS constructs are themselves uncorrelated ($r = -.06$, $p > .1$; J. R. Gray et al., submitted), this result confirms our original intuition that both cognitive and affective dimensions of individual differences may contribute to stable biases in cognitive control strategy, but through distinct causal pathways.

Insert Figure 5

A third and final finding was that the BIS trait was observed to correlate positively with ACC activity ($r(51) = .41$, $p < .05$). However, this correlation was found in a rostral, rather than caudal ACC region (see **Figure 5**). Moreover, we found that the correlation was selective to tonic activity levels, rather than trial-specific responses. Although this finding is somewhat different than our earlier results (since in those results the ACC correlation with BIS was in a caudal region), they might still be consistent with the DMC framework. In particular, rostral ACC is typically deactivated during the performance of demanding cognitive tasks (Drevets & Raichle, 1998). A standard interpretation of the function of this region is that it is involved with background monitoring of negative events, particularly those associated with bodily states. This monitoring function is postulated to get shut off during cognitive task performance in

order to free up resources for optimal performance. Thus, the failure of high BIS individuals to deactivate rostral ACC is consistent with the idea that they continue to monitor potential threats during n-back task performance in order to more effectively react to such threats if they appear. However, the increased background monitoring activity diverts resources away from proactive control processes, making them less effective.

The studies just discussed suggest an important way in which “non-cognitive” factors such as personality and affect might impact cognitive control strategy. Although work in this area is just in its infancy, we strongly believe that consideration of affective influences on cognitive control is essential for a full mechanistic understanding of WM and its sources of variation. The DMC framework provides one account for synthesizing and understanding why affect and personality might contribute to WM variation, by linking the more proximal constructs of reward-prediction and threat-detection (and their associated neural mechanisms) to proactive and reactive control modes, respectively. Nevertheless, the relationship between affect/personality and cognitive control is likely to be somewhat more complex than our original formulation, as these initial studies indicate (i.e., we had initially predicted that BIS would be associated with increased trial-specific activity in caudal ACC, but actually found an association with tonic activity in rostral ACC). Thus, further progress in this area may require more focused attention to designing WM experiments in a manner that will provide enhanced sensitivity to influences of affect/personality on cognitive control strategy, via manipulation of factors such as motivational incentives, ego threats, or emotionally evocative stimuli.

Other Sources of WM Variation

In the preceding sections we have provided evidence that many aspects of variation in WM function – within-individual effects, individual differences, effects of age and other certain types of neural dysfunction, and non-cognitive influences – can all be explained by appeal to a dual-process architecture of cognitive control, that we term the DMC account. In this respect, we share a common goal with the other contributors to this volume of trying to understand the common or distinct mechanisms underlying the many varieties of WM variation. In this section, we discuss how the DMC account relates to the other accounts of WM variation put forth in this volume, and more generally consider whether additional sources of variation are needed to account for the full range of empirical phenomena related to WM function (i.e., **Question #4**). In particular, we consider a number of outstanding issues related to variation in WM: neural and computational mechanisms, dual-process accounts, inhibition, domain-specificity vs. domain-generality, development, and genetics.

Neural and computational mechanisms. Our view of WM variation is highly similar to the account put forward by Munakata et al., in terms of relating active maintenance and updating to the interactive function of the PFC and DA system. Likewise, we share with them a deep interest in translating WM constructs into explicit neural and computational mechanisms. The similarity of our frameworks and approach is no coincidence, as we are frequent collaborators and have developed our central theoretical ideas, for the most part, in tandem. Nevertheless, Munakata et al place a

central emphasis on the role of the basal ganglia in mediating WM updating via phasic gating signals. This idea is very similar to our own ideas regarding DA and gating, but is also subtly different, focusing on how the architecture of the BG can enable hierarchical updating to occur within complex WM tasks. This is a potentially important direction for understanding of WM, and its potential breakdown in diseases such as Parkinsons. It is not yet clear whether such distinctions will have any implications for the development of the DMC account.

Reuter-Lorenz et al. also have a neural systems-oriented view of WM variation. In their account, lateral PFC areas serve attentional control functions in WM tasks, but they also postulate that all WM tasks require some degree of control. Additionally, Reuter-Lorenz et al. call attention to the fact that even very subtle task manipulations can lead to substantial changes in behavioral performance and PFC activity, by altering control demands. These views are highly similar to our own, except that we further suggest that it is important to distinguish between the demands placed on proactive vs. reactive control, and to specify which mechanism is likely to be dominant in a given task context. Such distinctions in control will have important ramifications for the way in which different PFC regions are engaged in WM tasks: with either sustained or transient dynamics; and in either a cue-specific or more global manner.

Dual-process frameworks. The executive attention account described by Kane et al. is also highly compatible with our own, and has highly influenced our thinking regarding the role of cognitive individual differences in WM. Like ourselves, Kane et al. posit that variation in WM performance is primarily linked to the active

maintenance of goal-relevant information rather than storage capacity per se. Kane et al. also argue that active goal maintenance, which in our terminology would refer to proactive control, is most critical when PI effects are prominent and must be overcome. Interestingly, Kane et al have also begun to develop a dual-process account of executive attention, which contrasts active goal maintenance with conflict resolution. This account seems very similar to our own distinction between proactive and reactive control, since we argue that reactive control occurs precisely under conditions where high conflict is detected, but not anticipated or prevented via proactive control. Kane et al. make their distinction based on data from the Stroop task that indicates low WM span individuals show heightened interference (and facilitation) effects selectively under low interference expectancy conditions. This finding seemingly parallels our own results from the recent negative Sternberg task (Burgess & Braver, 2004), in which low gF individuals exhibited increased interference effects related to expectancy. However, in one way our results are exactly opposite to Kane et al.'s since in our study gF differences were present selectively in the high interference expectancy rather than low expectancy condition. The discrepancy between these two sets of results is puzzling, but may be due to subtle cross-study differences in tasks (Stroop vs. Sternberg) and individual difference constructs (WM span vs. gF). Nevertheless, further investigation of the issue seems warranted.

Inhibition. An important component of the DMC model is that both proactive and reactive control are often invoked in the service of interference management. This view is similar to that espoused by Hasher et al., who highlight changes in the efficacy of inhibitory control processes as a major source of both age-

related and within-individual (e.g., time-of-day effects) WM variation. Like Kane et al., Hasher et al have convincingly demonstrated through a series of studies that differences in WM function are unlikely to be due to storage capacity. However, Hasher et al go further by postulating three distinct forms of inhibitory control relevant to WM: access, deletion and restraint. Although we are sympathetic to the appeal of these types of constructs, an important distinction between the account of Hasher et al and our own (and that of Kane et al and Munakata et al as well) is the causal primacy attributed to inhibitory control. In the DMC account, proactive control mechanisms serve to prevent interference, while reactive control processes can detect and suppress interference when it occurs. However, the control mechanisms themselves are not inhibitory per se, but rather achieve inhibition as an emergent consequence of active goal maintenance exerting a top-down bias on local competition within posterior brain systems. These types of emergent effects are most easily understood through the use of computational models which translate psychological constructs into specific underlying mechanisms, in often a non-one-to-one manner. Thus, we might argue that the “access” and “restraint” inhibitory functions might both relate to consequences of proactive control, but under different task contexts. Similarly, “deletion” might relate to effective DA-mediated updating in PFC. However, explicit simulations of tasks and behavioral phenomena would be required to determine whether such mappings are truly applicable.

Domain-specificity vs. domain-generality. The DMC account can be considered a domain-general model of WM variation, since we postulate that a single source of variability, between proactive and reactive control, can account for empirical

phenomena in a wide range of circumstances. There are other accounts of WM variation that are also domain-general, but which posit very distinct sources of variability. For example, a domain-general account of WM variation discussed by Hale et al. in their chapter, is the widely-known processing speed model. Much attention has been given to the processing speed construct in the WM literature, especially with regard to aging, and it appears to be highly successful as a source of explanation for WM variability (Salthouse, 1994). It is our hope that the construct can be fleshed out further into mechanistic terms so that its interactions with other dimensions of information processing can be better appreciated. For example, in other recent work, Hale, Myerson & colleagues present a mathematical model that specifies how computational speed might interact with individual differences, group differences and task complexity to produce the diversity of speed-related behavioral phenomena that have been observed in cognitive performance (Myerson, Hale, Zheng, Jenkins, & Widaman, 2003).

It is clear that any comprehensive account of WM variation will also have to deal with the obvious variation that must be occurring across individuals (and developmentally, within individuals) in regard to domain-specific knowledge. The brain is an organ defined by experience-dependent plasticity. Thus, individuals with different experiences are surely to have differential knowledge stored in the various brain systems specialized for coding these experiences. Likewise, just as some individuals have greater perceptual acuity than others, likely as a result of domain-specific genetic variation, so might there be domain-specific differences in cognitive abilities, such as verbal and spatial reasoning, that will likely impact WM function. Indeed, these

domain-specific individual differences may be as an important source of WM variation as domain-general factors. A number of chapters have provided convincing evidence supporting such a position (e.g., Hale et al., Jarrold et al.). A critical future direction for studies of WM will be to discover and explore the nature of interaction between domain-specific and domain-general sources of variability.

Development. In addition to the accounts and views of WM variation with which we hope our work intersects, we also recognize that there are likely other sources of important variation that are relevant for understanding WM function, but are not within the purview of our current model. For example, developmental approaches to WM are extensively considered by a number of investigators within this volume (e.g. Munakata et al., Hale et al., Jarrold et al., Hitch & Towse). The developmental maturation of the cognitive system and the concomitant neural changes that occur with it undoubtedly serve as both important sources of variation and important tools for discovering the causal mechanisms that underlie cognitive developmental variability. We have not explored yet whether the DMC account would be useful for understanding the nature of cognitive control in young children, but this may be an important avenue of exploration. An intriguing notion is that developmental changes in WM function may be linked to the developmental trajectory of DA function in PFC (e.g., Diamond, 2002).

Genetics. Finally, the future of scientific investigation on WM function will likely be strongly influenced by upcoming developments in cognitive-genetic approaches. The rapid development of easily accessible genotyping methods has already provided new knowledge regarding how genetic variation in certain alleles may relate to phenotypic variation in cognitive and neural function among healthy individuals. For

example, recent work has suggested that variations in the COMT (catechol O-methyltransferase) gene, which helps breakdown DA in PFC, might be strongly linked to individual difference variation in PFC activity and behavioral performance in WM tasks such as the n-back (Mattay et al., 2003). Further studies incorporating genetically-derived independent measures of variation may provide crucial information regarding the first causal link in the pathway from biology to behavior during performance of WM tasks.

Summary and General Contributions of the DMC Theory

In the preceding sections we have laid out what we believe is an important new direction for research into cognitive control and WM. We have argued that a comprehensive theory of cognitive control in WM requires the inclusion of at least two distinguishable and potentially independent control modes -- proactive and reactive. Proactive and reactive control can be differentiated on the basis of their information processing characteristics, computational properties, temporal dynamics, and underlying neural systems. The existence of dual mechanisms of control is suggested because of the inherent computational tradeoffs associated with each specialized mechanism. Thus, there are both costs and benefits, advantages and limitations to the exclusive use of either proactive or reactive control strategies. Consequently, the cognitive system is likely to optimize processing by utilizing both strategies to differing degrees, such that, in most individuals and in most task situations, a shifting mixture of both control mechanisms will be invoked.

We believe that the DMC framework contributes significantly to a general theoretical understanding of WM in a number of ways (i.e., **Question #4**):

- By providing clear predictions regarding how changes in cognitive control strategy will translate to characteristic changes in WM task performance .

Example: The double dissociation in immediate vs. delayed recognition in the Speer et al. (2003) Sternberg study.

- By clarifying the nature and temporal dynamics of lateral PFC involvement in WM tasks in terms of shifts in cognitive control mode.

Examples: The increased sustained delay-related PFC activity associated with low expected WM load (i.e., proactive control) in the Speer et al. (2003) Sternberg study. The decreased transient probe-related PFC activity and reduced behavioral interference effects in high gF individuals associated with high interference expectancy (i.e., proactive control) in the Burgess & Braver (2004) Sternberg study.

- By conceptualizing natural developmental processes, such as healthy aging, and certain types of neural dysfunction (e.g., schizophrenia) as reflecting a relatively stable shift in cognitive control strategy, with associated consequences .

Example: The pattern of changes in PFC activity exhibited by older adults in the AX-CPT task, with generalized task-related activation becoming increased while specific-delay related activity decreases (Barch et al., submitted).

- By highlighting the variety of task and individual difference factors – many of which are either subtle in nature, or not in the traditional purview of cognitive

scientists – that can influence WM task performance, by shifting which control strategy is dominant.

Example: The influence of the personality traits BIS and BAS on ACC and lateral PFC activity during performance of the n-back task (J. R. Gray et al., submitted).

Insert Table 2

Probably the most important take home message of our theoretical account to general WM theory is that of an appreciation of WM variability itself (see **Table 2** for a summary statement of our answers to the four central chapter questions). We suggest that understanding the variability between proactive and reactive control is fundamental to understanding the core mechanisms of WM. The critical point of the DMC account is that variability between dual control mechanisms can be a naturally occurring part of cognition, but can also become more prominent under various changes in internal states and external situations. Moreover, the DMC account does not posit a distinction between the types of WM variation that occur on an intra-individual basis from those that occur on an inter-individual basis. In other words, regardless of the source of WM variation – task factors, state factors, cognitive individual differences, personality differences or population differences – the proximal mechanisms of variation remain the same and have the same impact on brain activity and behavior. Thus, the DMC framework provides a unifying account that has the potential to synthesize and integrate a large body of literatures regarding WM function. By recognizing that there are multiple alternative routes to cognitive control, investigators may be in a better position to

explore and investigate the complexity of empirical findings, and as such more effectively manage the heretofore impossibly difficult task of defining the unifying latent WM constructs that will replicate across tasks, individuals and cognitive domains.

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TABLE 1: Distinctions between proactive and reactive control

	Proactive Control	Reactive Control
Computational Properties	Future-oriented, early selection, preparatory attention	Past-oriented, late correction, interference resolution
Information Processing	Strong goal-relevant focus, global control effects	Increased goal-irrelevant processing, item-specific control
Temporal Dynamics	Sustained, activation prior to imperative stimulus	Transient, activation after imperative stimulus
Neural Substrates	Lateral PFC, midbrain DA (phasic activity)	ACC, lateral PFC (transient response), MTL, others

TABLE 2: Summary answers to chapter questions

Question 1: Overarching Theory of WM

Our general approach is to link psychological constructs of WM to underlying neural and computational mechanisms. We suggest that WM is an emergent phenomenon arising from the interaction of multiple mechanisms (active context representation, dynamic updating, conflict detection, and binding). However, we give particular focus to the influential role of lateral PFC in mediating top-down biases over processing via actively maintained context or goal representations.

Question 2: Critical Sources of WM variation

We suggest that the distinction between proactive and reactive cognitive control may be the core source of WM variation. Proactive control enables the optimal task preparation and prevention of interference via sustained goal maintenance in lateral PFC. Reactive control provides an as-needed, just-in-time form of interference resolution or context retrieval via transient activation of PFC or related brain systems (e.g., MTL, ACC). Because these dual-mechanisms of control each have computational advantages and disadvantages, shifts in the dominant cognitive control mode can arise due to situational factors (intra-individual variation), individual differences, neural dysfunction, and non-cognitive factors such as mood and personality.

Question 3: Other Sources of WM variation

Many other sources of variation should be included in a comprehensive WM theory. We consider some of the differing sources discussed by other contributors to this volume: neural mechanisms (e.g., the basal ganglia; Munakata et al), dual-process accounts (Kane et al), inhibition (Hasher et al), processing speed (Hale et al), domain-specific mechanisms (Jarrod et al), and development (Hitch & Towse). Additionally, we think that genetic variation will be an important focus of future WM research.

Question 4: Contributions to General WM Theory

We believe that the DMC model put forward here can provide a unifying framework for understanding the many varieties of WM variation. The model: a) indicates the task and individual difference factors that should influence WM task performance; b) clarifies the nature and dynamics of PFC activity in WM tasks; and c) links specific forms of neural dysfunction to stable shifts in cognitive control strategy. The conceptualization of cognitive control mechanisms in terms of computational specialization and tradeoffs provides a coherent causal explanation for why variability occurs in complex cognitive activities, such as WM.

Figure Captions

Figure 1. Schematic diagram of WM theoretical framework. Lines with single arrowheads reflect excitatory interconnection; double arrowheads reflect encoding / retrieval of traces via episodic memory. The excitatory connection from PFC back to itself represents recurrent connectivity in PFC that mediates active maintenance. The square arrowhead reflects the ability of dopaminergic projections to modulate or gate inputs into PFC; the circular arrowhead reflects gradual learning and plasticity involved in reward prediction. PFC = prefrontal cortex in all figures.

Figure 2. Memory strategy effects on PFC activity (Speer et al., 2003) . Left Panel: Left dorsolateral PFC region showing anticipatory, delay-related activation in low-load expectancy condition. Right Panel: Left anterior PFC region showing increased probe-related activity in high-load expectancy condition. X-axis refers to the timecourse of activity. Y-axis refers to average percentage fMRI signal change (from baseline).

Figure 3. Interactions between gF and interference expectancy in lateral PFC activity (Burgess & Braver, 2004). Top panel: High gF group shows increased delay-related activity in left VLPFC compared to low gF, but only during high expectancy condition. Bottom panel: In high expectancy condition, low gF group shows increased probe-related activity in a nearby left VLPFC region for recent negatives, but high gF group does not. VLPFC = ventrolateral prefrontal cortex.

Figure 4. Age-related changes in PFC activity in the AX-CPT task (Barch et al., submitted). Upper panel: Left dorsolateral PFC region showing reduction in

delay-related activation in older adults in long delay. Lower Panel: Brain regions (including PFC) showing generalized age-related increase in activation. Z values refer to superior-inferior plane of brain section.

Figure 5. Contributions of personality to ACC activity (J. R. Gray et al., submitted).

Left Panel: Positive association between BIS (punishment-sensitivity) and tonic activity in rostral ACC. Right Panel: Negative association between BAS (reward-sensitivity) and trial-specific activity in caudal ACC. Y-axis is percentage fMRI signal change (from baseline). ACC = anterior cingulate; BIS = behavioral inhibition system; BAS = behavioral approach system.

Figure 1

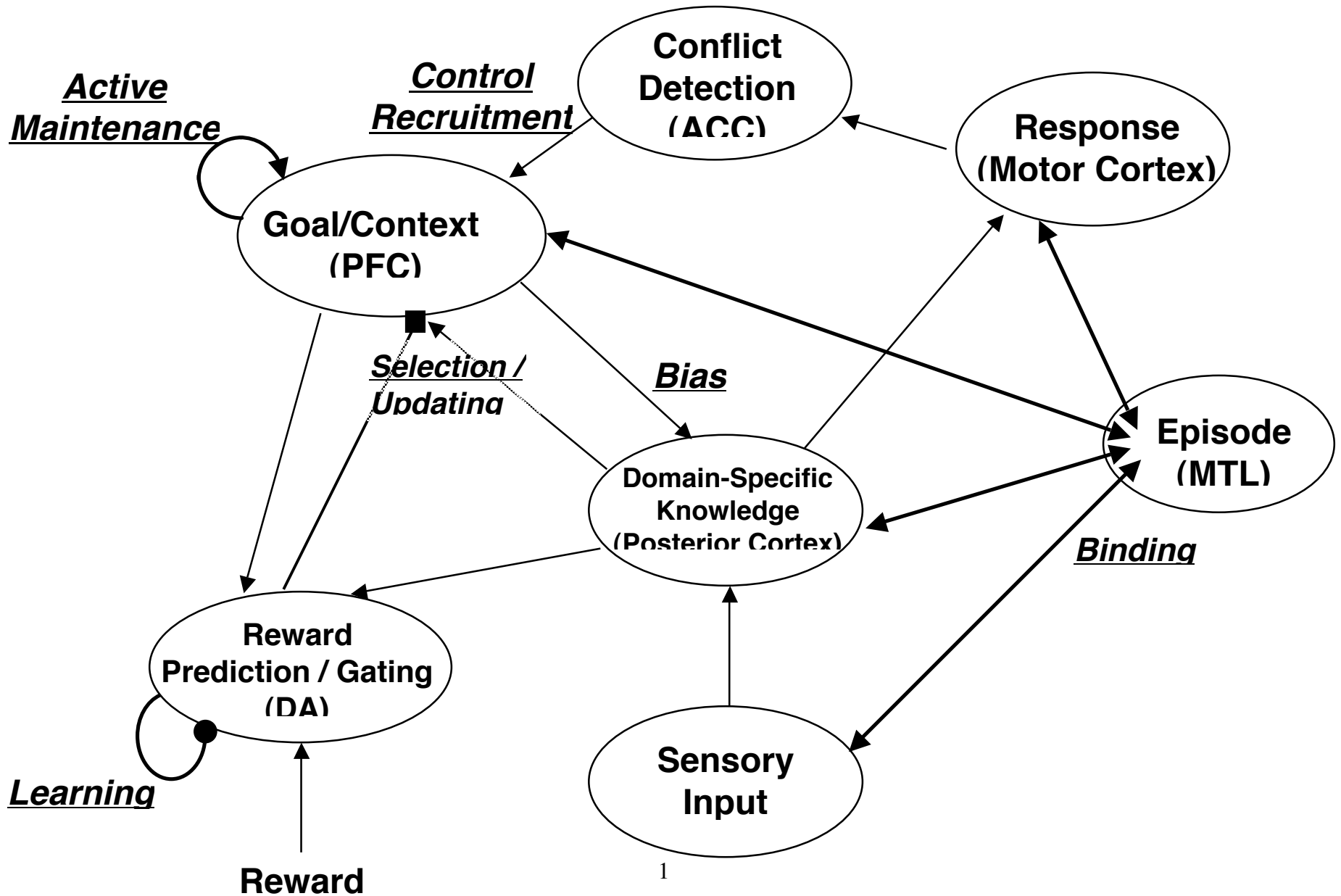


Figure 2

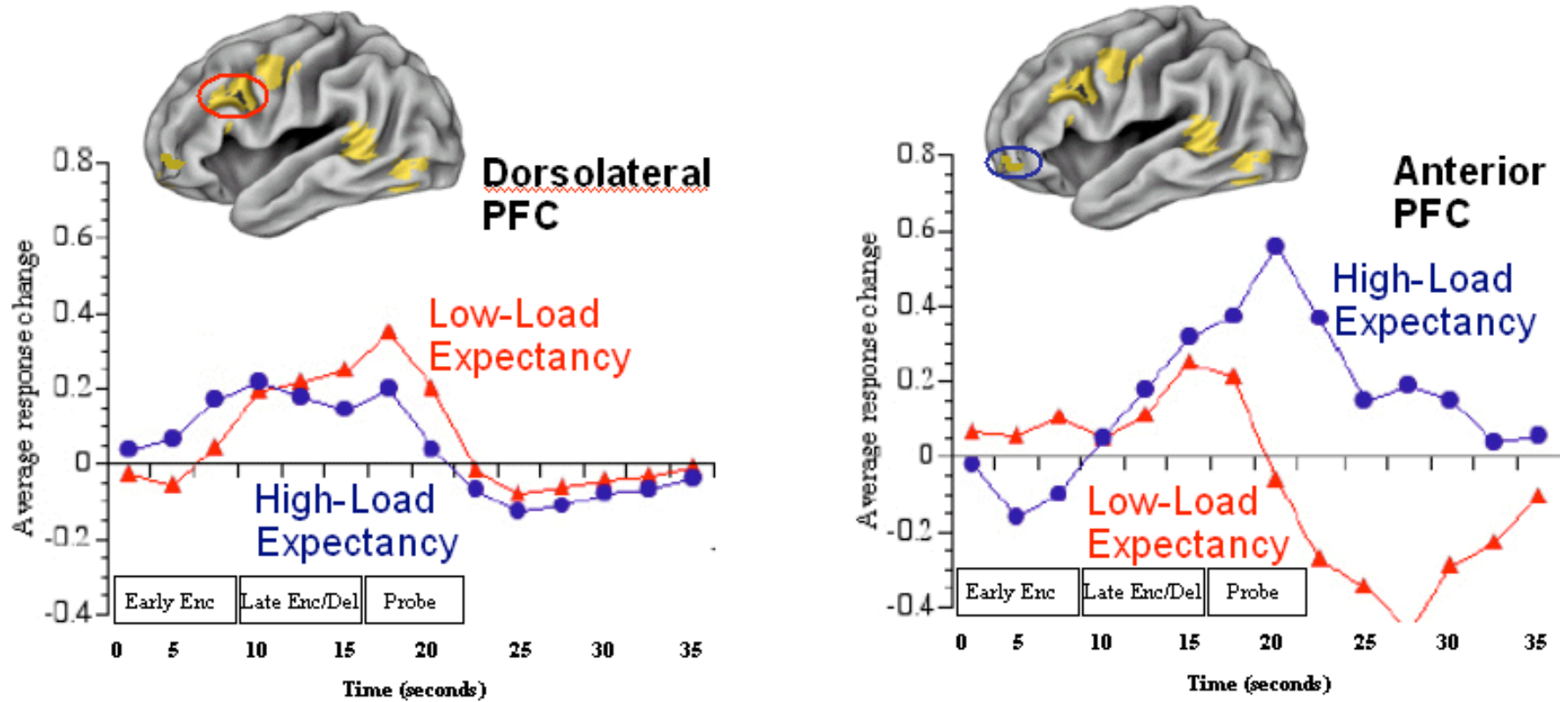


Figure 3

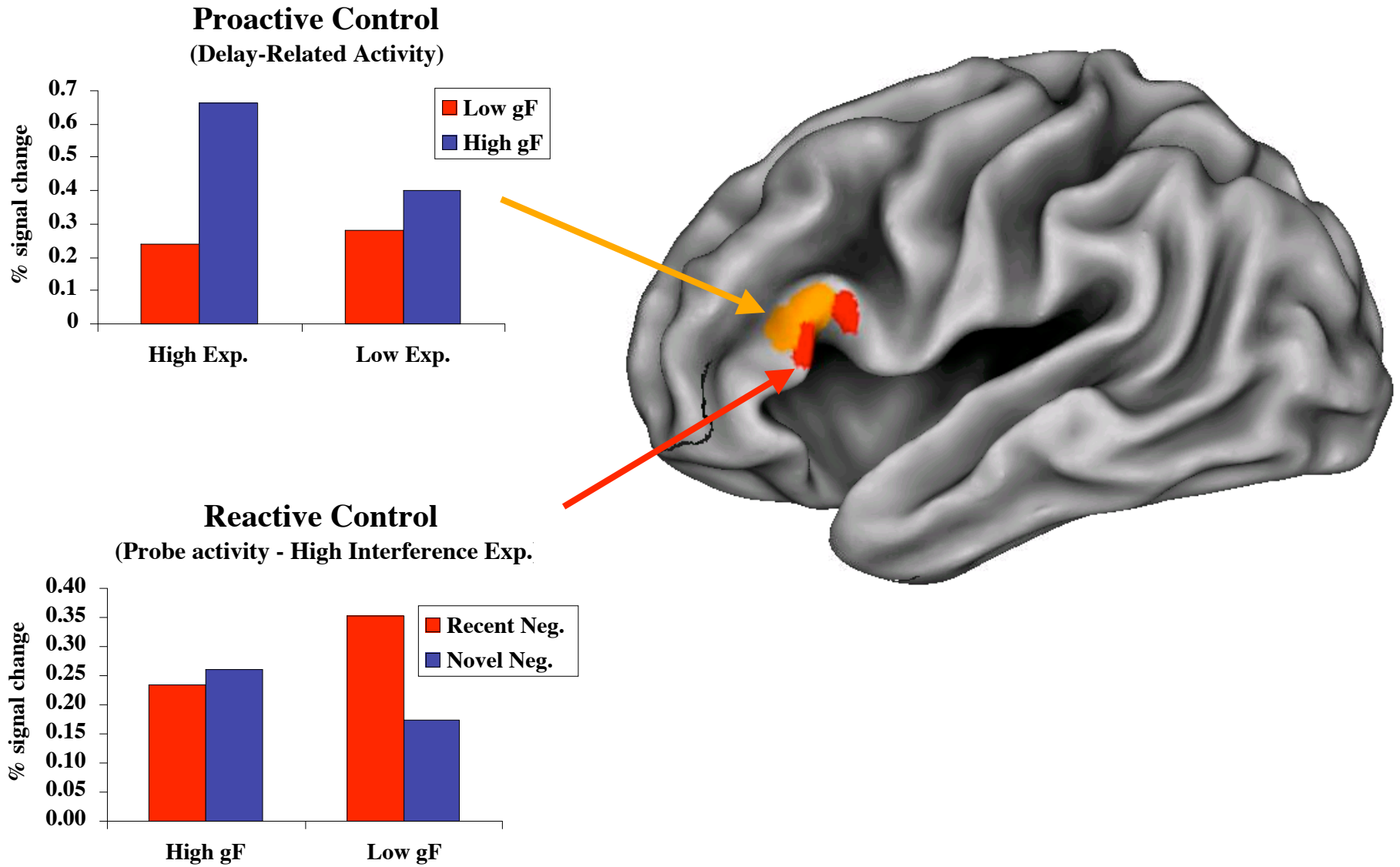
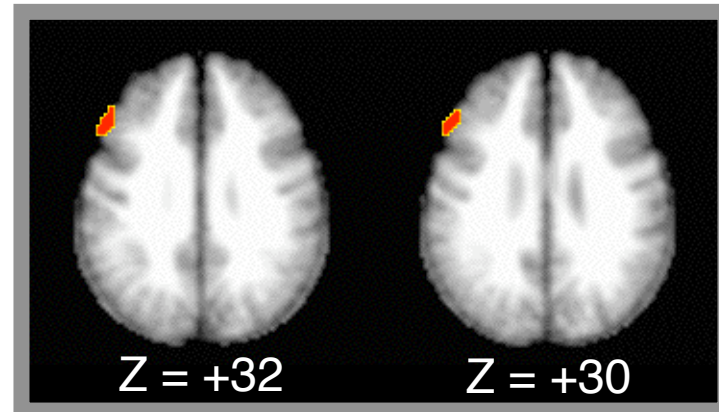
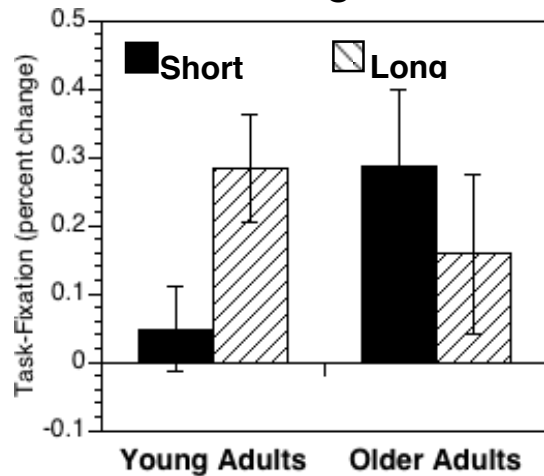


Figure 4

Significant Age x Delay



Task-Related Activations Greater in Older Than Younger Adults

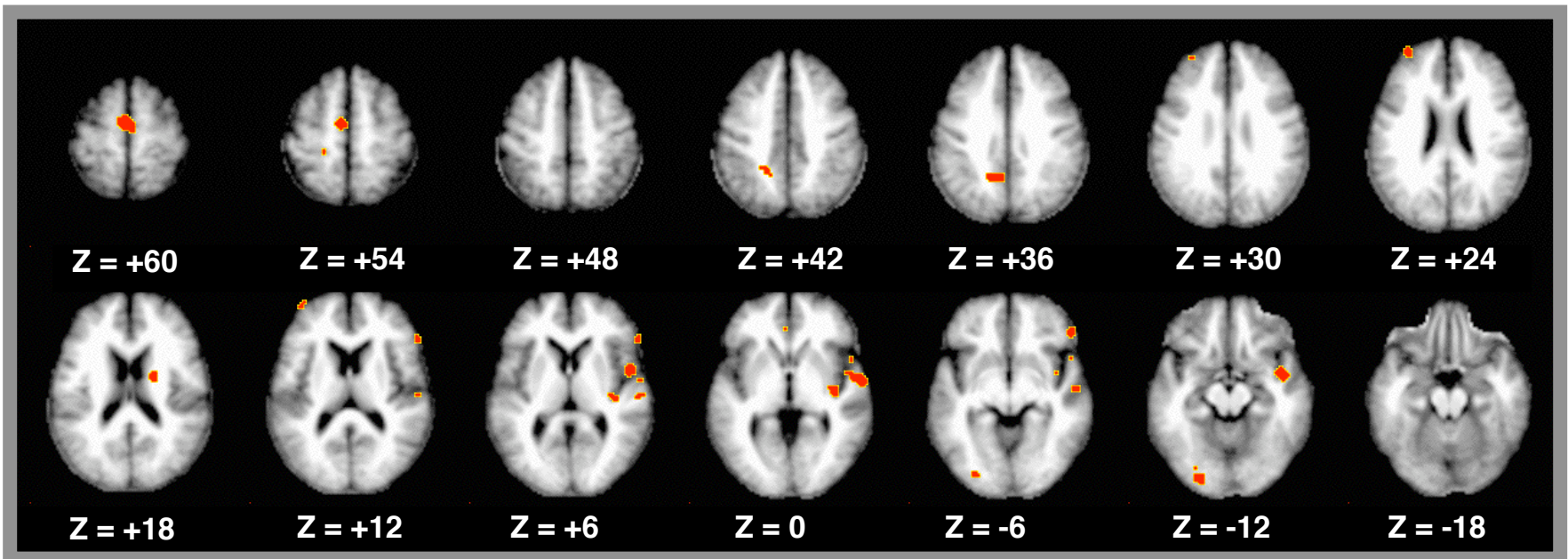
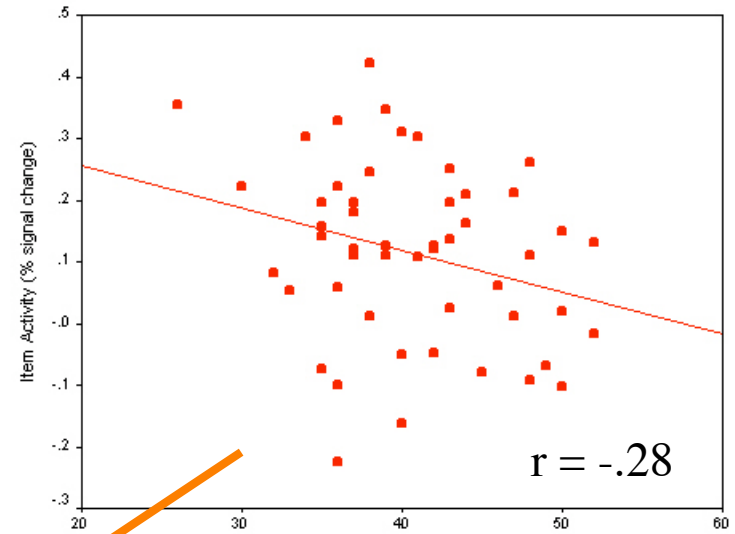
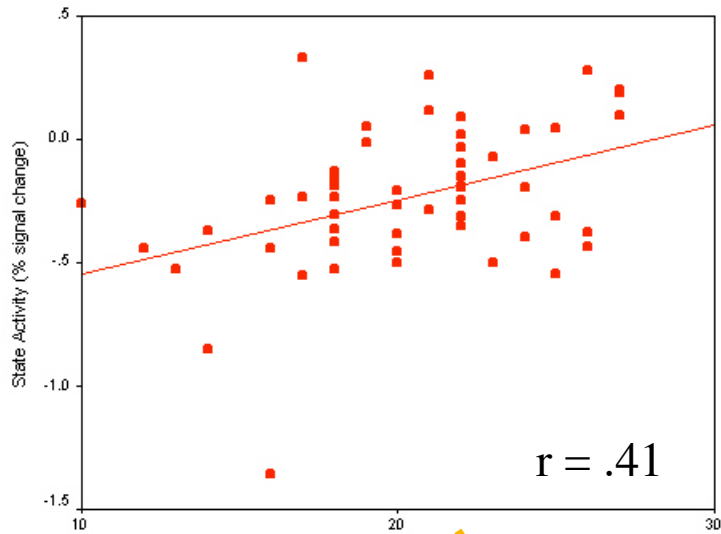


Figure 5



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