

Context Processing and Cognitive Control

From Gating Models to Dual Mechanisms

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The ability to maintain and flexibly regulate thoughts and action plans in pursuit of internally represented behavioural goals is central to the psychological construct of *cognitive control* and critical to adaptive human behaviour. This ability requires a complex balance between maintaining current goal representations against distracting information, while also flexibly updating these representations as goals and environmental factors change. In the present chapter, we review evidence that the balance between control stability and flexibility is supported by context maintenance in the prefrontal cortex and flexible representation updating via a dopaminergic gating mechanism. We will then discuss how context processing can be understood as supporting dual mechanisms of cognitive control characterised by distinct temporal dynamics, by reviewing evidence for the dual mechanisms of control (DMC) framework (Braver, 2012; Braver, Gray, & Burgess, 2007). We will also outline methodological approaches and tools that have been fruitful in empirical investigation within the DMC framework and discuss future directions for investigation stemming from this perspective. Given past evidence and future directions within this line of research, we propose that the core utility of the DMC framework lies in its ability to account for and generate specific, testable predictions regarding variability in cognitive control dynamics across a broad variety of task paradigms and at multiple levels of analysis.

Context Processing and Gating Models

Context can be broadly described as task-relevant information represented in such a form so as to bias selection of the appropriate task response. Internal, active representations of context in working memory play a critical role in guiding executive, goal-oriented behaviour (Braver, Barch, & Cohen, 2002; J. D. Cohen & Servan-Schreiber, 1992). These representations may bias attention to task-relevant information, promote inhibition of task-irrelevant information, and structure encoding, maintenance, and retrieval of information in working and long-term memory, while generally supporting the planning and execution of adaptive goal-directed actions and behaviour. These cognitive processes correspond closely to the putative functions of the prefrontal cortex (PFC), based on early lesion and neuroimaging studies in humans

(Stuss & Knight, 2013) as well as neurophysiological studies in primates (Goldman-Rakic & Friedman, 1991). Along with identifying the PFC as a neural substrate supporting executive function, studies from this body of work further identified the dopamine (DA) neurotransmitter system as a major modulator of goal-oriented behaviour and PFC activity: that is, studies of disrupted cognitive function and DA systems in schizophrenia (J. D. Cohen & Servan-Schreiber, 1992) as well as studies in primates suggesting that pharmacological manipulations of the DA system alter working-memory-related activity in PFC neurons (Sawaguchi & Goldman-Rakic, 1991). Although this work was critical in identifying functional brain areas supporting context processing and the implementation of goal-directed behaviour, these early studies were largely agnostic on the mechanisms underlying active learning, maintenance, and updating of context representations and their use in the execution of adaptive task behaviour.

Braver and Cohen (Braver & Cohen, 1999, 2000) proposed a gating model aimed at addressing this theoretical gap by identifying and testing a plausible mechanistic means by which DA could modulate active context processing in the PFC, supporting controlled behaviour. This connectionist model posits that selection, updating, and maintenance of context occur through interactions between the PFC and the DA neuromodulatory system. Specifically, this model posits that phasic bursts of DA act as a gating mechanism, regulating information access to active memory mechanisms subserved by the PFC (Braver, Barch, & Cohen, 1999). Further, DA plays a learning function (via phasic firing in response to prediction errors; i.e., situations where reward outcomes are either greater or lesser than anticipated), allowing the system to discover what information is relevant for selection as context (Braver & Cohen, 2000).

These assertions were tested in a simulation of the model using the *AX Continuous Performance Task* (AX-CPT; J. D. Cohen & Servan-Schreiber, 1992). The AX-CPT is a delayed-response task requiring context maintenance and updating for successful performance (see Figure 9.1a). On each experimental trial of the AX-CPT, participants must respond to a cue–probe pair presented sequentially (typically, letter stimuli). One specific combination requires a target response (i.e., the letter ‘A’ followed by the letter ‘X’; AX trial), whereas all other combinations of cue and probe require a non-target response. Target (AX) trials occur at a high frequency (typically 70%), leading to associations between the target cue (the letter A) and target response, and between the target probe (the letter X) and the target response. These associations subsequently lead to interference for two low-frequency cue–probe pairs (typically occurring at 10% each): AY trials (target cue, non-target probe), where contextual cue leads to a bias towards target response that must be overcome; and BX (non-target cue, target probe) trials, where the contextual information must be used to inhibit the probe-related tendency towards target response. BY (non-target cue, non-target probe) trials also occur at a low-frequency (10%) control condition.

Simulations with this model (schematic in Figure 9.1b) suggested that it is biologically plausible for DA to successfully gate information into active memory in the PFC and, in response to reward prediction errors, strengthen stimulus–response associations supporting learning (in turn optimising reward pursuit and goal-oriented behaviour). Phasic DA activity as a gating mechanism was thus posited to provide a means by which context information could be actively maintained in the PFC, remain protected against interference yet flexible to updating, and used to bias action responses in the service of goal-oriented behaviour. The gating model provides an account consistent with behavioural and neurobiological evidence for altered context processing in populations including schizophrenic patients (Braver et al., 2002; J. D. Cohen, Barch, Carter, & Servan-Schreiber, 1999; Chapter 31 by Barch & Sheffield in this volume) and healthy older adults and individuals with Alzheimer’s disease (Braver et al., 2002). Interestingly, these empirical studies suggested that impaired cognitive

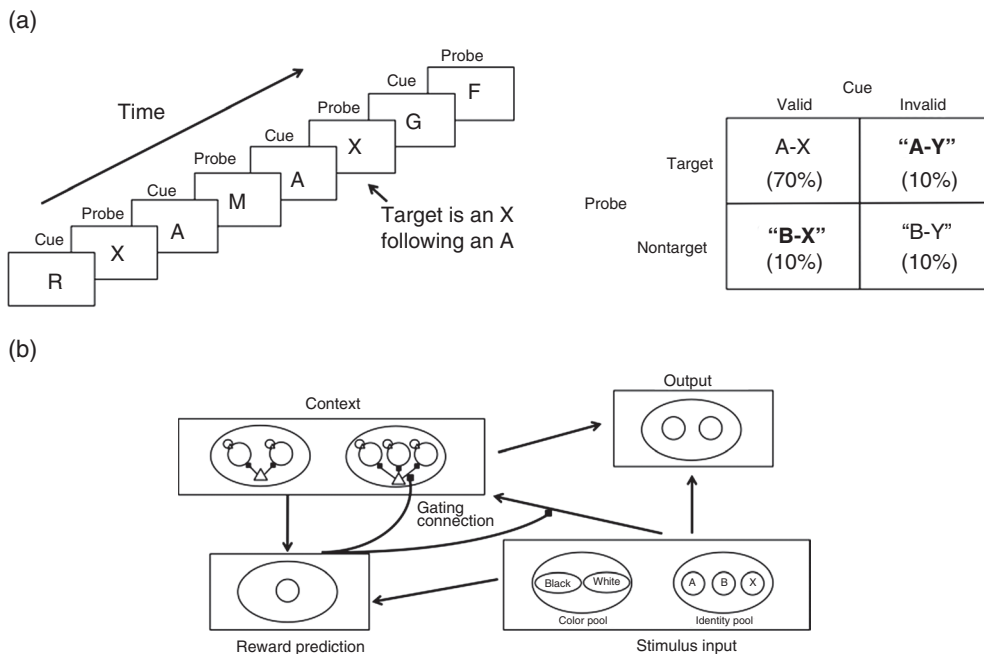


Figure 9.1 (a) Schematic of the AX-CPT paradigm. Single letters are visually displayed as a series of cue–probe pairs. In this example, a target is defined as the occurrence of an ‘X’ probe immediately following an ‘A’ cue and occurs at high frequency (70% of trials). Three types of non-target trials occur with equal frequency (10%): AY, BX, and BY (where B refers to any non-A cue, and Y refers to any non-X probe). (b) Schematic of the learning/gating model used in simulation of AX-CPT (following Braver & Cohen, 2000). Excitatory connections exist between layers, as indicated by arrows; lateral inhibitory connections (not pictured) exist within each layer. Context units have self-excitatory connections allowing for active context maintenance. Low levels of baseline activity in the context layer are enforced by local inhibitory bias units (indicated by small triangles). Input and context layers are fully connected to the reward prediction/gating (RPG) unit, which in turn makes a gating connection with both excitatory and inhibitory input to the context layer. The RPG unit also modulates learning in all modifiable network connections. Source: Adapted from Braver and Cohen, 2000.

control performance in such populations, relative to healthy controls, might be best characterised by selective impairments in specific components of context processing, as opposed to a global cognitive deficit. Specifically, both schizophrenic patients and healthy older adults showed worsened BX performance and improved AY performance relative to healthy young adults. Evidence of superior AY performance in these populations relative to young adults is notable, as generally their cognitive performance is comparatively impaired. Successful performance on AY trials in the AX-CPT is specifically attributed to the ability to overcome response bias associated with the contextual cue gated by DA and maintained within the PFC; task performance suggests that in these populations, the cue representation may not be maintained as strongly as in healthy young adults. Early experimental work, using fMRI, provided evidence consistent with this idea, showing cue-related activation in the dorsolateral PFC during performance of the AX-CPT (Braver et al., 2002). Other later work demonstrated reductions in cue-related dorsolateral PFC activity during AX-CPT performance in both patients with schizophrenia (MacDonald & Carter, 2003) and older adults (Paxton, Barch, Racine, & Braver, 2008).

A recent fMRI study provided more direct support for the gating account, both by directly imaging the midbrain DA system during working memory updating, and by using transcranial magnetic stimulation (TMS) to disrupt activity within the PFC (D'Ardenne et al., 2012). Specifically, in this study, activity in the DA midbrain (ventral tegmental area, substantia nigra) was found to phasically increase in response to contextual cues in an AX- CPT variant, and this activation was correlated with cue-related activation observed in the right dorsolateral PFC. Furthermore, phasic TMS applied to this same dorsolateral PFC region, immediately after cue presentation, led to task performance decrements.

Subsequent computational models have built upon the gating model while retaining the core principle that DA may regulate information flow and updating in the PFC. O'Reilly, Frank, and colleagues (Frank, Loughry, & O'Reilly, 2001; O'Reilly & Frank, 2006) developed a computational model of working memory similarly built on the premise that a dopaminergic gating mechanism controls information access to the PFC, but refined this model by positing a specific role for the basal ganglia in releasing inhibition on specific subregions of the frontal cortex (Figure 9.2b). Thus, in this model, known as the prefrontal-cortex basal-ganglia working memory (PBWM) model, phasic DA activity controls the learning of more spatially targeted gating signals within the basal ganglia, which enable selective updating within the PFC (as opposed to the relatively global effect that diffuse DA broadcast would cause; Figure 9.2c). The PBWM gating model has been shown to be especially powerful in understanding hierarchically structured working memory tasks, in which some representations (e.g., subgoals, 'inner loop') need to be updated following presentation of contextual cues, while others must still be maintained during this period (i.e., higher-order goals, 'outer loop'). For example, the PBWM model can simulate a hierarchically structured version of the AX-CPT, known as the 1-2-AX task (Nee & Brown, 2012; O'Reilly & Frank, 2006), in which contextual cues need to be referenced to the higher-order context (1 or 2) present throughout a block of trials (see Figure 9.2a). This type of hierarchically structured context processing task would be difficult to simulate with a global dopamine gating model.

More recently, the gating model has been even further refined, adding not only an input gate to the PFC mediated by corticostriatal interactions, but also a second striatally based output gate that may determine what PFC-maintained active representations are utilised for behaviour (Chatham, Frank, & Badre, 2014) and a third striatally based mechanism that re-allocates working memory capacity when representations are no longer relevant (Chatham & Badre, 2015; see also Chapter 21 by Bhandari, Badre, & Frank in this volume).

The DMC Framework

Although clarifying the mechanisms by which context representations are gated into the PFC and selected for action remains an active area of research, models of context maintenance and updating in the PFC have also been expanded through the development of the DMC framework. The DMC framework aims to address and account for variation in cognitive control performance at multiple levels of analysis (Braver, 2012; Braver et al., 2007). This framework proposes that cognitive control can be understood as operating in two primary modes: *pro-active* and *reactive*. Proactive control is characterised by the active maintenance of context representations in the PFC; this information enters and is maintained via the phasic DA gating mechanism that the gating model describes. Because the gating mechanism allows for active maintenance of information relatively protected from interference, proactive control is thought to be relatively tonic in nature. In contrast, reactive control is implemented as a

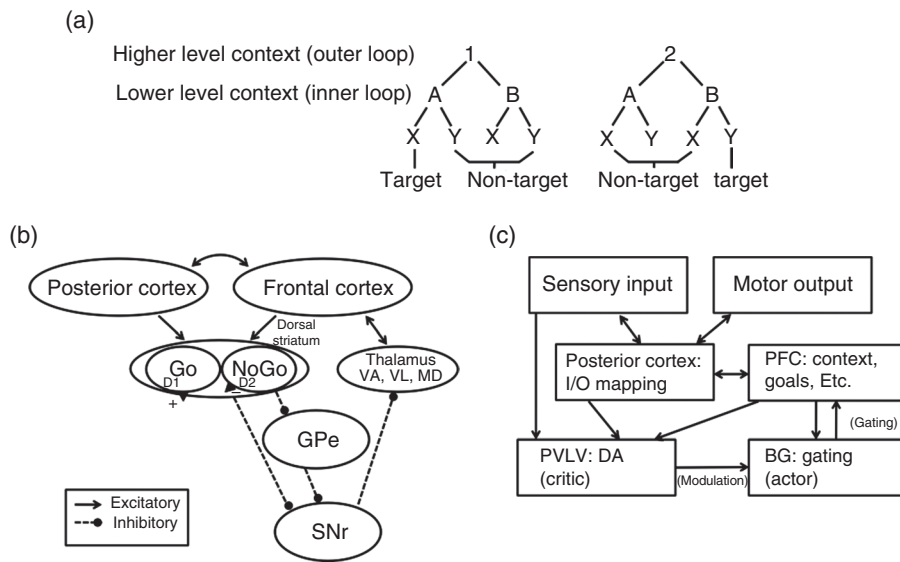


Figure 9.2 (a) Nesting rule structure of the 1-2-AX, hierarchical context updating paradigm (adapted from Nee and Brown, 2012). Subjects respond to ‘X’ and ‘Y’ stimuli based upon a nested series of cues. Under the ‘1’ higher-level context (cued prior to trial), subjects make a target response to the letter ‘X’ if within the ‘A’ lower-level context (non-target response otherwise). Under the ‘2’ higher-level context, subjects made a target response to the letter ‘Y’ if within the ‘B’ lower-level context (non-target response otherwise). (b) Interconnections between the basal ganglia and the frontal cortex through a series of parallel loops (Source: adapted from O’Reilly and Frank, 2006). The thalamus is bidirectionally excitatory with frontal cortex; the SNr (substantia nigra pars reticulata) is tonically active and inhibiting this excitatory circuit. When direct pathway ‘Go’ neurons in dorsal striatum fire, they inhibit the SNr and thus disinhibit the frontal cortex, producing a gating-like modulation argued to trigger the update of working memory representations in the prefrontal cortex. The indirect pathway ‘NoGo’ neurons of the dorsal striatum counteract this effect by inhibiting the inhibitory GPe (globus pallidus, external segment). (c) Overall architecture of the PBWM model implemented to capture hierarchical updating tasks such as the 1-2-AX (adapted from O’Reilly and Frank, 2006). Sensory inputs are mapped to motor outputs via posterior cortical (‘hidden’) layers. The PFC contextualizes this mapping by representing relevant prior information and goals. The basal ganglia (BG) and the primary value learned value (PVLV) system drive DA modulation of BG so it can learn when to update.

transient, phasic form of ‘late correction’ that occurs in response to changing environmental demands (i.e., in response to performance monitoring) or stimulus-triggered associative retrieval, and is posited to operate in the absence of the gating mechanism. Each mode of control has advantages and drawbacks, leading to an inherent computational trade-off between the two; the emergence of these specialised modes is thought to make possible dynamic shifting of control, towards optimisation of the balance between them. On account of explicit acknowledgement that the two modes of control can dynamically shift as a result of multiple influences, the DMC framework can provide a coherent theoretical account for variability in cognitive control processing from multiple sources, including within-individual, within-group, and between-group variability (Braver, 2012). The DMC framework’s ability to account for altered context processing and cognitive performance in different populations

and to generate new, testable hypotheses regarding sources of variability in cognitive control has yielded a wealth of empirical research. These studies have utilised different experimental paradigms and methodological approaches, motivational and affective manipulations, and comparisons between population groups and individuals as critical sources of variation in cognitive control. We discuss the highlights of this research below.

Cognitive Paradigms

One of the key contributions of the DMC framework is that it provides a means of understanding the potential sources of cognitive control variability that have been noted and observed across a wide range of experimental paradigms that are typically used in the cognitive control literature. These include context processing, cued task switching, selective attention / stimulus–response compatibility, working memory, prospective memory, and response inhibition. Here we briefly review each of these domains.

As a theoretical expansion of the gating model, the DMC framework has been most extensively employed to interpret variability in context processing tasks, in which contextual cues indicate how to appropriately respond to target items. The most widely investigated variant of context processing is the AX-CPT task. In the DMC interpretation of the AX-CPT, interference on AY trials is attributable to maintenance of contextual target cue ('A') that must be overcome upon presentation of the non-target probe ('Y'), and AY trial interference is thought to reflect a relatively preparatory, or proactive control. In contrast, in BX trials, interference arises via a target response bias to the target probe ('X') that must be inhibited on the basis of a prior contextual cue; BX trial interference is thus thought to reflect relatively reactive control. The utilisation of reactive control (rather than a complete failure of control) would be represented in BX interference coming primarily in the form of reaction time slowing (reflecting the time to engage control following probe presentation), rather than a large increase in BX error rates. Thus, the extent to which interference is experienced in AY and BX trial conditions during task performance may serve as an indicator of relative tendencies towards proactive versus reactive control. Studies of variability in AX-CPT performance and associated neural and physiological activity as a result of experimental manipulations or comparisons between groups have provided evidence that cognitive control during the task can be understood as operating in two primary modes. These findings will be outlined in further detail below (see the sections titled 'Individual Differences' and 'Comparison Between Populations').

A more complex category of the context processing paradigm is cued task switching (for a review, see Chapter 2 by Monsell in this volume). Here, the task varies randomly from trial to trial, and advance cues specify which task is relevant for the upcoming trial. The cognitive control demands of task switching are evidenced by the presence of both switching costs and mixing costs, which reflect performance decrements on, respectively: (a) trials in which the task switches compared to when it repeats; and (b) task-switch blocks compared to single-task blocks (controlling for task-switch trials; Kiesel et al., 2010; Monsell, 2003; Vandierendonck, Liefooghe, & Verbruggen, 2010). The finding that these costs are significantly reduced with increased preparation time following task cues suggests the presence of proactive control (Meiran, Chorev, & Sapir, 2000; Monsell, 2003). Conversely, the fact that the costs are almost never eliminated (i.e., residual), even with long preparation times, and also impacted by target-related factors such as task-rule congruency (whether the target stimulus elicits the same or conflicting responses, on the basis of which task is relevant), suggests the presence of, and demand for, reactive control as well (Kessler & Meiran, 2008; Meiran, Kessler, & Adi-Japha, 2008). Indeed, a primary area of unresolved debate and controversy is the extent to which cued task switching is thought to be accomplished primarily by proactive

(e.g., preparatory task set maintenance and biasing) or reactive control mechanisms (e.g., target-driven priming or conflict-triggered rule retrieval; Arrington, Logan, & Schneider, 2007; Koch & Allport, 2006; Monsell, 2003; Chapter 2 by Monsell in this volume). According to the DMC framework, the weighting or bias towards each control mode is related to a variety of task factors, such as reward motivation or expectation of interference (Bugg & Braver, in press; Bugg, Diede, Cohen-Shikora, & Selmecky, 2015; Dreisbach, Haider, & Kluwe, 2002; Nieuwenhuis & Monsell, 2002). Indeed, in one computational model, we simulated how shifts between proactive and reactive control might even be implemented on a trial-by-trial basis, in response to random fluctuations of the DA gating mechanism, and how this could account for some of the performance variability observed experimentally (Reynolds, Braver, Brown, & Van der Stigchel, 2006).

Working memory tasks, although typically conceived of as being distinct from context processing and task-switching paradigms, also often have a context-target structure. In this case, the contextual information consists of items that should be stored in short-term memory over a delay interval, but also used to guide responding to the target. Although it is typically assumed that working memory tasks predominantly depend upon proactive control, in order to keep memory items actively maintained over the delay, more recent attention has been given to target-evoked interference effects that also suggest the presence and demand for reactive control (Berman, Jonides, & Lewis, 2009; Irlbacher, Kraft, Kehler, & Brandt, 2014). Indeed, it is important to note that the DMC framework does not imply an equivalence between short-term memory storage and proactive control. Rather, proactive control refers to processes that select specific items in short-term storage for further attentional processing, such as in the case of the n-back or directed-forgetting-type paradigms, or bias attention towards only task-relevant features of probe items, as in recent negative probe paradigms (Irlbacher et al., 2014). In prior work, we and others have shown that biases towards proactive versus reactive control can be modulated in these paradigms by various manipulations (Irlbacher et al., 2014), such as the expected working memory load (Speer, Jacoby, & Braver, 2003) and the frequency of target-related interference (Burgess & Braver, 2010).

Even in memory tasks that involve much longer delays than standard working memory paradigms, the DMC framework can be used to help understand variability in the cognitive strategies and behavioural markers of cognitive control engaged for task performance. Although there have been very few studies directly examining proactive and reactive control within the episodic memory domain (Dobbins & Han, 2006; Velanova et al., 2003), within the domain of prospective memory, there have been explicit theoretical accounts focusing on variability in the control mechanisms used to support memory for delayed intentions (Einstein et al., 2005). Specifically, it has been recently noted that the influential multi-process account of prospective memory, which postulates a key distinction between sustained attentional monitoring and spontaneous retrieval processes, aligns well to distinctions between proactive and reactive control (Bugg, Scullin, & McDaniel, 2013). A variety of factors are thought to influence whether control is biased towards proactive (attentional monitoring) or reactive (spontaneous retrieval) strategies, but one of the key variables is whether cues indicating the prospective memory target are salient and focally processed as part of the ongoing task or not. In recent work, we have shown that a subtle distinction between the use of focal versus non-focal prospective memory targets had a strong influence on both task performance and the dynamics and location of prefrontal control regions (McDaniel, Lamontagne, Beck, Scullin, & Braver, 2013).

The DMC framework has also been extensively applied in contexts that do not involve cue-target designs or strong memory requirements, but rather primarily tap into selective attention and inhibition or interference control. For example, in the classic Stroop paradigm (Stroop, 1935), cognitive control demands are thought to vary as a function of the

proportion of congruent (word name and ink colour match) to incongruent items (word indicates a different colour name than the ink colour [Chapter 5 by Bugg in this volume; Bugg & Crump, 2012; Jacoby, Lindsay, & Hessels, 2003; Logan & Zbrodoff, 1979]). For block-wise manipulations of proportion congruency, it is intuitive to think that proactive control would increase when the tonic, global expectation for interference is high relative to when it is low. Conversely, when proportion congruency is manipulated in an item-specific manner (e.g., certain colours, such as red, are mostly congruent, whereas others, such as blue, are mostly incongruent), but overall block-wise expectations for interference are low, then reactive control might be the dominant mode. Recent work has supported this distinction with reductions of Stroop interference observed following both block-wise and item-specific proportion congruency manipulations (Bugg, Jacoby, & Toth, 2008); however, the two different manipulations have been associated with distinct behavioural and neural signatures (Bugg & Hutchison, 2013; Bugg, Jacoby, & Chanani, 2011; De Pisapia, Slomski, & Braver, 2007; Gonthier, Braver, & Bugg, in revision; Grandjean et al., 2012; Wilk, Ezekiel, & Morton, 2012).

Although less extensively studied, the same types of proportion congruency manipulations can easily be applied and may produce the similar dissociations in related attentional and stimulus-response compatibility paradigms, such as the flanker task (Gratton, Coles, & Donchin, 1992) and the Simon task (Torres-Quesada, Funes, & Lupianez, 2013). These paradigms are also beginning to be explored with precuing manipulations, with the hypothesis that congruency precues might produce preparatory (proactive) control patterns (Bugg & Smallwood, 2014; Chiew & Braver, 2016; Czernochowski, 2015). Finally, a related strategy of precuing control demands has also begun to be explored within the domain of response inhibition, in paradigms such as the go-no go and stop signal (Aron, 2011; King, Korb, von Cramon, & Ullsperger, 2010). In this literature, it has been somewhat surprising that response inhibition, which in some sense represents the most extreme example of reactive control (see Chapter 6 by Verbruggen & Logan in this volume), can show evidence of implementation of proactive control strategies under conditions in which inhibitory demands can be anticipated (Berkman, Kahn, & Merchant, 2014; Verbruggen & Logan, 2009).

Temporal Dynamics and Neural Bases of DMC

The DMC framework makes strong predictions regarding the temporal dynamics of proactive and reactive control. Proactive control is thought to be characterised by sustained and/or anticipatory neural activity, reflecting the active maintenance of context representations, whereas reactive control is thought to be engaged on an as-needed basis, and is thus characterised by rapid engagement of transient neural activity just prior to responding (see Figure 9.3a for a schematic diagram of control dynamics). A range of methods has been used to characterise the anatomical localisation and temporal dynamics of these control mechanisms, with different advantages and disadvantages in terms of spatial and temporal resolution. These techniques have included fMRI, event-related potentials (ERPs), and pupillometry.

Functional neuroimaging using fMRI has played a key role in investigations of cognitive control within the DMC framework. We do not intend to provide an exhaustive review of this line of research here, but instead specifically highlight how fMRI has made neural investigation of separate control modes with distinct temporal dynamics possible. As noted before, the DMC framework predicts that proactive control is associated with relatively sustained and/or anticipatory activity, whereas reactive control is associated with relatively transient activity. fMRI studies of cognitive control have been consistent with the idea that a proactive control mode is associated with sustained activity in the PFC (Braver, 2012), whereas reactive

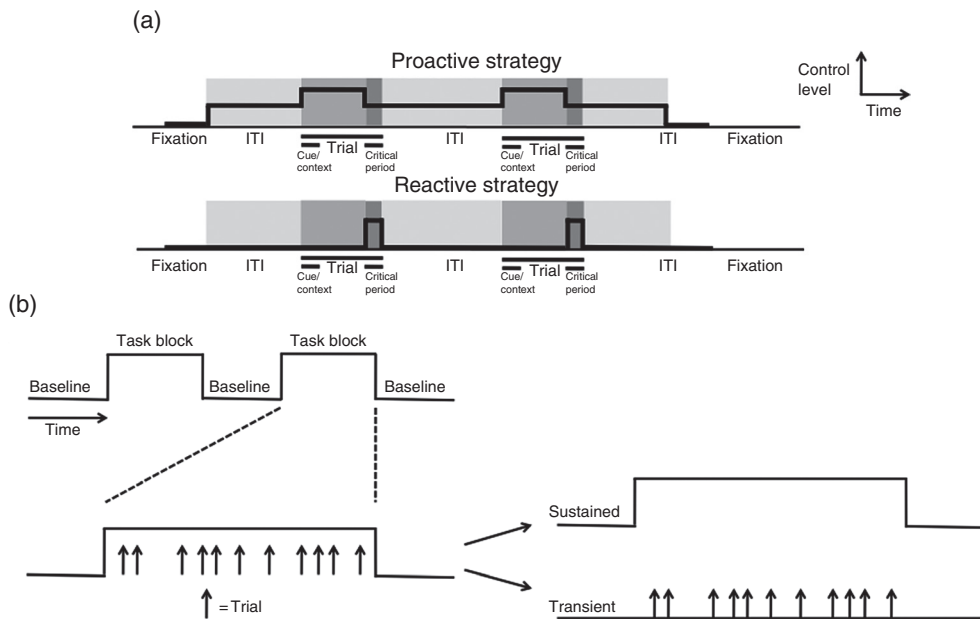


Figure 9.3 (a) Schematic of the temporal dynamics of proactive and reactive control in a context-processing task (such as the AX-CPT), as predicted by the DMC framework. Proactive control is characterised by sustained, preparatory control maintained over time (i.e., increased both tonically throughout a block and/or in an anticipatory fashion, following advance contextual cues), whereas reactive control is characterised by transient activity recruited just prior to responding. (b) The mixed block/event-related experimental design allows for simultaneous modelling of transient, trial-related activity and the sustained task-related activity.

control may rely on transient activity in a more distributed set of brain regions, including the PFC but also implicating an important role for other neural regions including the anterior cingulate, which has been implicated in the detection of conflict, error detection, or performance monitoring signalling the need for changes in control demand (Botvinick, Cohen, & Carter, 2004; Chapter 15 by Brown in this volume; Brown & Braver, 2005; van Veen & Carter, 2002; Chapter 17 by Ullsperger in this volume); all of these control functions can be considered highly reactive in nature.

Block and event-related fMRI designs allow characterisation of sustained and transient neural activity, respectively (Buckner, 1998), but do not allow dissociation of activations at different temporal dynamics. The *mixed block/event design* was developed for use with fMRI to address this issue, permitting disentanglement of relatively block versus event-related effects, originally in the context of visual processing (Visscher et al., 2003), but subsequently with a wealth of cognitive tasks (see Figure 9.3b). Employment of this design in conjunction with fMRI has been very useful in delineating both sustained and transient neural activity associated with cognitive control performance, providing evidence in support of the DMC framework. For example, using a mixed block/event fMRI design in combination with a task-switching paradigm (Braver, Reynolds, & Donaldson, 2003), changes in sustained activity in control-related brain areas were observed to relate to task set (i.e., task switching vs. single-task blocks), but additionally, transient activity in control-related regions was observed on a trial-by-trial basis with changing task demands (i.e., repeat vs. switch trials) and response speed. Likewise, within prospective memory, this design enabled dissociation of a

primarily sustained dynamics observed in anterior and dorsolateral PFC under nonfocal (proactive) conditions, but only transient activity in ventral PFC, ACC, and medial parietal regions during focal (reactive) conditions (Braver et al., 2003).

Other event-related designs have enabled dissociation and characterisation of distinct events within a given trial, such as cue/delay versus target periods in cued task switching and context processing paradigms (Ruge, Goschke, & Braver, 2009) and encoding/retention versus probe periods in working memory paradigms (Jimura, Locke, & Braver, 2010). These types of designs have been useful in demonstrating distinct patterns of temporal dynamics in task conditions associated with proactive versus reactive control, as well as shifts in dynamics that can occur even within the same lateral PFC regions, as was observed as a function of both cognitive training and motivational incentives in the AX-CPT task (Braver, Paxton, Locke, & Barch, 2009) (Figure 9.4).

Although fMRI has been a critical tool in investigating the temporal dynamics of cognitive control within the PFC and other neural areas, other methodologies have also

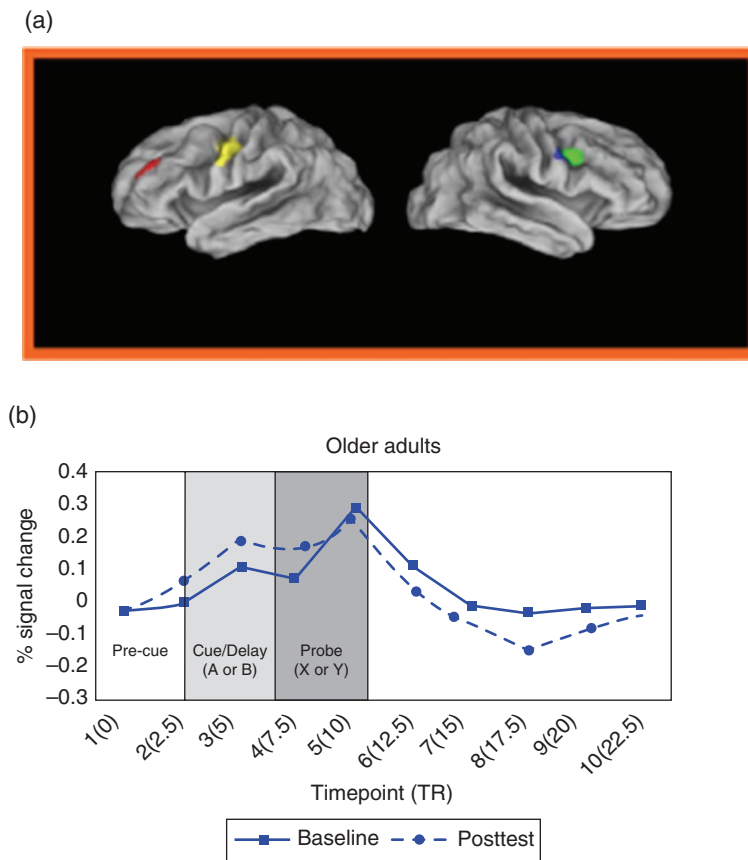


Figure 9.4 Dynamic shifts in cognitive control-related activity in the lateral PFC as a result of training and incentive manipulations. (a) Regions (see Braver et al., 2009, for exact coordinates) demonstrating training-related proactive shift (increased cue-related and decreased probe-related activity) in older adults and penalty-related reactive shift (decreased cue-related and increased probe-related activity) in young adults. (b) Activation dynamics for older adults at baseline and post-test conditions in brain regions identified in (a).

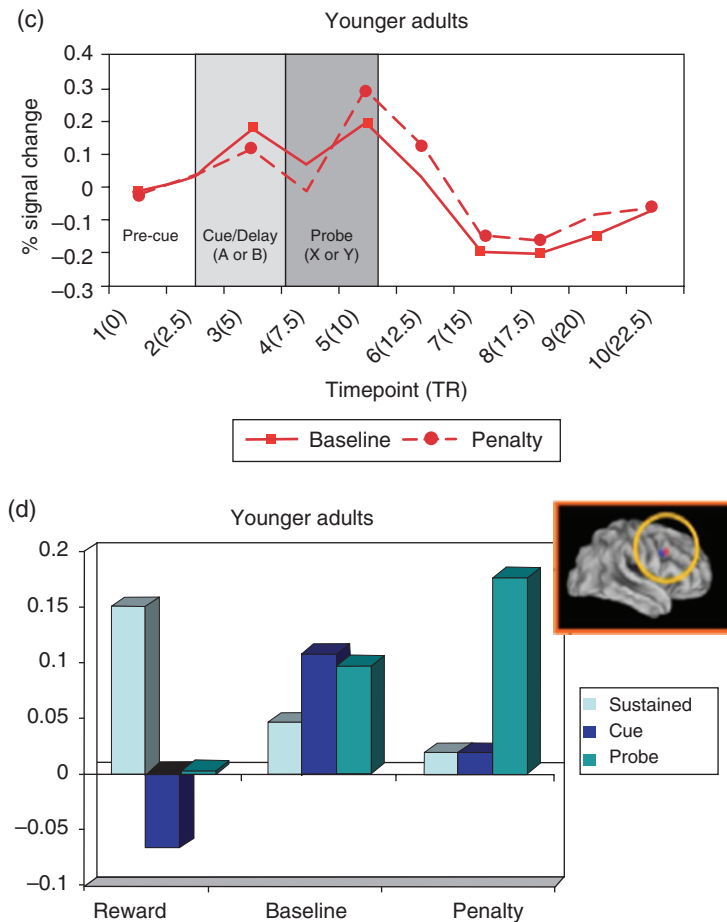


Figure 9.4 (Continued) (c) Activation dynamics for younger adults at baseline and penalty conditions in brain regions identified in (a). (d) Shift from sustained to relatively cue-related to relatively probe-related activation dynamics in the right inferior frontal junction across reward, baseline, and penalty AX-CPT conditions. Source: Braver 2009. Reproduced with permission from Braver.

emerged as useful tools for investigation of cognitive control within the DMC framework. Tools such as ERPs and pupillometry may provide higher temporal resolution (although with a trade-off in terms of spatial resolution) than fMRI as well as cheaper and easier data collection, providing a methodological advantage for some investigations. ERP investigations of cognitive control within the DMC framework are still somewhat limited in number, but existing studies have reported evidence consistent with the concept of functional neural dissociation between two control modes. These include investigations of the neural correlates of top-down control versus conflict monitoring (West, 2003) and investigations of conflict and error monitoring and subsequent control adjustment implicating a role for the anterior cingulate (Gehring, Goss, Coles, Meyer, & Donchin, 1993; van Veen & Carter, 2002).

Studies focussed on examining the differential temporal dynamics of cognitive control in relation to the DMC framework have observed changes to ERP component dynamics in

response to (a) proportion congruency manipulations in a Stroop task, in line with behavioural evidence of changes in task performance with such manipulations (West & Bailey, 2012); (b) effects of proactive cueing on task-switching performance (Czernochowski, 2015); and (c) age-related changes in the AX-CPT (Hammerer, Li, Muller, & Lindenberger, 2010; Schmitt, Ferdinand, & Kray, 2015). In particular, these studies have revealed double dissociations between distinct negative medial components associated with proactive and reactive control (greater medial frontal negativity associated with proactive control, vs. greater medial posterior negativity associated with reactive control; West & Bailey, 2012) as well as evidence of sustained slow-wave activity while in a proactive control mode, versus the absence of such activity in a reactive control mode (Czernochowski, 2015). Such findings support the utility of ERP measures for identifying neural components of proactive and reactive modes of control operating with distinct temporal dynamics, thus both supporting the DMC framework while clarifying underlying mechanisms of the two proposed control modes. Thus, continued use of this methodology in future work seems especially promising.

In addition to ERP measures, pupillometry has recently emerged as a tool of interest in investigating the temporal dynamics of cognitive control. Based on predictions that proactive control would manifest as preparatory and/or sustained dilation whereas reactive control would manifest as post-stimulus transient dilation, pupil dilation was used to index developmental changes in a modified AX-CPT paradigm, demonstrating a shift from predominantly reactive to proactive control over childhood (Chatham, Frank, & Munakata, 2009). More recently, we demonstrated that pupillometry can be combined with a mixed block/event experimental design to examine changes in cognitive control dynamics (Chiew & Braver, 2013, 2014), specifically by examining the effects of reward incentives on AX-CPT performance and concurrent pupil dilation. We demonstrated that incentives were associated with enhanced performance and pupil dilation (i.e., indicative of increased control), both on a sustained basis (comparing reward vs. baseline blocks) and a transient, trial-evoked basis (comparing incentive trials vs. non-incentive trials within a single block), suggesting a shift towards enhanced proactive control (see Figure 9.5). However, pupillometric investigations of cognitive control are still at a relatively early stage, and underlying neural contributions to the pupil signal are still being elucidated. Nevertheless, a particularly exciting direction for this work is the potential utility of pupillometry (and other oculometric measures) in examining the dynamics of neuromodulatory influences on control, as a potential peripheral marker of both noradrenergic and potentially dopaminergic effects (Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; van Bochove, Van der Haegen, Notebaert, & Verguts, 2013).

Affective and Motivational Influences

A major thrust of the DMC framework has been to advance the understanding of cognitive control in terms of ‘non-cognitive’ factors, such as affect and motivational influences. Specifically, in the DMC framework, these factors can also contribute to the balance between proactive and reactive control, and thus variability in control performance. Investigations focussed on affective (Chapter 22 by Pessoa in this volume) and motivational influences (Chapter 24 by Krebs & Woldorff in this volume) on cognitive control have become a fast-growing field of study, within which the DMC framework has acted as a useful theoretical tool for interpretation of data and generation of future predictions. There are two theoretical components of the DMC framework that provide relevant conceptual assumptions and hypotheses regarding affect and motivational factors. First, proactive control should maximise harvesting of available rewards, given that a preparatory, planning-based mode should optimise the use of contextual, reward-predictive cues, as well as more tonic indicators of the

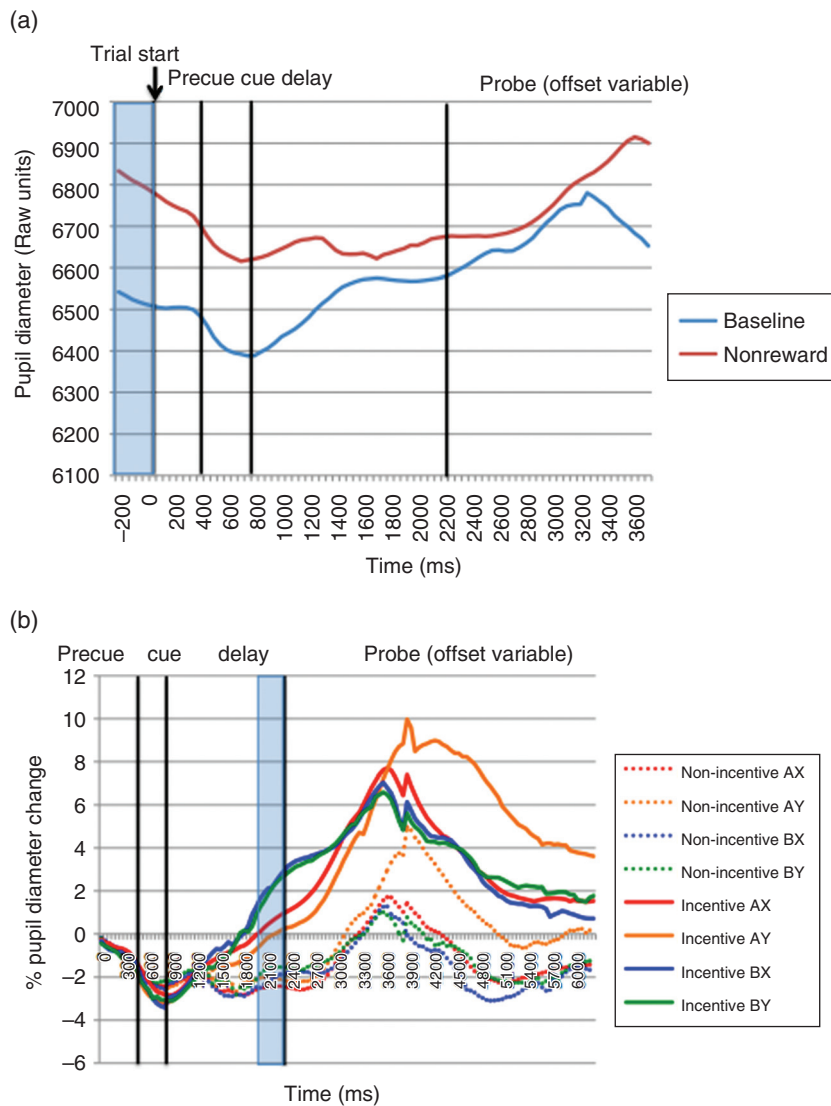


Figure 9.5 Sustained and transient changes in pupil dilation activity as a function of reward incentives in the AX-CPT task. (a) Pupil timecourses as a function of incentive status for the sustained (block) contrast: baseline block trials versus non-incentivized trials within reward block, averaged across trial types. (b) Pupil timecourses as a function of incentive status for the transient contrast: non-incentivized versus incentivized trials within the reward block.

current reward context. Conversely, because such reward signals are known to result in phasic (and potentially tonic; Niv, Daw, Joel, & Dayan, 2007) DA responses (Schultz, Dayan, & Montague, 1997), these should enhance the ability to actively maintain goal representations within the lateral PFC. Thus, according to the DMC framework, enhancement of such reward signals should facilitate implementation of proactive control. Second, the reactive mode should be preferred when control resources need to be deployed towards background monitoring of the external (and internal) environment for the presence of potential threats. This is because proactive control makes the cognitive system less sensitive to goal-incongruent

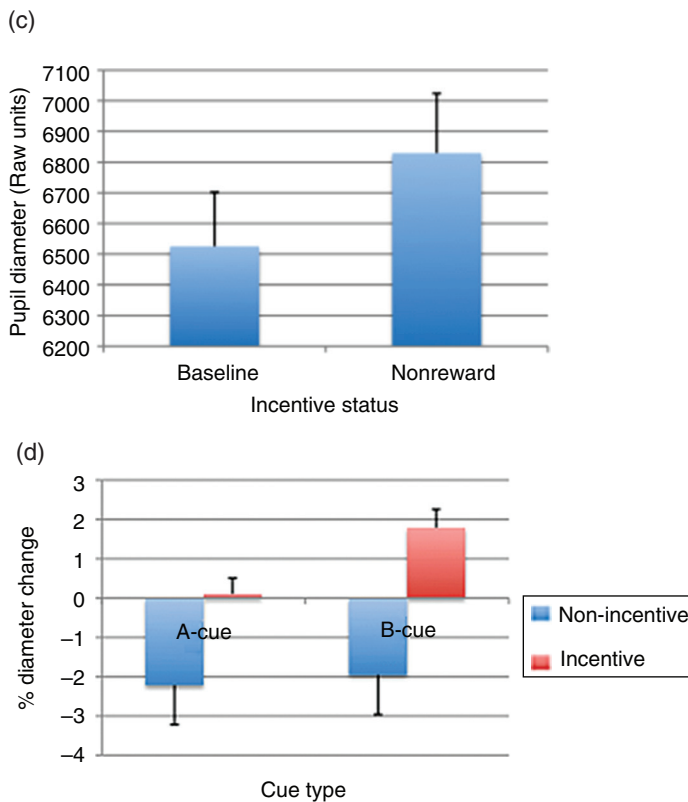


Figure 9.5 (Continued) (c) Sustained incentive effects (i.e., an increase in averaged pupil magnitudes) at the pre-trial period (–200 to 0 ms). (d) Transient incentive effects (i.e., an increase averaged pupil magnitudes) during cue maintenance prior to probe onset (1,950 to 2,200 ms). The transient effects also show an additional increase in pupil dilation following the high control-demand B-cues. Source: Adapted from Chiew and Braver 2013.

or incidental features of the environment, which might be threat relevant. Thus, according to the DMC framework, high demands or a pre-existing bias towards background threat monitoring should predispose cognitive control towards the reactive mode.

In recent years, there has been an upsurge in research specifically examining the relationship between reward motivation and cognitive control (Botvinick & Braver, 2015; Braver et al., 2014; Pessoa, 2009; Chapter 22 by Pessoa in this volume; Chapter 24 by Krebs & Woldorff in this volume) in studies utilising manipulation of reward incentives. Observed changes in task performance under reward incentives have been consistent with the hypothesis of enhanced proactive control across several cognitive control tasks, including the AX-CPT (Chiew & Braver, 2013; Locke & Braver, 2008), task-switching (Umemoto & Holroyd, 2014) and working memory tasks (Beck, Locke, Savine, Jimura, & Braver, 2010; Savine, Beck, Edwards, Chiew, & Braver, 2010), and Stroop-type paradigms (Soutschek, Stelzel, Paschke, Walter, & Schubert, 2015).

In addition, our research has utilised the DMC framework to develop and test predictions about the extent to which positive affect (i.e., positively valenced subjective experience) and reward incentive influences on cognitive control should be considered a common construct or dissociable in nature (Chiew & Braver, 2011, 2014). This investigation drew on prior

findings suggesting that positive affect is associated with more flexible, but also more easily distracted, performance (suggesting a more reactive mode of control; Dreisbach, 2006; Dreisbach & Goschke, 2004), although these results are not always consistent (Frober & Dreisbach, 2012). We contrasted these findings with evidence that reward incentives have been associated with enhanced context maintenance and proactive control, as described above (Locke & Braver, 2008). Direct comparison of positive affect and reward incentive influences on cognitive control as indexed by the AX-CPT and pupillometric measures suggested that both influences were associated with increased proactive control, although reward incentives led to a much larger shift in performance relative to baseline (Chiew & Braver, 2014). This and related investigations (Frober & Dreisbach, 2014; Goschke & Bolte, 2014) have led to more nuanced conceptualisations of dissociable hedonic and motivational influences on cognition, and predictions to be tested in future work (Notebaert & Braem, 2015).

Individual Differences

Individual variation in both cognitive factors (i.e., working memory capacity; Engle, 2002) and affective factors (i.e., personality) may influence cognitive and neural activity supporting goal-directed behaviour. There has been a recent upsurge of interest in these individual differences, based on the recognition that use of cognitive neuroscience methodologies may help clarify the core mechanisms that give rise to such variation, while establishment of brain-behaviour relationships can provide convergent evidence for theoretical hypotheses of cognition (Braver, Cole, & Yarkoni, 2010). Individual differences may act as important, stable sources of variance in the balance between proactive and reactive control, and may also determine the extent to which other manipulations influence the balance between modes of control, as we outline below.

Working memory capacity (WMC), which can be defined as the executive-attention element of the working memory system allowing information maintenance in the presence of interference, has been associated with PFC function and is of interest as a factor accounting for individual differences in cognitive performance (Kane & Engle, 2002). Individual variation in WMC has been associated with goal maintenance and context processing ability (Redick & Engle, 2011), and thus may act as an important potential determinant of proactive control. Consistent with this prediction, recent studies using adaptations of the AX-CPT paradigm suggest that task performance in high-WMC individuals thus tends towards proactive control (greater interference on AY trials and decreased interference in BX trials, relative to low-WMC individuals; Redick, 2014; Richmond, Redick, & Braver, 2015).

Individual differences in WMC, or related cognitive dimensions such as fluid intelligence (Burgess, Gray, Conway, & Braver, 2011; Kane & Engle, 2002), might also interact with other task factors to influence whether cognitive control shifts between proactive and reactive control modes. In one such study examining the interaction between experimental and individual difference factors (Burgess & Braver, 2010), it was found that increasing interference expectancy in a recent negative probes working memory paradigm led to a general shift towards proactive control, evidenced by reduced interference and a shift of PFC dynamics from being primarily (recent negative) probe driven to present during the cue and delay period. However, this pattern also interacted with individual differences in fluid intelligence (gF), with low-gF individuals showing some evidence of increased reactive control (rather than a shift to proactive control) under conditions of high interference expectancy, whereas in high-gF individuals there was an increased tendency towards the proactive control pattern being used even under low interference expectancy conditions.

Putatively ‘non-cognitive’ individual differences, such as personality traits, may also play an important role in determining the balance between proactive and reactive control, especially when considered in combination with other influences on control. Such traits may not have a direct influence on cognitive processing, but instead influence the relative costs versus benefits of engaging in one cognitive mode over another. For example, individual variation in reward sensitivity may play a key role in the extent to which reward incentives alter motivation to perform a given task. Experimental evidence suggests that reward-sensitive individuals demonstrate enhanced performance under incentive context on a working memory task, and that this performance change was accompanied by a shift from transient to tonic activity in the right lateral PFC, suggesting that individual variation in reward sensitivity was associated with variation in incentive-related enhancement in proactive control (Jimura et al., 2010).

Individual differences in (non-clinical) trait anxiety have also been found to influence the balance between proactive and reactive control during working memory performance (Fales et al., 2008): A mixed block/event fMRI design revealed a tendency towards reactive control (i.e., decreased sustained and increased transient PFC activity) during task performance as a function of trait anxiety. This is consistent with the idea that individuals with increased anxiety may expend more cognitive resources on worrying or background monitoring for the presence of environmental threats, thus tending towards reactive control as a less efficient but also less effortful task strategy (Eysenck & Calvo, 1992).

Comparisons Between Populations

Initial development of the gating model and subsequent development of the DMC framework drew on observations of impaired context processing and altered DA activity in individuals with schizophrenia (Chapter 31 by Barch & Sheffield in this volume), identifying DA modulation as a candidate gating mechanism regulating information access to the cortex. Subsequently, the DMC framework has provided a powerful means by which to interpret data and generate predictions regarding differences in context processing and cognitive control performance between different populations.

The DMC model has been proved to be especially fruitful for examining age-related changes in cognitive control, both in older adults and during developmental periods (see also Chapter 27 by Zanto & Gazzaley in this volume). Healthy ageing is associated with impairments in cognitive performance and declines in DA neuromodulation due to DA neuron and receptor loss (Backman, Nyberg, Lindenberger, Li, & Farde, 2006; Li, Lindenberger, & Sikstrom, 2001). Systematic investigation of age-related changes in performance in terms of dual control modes has revealed that cognitive performance does not decline globally with ageing, but instead older adults may demonstrate a specific decline in proactive control mechanisms, while reactive control mechanisms remain relatively intact. Behavioural studies of AX-CPT performance in younger and older adults provided have demonstrated improved AY trial performance and worsened BX trial performance with age, consistent with a specific decrement in context maintenance (Braver et al., 2001; Braver, Satpute, Rush, Racine, & Barch, 2005). Following up on these results, a neuroimaging study examined the effects of aging on AX-CPT performance and neural activity using a mixed block/event design to dissociate sustained and transient activations (Paxton et al., 2008). fMRI revealed decreased activity during the cue/delay period and increased activity during the probe period in older relative to younger results, providing neural evidence of decreased proactive and increased reactive control with ageing, complementary to evidence from behavioural performance.

However, it is important to note that the shift from proactive to reactive control might reflect a strategic decision (though not necessarily a conscious or volitional one) made from changes in cost-benefit weightings in the two modes. Support for this idea was found in later studies that examined the degree to which reactive control shifts could be reversed, or at least minimised, following focussed cognitive training. In particular, studies using the AX-CPT task found that training in the explicit utilisation of contextual cues to prepare probe responding led to a shift in both behavioural performance profiles and neural activation dynamics among older adults, to bring them closer to the young adult pattern observed in the task (Braver et al., 2009; Paxton, Barch, Storandt, & Braver, 2006; see Figure 9.4). Work using highly similar training and experimental protocols also observed similar ‘normalisation’ effects among individuals with schizophrenia in the AX-CPT (Edwards, Barch, & Braver, 2010).

As described earlier, studies using other methodologies, such as ERP, have also been employed to provide evidence for reactive shifts in older adults (Czernochowski, Nessler, & Friedman, 2010; Schmitt et al., 2015). Similar approaches have been used at the other end of the lifespan to demonstrate enhanced reactive control tendencies in younger children and adolescents (Andrews-Hanna et al., 2011). For example, Chatham et al. (2009) used pupillometric and behavioural performance measures to provide evidence for a shift from reactive to proactive control from 3.5- to 8-year-old children in the AX-CPT. These investigations demonstrate the utility and versatility of the DMC framework as a theoretical and experimental tool for understanding how cognitive control processes might change across different population groups. Most critically, the framework provides a more nuanced account of such cognitive control differences, as not simply reflecting intact versus poor cognitive control, but rather a shift in which the type of control strategy tends to be engaged, and how these might be influenced by both task factors and cost-benefit calculations.

Directions for Future Research

As we have attempted to illustrate through this brief review, considering cognitive control in terms of context processing and proactive versus reactive mechanisms has proved to be useful in understanding the adaptive quality of goal-directed behaviour. The DMC framework posits a neurobiologically grounded mechanistic account of cognitive control that can be experimentally tested, across a variety of task paradigms, with a range of cognitive neuroscience methodologies, and in terms of individual and population group differences. These advances have also opened up new questions for future research to address. A number of these outstanding questions, regarding further clarification of gating mechanisms, affective and motivational influences, and the role of individual differences, have been discussed throughout the body of the present chapter. In the present section, we wish to highlight research directions that are somewhat broader than these previously discussed issues, aiming to advance understanding of cognitively controlled behaviour within the DMC framework and within the broader landscape of current cognitive neuroscience research.

An important issue that remains to be resolved is the extent to which proactive and reactive control constitute independent mechanisms. The DMC framework in its present form postulates that the two control modes will be necessarily inversely correlated, in that increased utilisation of proactive control should reduce the demand on reactive control, and vice versa. Likewise, given the distinct computational costs and benefits associated with each mode, the circumstances in which one mode is advantageous are generally circumstances in which the other is not. Nevertheless, it is still an open question whether it is best to think of proactive and reactive control as opposite poles of a single dimension, or rather, two (semi-) independent dimensions of control, that can be modulated in isolation. Thus, an important

larger-scale project of interest is to determine whether experimental task manipulations can be designed that influence one control mode, while not affecting the other, across the range of domains and paradigms for which the DMC framework has already proved to be useful (i.e., context processing, cued task switching, working memory, selective attention, prospective memory, and response inhibition).

Initial findings in this endeavour have proved promising. Within the Stroop task, double dissociations have been established, demonstrating that block-wise proportion congruency manipulations show distinct behavioural signatures from item-specific manipulations, with each consistent with selective changes to proactive and reactive control, respectively (Gonthier et al., in revision). In addition, recent work has suggested that positive affect can lead to decreased proactive control without alterations in reactive control (Frober & Dreisbach, 2012). Further work is required, however, to establish whether these control modes can be considered fully independent, and yield not only doubly dissociable behavioural signatures, but also neural ones as well.

Another issue that remains to be addressed is the reconciliation of the DMC framework with other models of cognitive control. One important alternative model posits that cognitive control can be understood in terms of hierarchically organised rule representations and that this organisation is supported neuroanatomically, from low-level to high-level control, by caudal to rostral subregions of the PFC (Badre, 2008; Chapter 12 by Duverne & Koechlin in this volume). Although empirical evidence exists for the hierarchical model framework, initial attempts to reconcile the hierarchical and DMC frameworks have not met with success and, in fact, have shown evidence against a strict hierarchical account in favour of a dynamically flexible one (Reynolds, O'Reilly, Cohen, & Braver, 2012). A recent study by Bahlmann and colleagues (Bahlmann, Aarts, & D'Esposito, 2015) examined the effect of reward incentives on hierarchically organised cognitive control performance and task-related fMRI activity in the PFC and observed that incentive-related benefits in performance were greatest at mid-level (vs. high-level or low-level) control. Given extensive evidence from studies within the DMC framework that reward incentives may enhance proactive control, future studies could potentially explore whether hierarchical and temporal dimensions of control are orthogonal or interactive: That is, it may be possible that control of mid- and high-level task representations (those that are more abstract) involve proactive control in a manner that is not necessary for lower-level ones.

A third issue for future research within the DMC framework to consider is the adoption of a particular cognitive control strategy in terms of cost-benefit decision making. Recent evidence suggests that individuals are inclined to minimise cognitive effort, consistent with the 'law of less work' (Kool, McGuire, Rosen, & Botvinick, 2010; see also Chapter 10 by Kool, Shenhav, & Botvinick in this volume) but may decide to engage cognitive effort based on the anticipated reward value of doing so (Dixon & Christoff, 2012). Moreover, recent findings suggest that the subjective cost of cognitive effort may vary based on both within-individual factors including objective load and anticipated reward, individual difference factors such as trait cognitive motivation, and population differences such as older age (Westbrook, Kester, & Braver, 2013). The sensitivity of subjective cognitive effort costs to all three of these dimensions of variability suggests an important point of potential contact with the DMC framework. In particular, it may be the case that it is specifically the utilisation or demand for proactive control that may underlie the subjective cost of cognitive performance (Westbrook & Braver, 2015). However, direct evidence for this possibility is still lacking. Nevertheless, an important direction for future research is to better understand variability in cognitive control strategies, such as that postulated in the DMC framework, in terms of subjective value and costs, and more generally, from within a framework of cost-benefit decision making (Botvinick & Braver, 2015).

Conclusion

As this review has aimed to demonstrate, the DMC framework has provided an important conceptual account aiming to clarify the computational and neural mechanisms underlying variation in cognitive control, using different cognitive paradigms, methodologies, and comparison groups. Research within this framework has illustrated the importance of considering the temporal dynamics of cognitive and neural processes underlying adaptive, goal-directed behaviour and has illustrated how ‘non-cognitive’ factors such as affect, motivation, and individual differences may be important determining factors in the engagement of cognitive control, even though they may not influence the efficacy of cognitive function directly. Many questions remain for future research; critical among these is the question of how key principles and findings of the DMC framework can be integrated with evidence from other models and accounts of cognitive control. Addressing this question will be critical in developing an improved and more integrative theoretical framework to further advance our understanding of human higher cognitive function.

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