Author's personal copy

Opinion

Cell PRESS

The variable nature of cognitive control: a dual mechanisms framework

Todd S. Braver[1,2*]

[1] Department of Psychology, Washington University in St. Louis, St. Louis, MO 63130, USA
[2] Department of Radiology, Washington University in St. Louis, St. Louis, MO 63130, USA

A core component of cognitive control – the ability to regulate thoughts and actions in accordance with internally represented behavioral goals – might be its intrinsic variability. In this article, I describe the dual mechanisms of control (DMC) framework, which postulates that this variability might arise from qualitative distinctions in temporal dynamics between proactive and reactive modes of control. Proactive control reflects the sustained and anticipatory maintenance of goal-relevant information within lateral prefrontal cortex (PFC) to enable optimal cognitive performance, whereas reactive control reflects transient stimulus-driven goal reactivation that recruits lateral PFC (plus a wider brain network) based on interference demands or episodic associations. I summarize recent research that demonstrates how the DMC framework provides a coherent explanation of three sources of cognitive control variation – intra-individual, inter-individual and between-groups – in terms of proactive versus reactive control biases.

Shifting the emphasis to variability in cognitive control

One of the most fascinating mysteries of human cognition is the capacity for cognitive control: the ability to regulate, coordinate, and sequence thoughts and actions in accordance with internally maintained behavioral goals. Although it is clearly the case that substantial theoretical and experimental progress has occurred in the past 20 years regarding the mechanisms that enable cognitive control [1–7], there is still a great deal that remains poorly understood, subject to debate, and without clear consensus among investigators working in this field.

The majority of research efforts have focused on accounting for the diversity, scope and range of cognitive control functions in terms of an ever expanding conceptual taxonomy or fine-grained anatomically oriented fractionation scheme [8–15]. In this article, instead, I discuss the DMC framework [16,17], which shifts the emphasis towards an exploration and appreciation of the intrinsic variability that may in fact be a core component of cognitive control, and a means of potentially capturing and explaining this variability in terms of the temporal dynamics of control processes.

The main tenet of the DMC account, first described in detail in 2007 [16], posits variation between two qualitatively distinct control modes. In the sections that follow, I lay out the DMC account, and draw upon recent research to demonstrate how it provides a coherent explanation of three empirically observed sources of variation in cognitive control function: intra-individual (i.e. state related or task related), inter-individual (i.e. trait related) and between-groups (i.e. related to changes in brain function or integrity in different populations).

The dual mechanisms of control framework

The central hypothesis of the DMC framework is that cognitive control operates via two distinct operating modes: 'proactive control' and 'reactive control'. The proactive control mode can be conceptualized as a form of 'early selection' in which goal-relevant information is actively maintained in a sustained manner, before the occurrence of cognitively demanding events, to optimally bias attention, perception and action systems in a goal-driven manner [1]. By contrast, in reactive control, attention is recruited as a 'late correction' mechanism that is mobilized only as needed, in a just-in-time manner, such as after a high interference event is detected [18]. Thus, proactive control relies upon the anticipation and prevention of interference before it occurs, whereas reactive control relies upon the detection and resolution of interference after its onset (Figure 1).

The DMC account provides a strong prediction about the temporal dynamics and location of brain activity under proactive versus reactive control. Proactive control should be associated with sustained and/or anticipatory activation of lateral PFC, which reflects the active maintenance of task goals. This goal maintenance activity serves as a source of top-down bias that can facilitate processing of expected upcoming events that have a high cognitive demand. By contrast, reactive control should be reflected in transient activation of lateral PFC, along with a wider network of additional brain regions. This transient activity might reflect the bottom-up reactivation of task goals, mediated either via the detection of interference (e.g. through the engagement of conflict monitoring regions such as the anterior cingulate cortex [ACC]; [5]) or via associative and episodic associations (as might occur through posterior cortical or medial temporal lobe regions). In addition, the two control mechanisms should differ in terms of the involvement of the dopaminergic (DA) system. The ability to actively sustain inputs in PFC requires a phasic DA-mediated gating signal occurring at the time when contextual cues are presented [19,20]. Without such a gating signal, PFC can only be transiently activated.

Corresponding author: Braver, T.S. (tbraver@artsci.wustl.edu)
* Current address: Department of Psychology, Washington University in St. Louis, CB1125, One Brookings Drive, St. Louis, MO 63130, USA.

 1364-6613/$ – see front matter © 2011 Elsevier Ltd. All rights reserved. doi:10.1016/j.tics.2011.12.010 Trends in Cognitive Sciences, February 2012, Vol. 16, No. 2

Author's personal copy

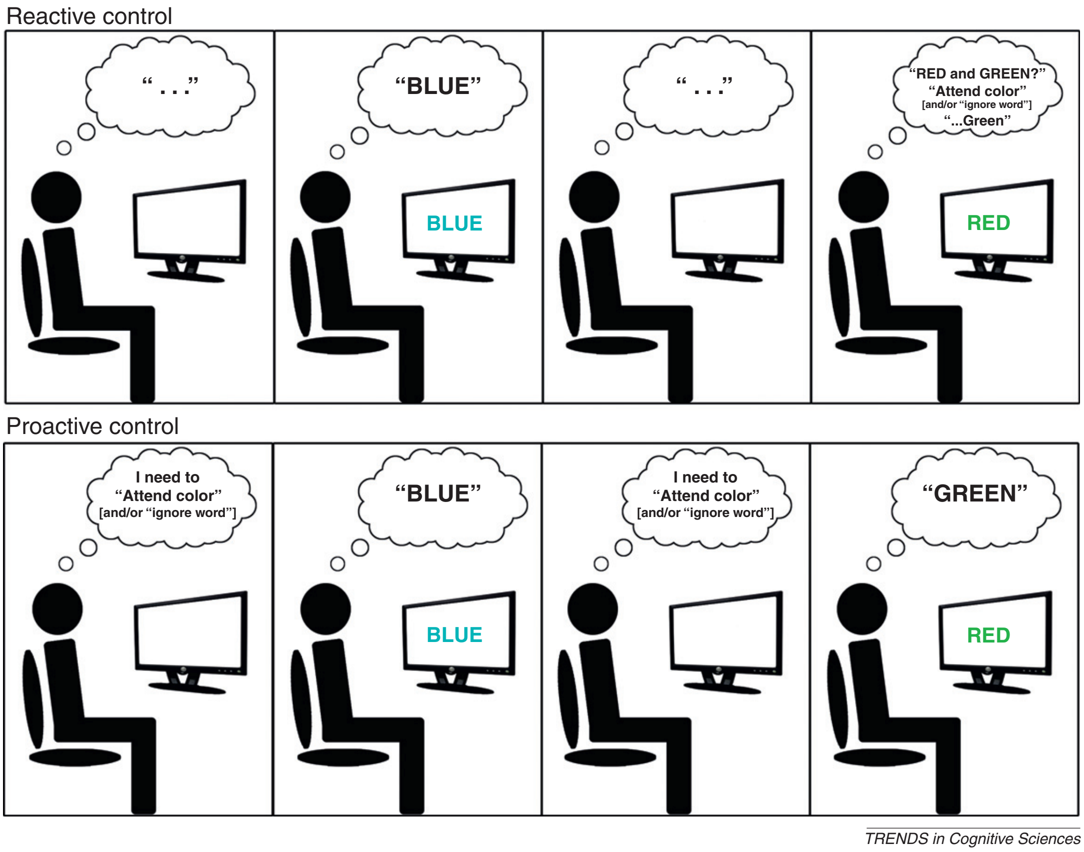

Figure 1. Conceptual distinction between reactive and proactive control, as illustrated in the classic Stroop color-naming task. Upper panel illustrates reactive control, which relies upon detection of interference (occurring in the last panel following presentation of an incongruent stimulus) to drive reactivation of task goals and enable successful responding (albeit with slower latencies). In this control mode, task goals are not actively maintained during intertrial periods (first and third panels), and may not be triggered following presentation of congruent stimuli. Lower panel illustrates proactive control, which does involve sustained active maintenance of task goals during intertrial intervals (first and third panels), and results in less conflict experienced during presentation of incongruent stimuli (last panel). It is important to note that the representation of task goals is illustrated in this manner purely for ease of description. The DMC framework makes no claims about whether these involve verbal coding or are consciously accessible.

Because both reactive and proactive cognitive control are postulated to be associated with complementary advantages and limitations (Box 1), successful cognition probably depends upon some mixture of both strategies. Indeed, it may be the case that the two systems are at least semi-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. These factors can be characteristics of the task situation but may also be characteristics of the individual. Indeed, the central aspect of the DMC account is that it provides a unifying framework for understanding both intra-individual and inter-individual variability in cognitive control function, as well as the changes in cognitive control that may be present in different populations, such as children and older adults, and groups with specific neuropsychiatric disorders.

Intra-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. Thus, the DMC account naturally leads to the idea that potentially subtle differences between otherwise similar tasks might lead to significant 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. Thus, we have utilized a research strategy of directly manipulating factors expected to influence the preferred mode of cognitive control during tasks with high control demands.

As an example of this approach, in one recent study, Burgess and Braver [21] focused on shifts in cognitive control mode that might be utilized to deal with interference during working memory, according to whether such interference can be anticipated or not. This issue was investigated with the recently popularized working memory paradigm known as the recent probes task [22], because prior studies with this paradigm have reliably observed activity in left inferior PFC occurring selectively following the presentation of high interference probes (recent negatives), suggesting the presence of a reactive control mechanism [23]. Participants performed the recent probes task under conditions of high and low interference expectancy. In the low expectancy condition, recent negative probes occurred only rarely, whereas in the high expectancy condition they were frequent (note that other

Author's personal copy

aspects of trials were also varied across conditions to compensate for the recent probe manipulation and actually served to make the expectancy effect very subtle). The expectancy manipulation led to a shift in the temporal dynamics and specificity of lateral PFC activation, in accordance with predictions of the DMC framework. Specifically, in the low expectancy condition, we replicated prior results by demonstrating that left inferior PFC (as well as other medial and lateral PFC regions) exhibited a probe-triggered increase in activity, specifically on recent negative probe trials, consistent with recruitment of reactive control (Figure 2a). By contrast, in the high expectancy condition (Figure 2a), lateral PFC activity (in adjacent regions) increased during the delay period, prior to probe onset, with this effect occurring globally (i.e. on all trials). In other words, when expectancy is high, proactive control is recruited instead of reactive control (which may be the default mode for this paradigm).

Other studies have shown similar findings when using distinct manipulations to induce shifts in cognitive control mode, or when exploring such effects within different task domains. For example, in another study of working memory, expected working memory load was manipulated across conditions, rather than interference expectancy [24]. The hypothesis was that when the expected load was low participants would be biased to adopt a proactive control strategy, using the items maintained in working memory to prepare for the upcoming probe. By contrast, when load was expected to be high (and beyond working memory capacity) participants would instead utilize the probe as a retrieval cue from which to query memory. Indeed, a distinct set of brain regions and activity dynamics were observed across conditions, even when considering trials that were matched on actual load. Specifically, in the low load condition, an anticipatory proactive pattern was observed, with activity increasing during the delay period; in the high load condition, the pattern was more reactive, with downward ramping delay activity but increased activation when the probe was presented. In studies of cued task-switching, activity dynamics within the same lateral PFC region have been found to shift on a trial-by-trial basis along with presumed shifts from reactive to proactive control. For example, on trials emphasizing high accuracy and speed (through motivational incentives), cue-related activation of a region of left dorsolateral PFC was increased, relative to intermixed low-incentive trials [25]. Such trial-by-trial shifts in control mode might even occur spontaneously: in another study, it was found that task-switching trials associated with fast performance were marked by increased cue-related and reduced probe-related activity within left lateral PFC

Box 1. Why dual mechanisms?

A key question that arises when considering these alternative modes of control is: what are the advantages of having a dual-mode system, given that it is less parsimonious than a single-mode system? This question can be answered by considering that there may be both costs and benefits associated with proactive and reactive control, such that a computational tradeoff exists. Thus, on purely computational grounds, it is sensible to argue that in the face of such tradeoffs a dual-process control mechanism is one that best optimizes information processing across the widest range of situations. Consider the following tradeoffs.

Under proactive control, goal representations are triggered in advance of their implementation, and maintained continuously during periods in which they are required, thus optimizing preparation while minimizing interference from internal or external sources of distraction. Consequently, the advantage of proactive control is that plans and behaviors can be continually adjusted to facilitate successful completion of the goal. However, the disadvantage of a proactive control strategy is that it is strongly resource consuming, requiring continuous goal maintenance. Given the clear and strong capacity limitations of goal representation in the focus of attention [48–50], the engagement of proactive control will substantially reduce available capacity for maintenance of other information that could be held in working memory. By contrast, under reactive control, goal representations are only activated (or retrieved) at the time in which they are needed. The reactive control strategy has the advantage of being computationally efficient, in that during the interval between when the intention is formed and completed, resources are freed up, such that other tasks and goals can be carried out more effectively. However, the disadvantage of this strategy is that it requires repeated reactivation of the goal rather than continuous maintenance. Thus, there is greater dependence on the trigger events themselves because if these are insufficiently salient or discriminative they will not drive reactivation.

A second form of tradeoff between proactive and reactive control is the attentional commitment required. The continuous maintenance of internal goals implements a form of sustained mental set that makes cognitive processing more brittle, and hence less sensitive to other unexpected but potentially relevant sources of bottom-up information (e.g. changing environmental contingencies). Relatedly, the engagement of proactive control is dependent on the availability of contextual cues that are strong and reliable enough to trigger goal activation and maintenance in advance of the time when those goals are needed. By contrast, because reactive control is stimulus driven and transient, it is by definition not dependent on advance contextual cues, and makes greatly reduced demands on attentional resources and commitment. However, because this form of control is stimulus dependent and late acting, it will be much more vulnerable to transient attentional capture or orienting effects that may disrupt the ability to trigger goal reactivation when necessary. In addition, reactive control will be reliant on strong bottom-up associative cues that enable stored goals to be retrieved and reaccessed, or on conflict detection mechanisms that signal when control needs to be rapidly mobilized.

A concrete example may make these contrasts clearer. Imagine a typical prospective memory situation [51], in which an intention is formed about a behavioral goal to be completed at some later point, such as stopping at the grocery store to go shopping before going home from work (Figure I). 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). By contrast, with a reactive control strategy the shopping goal would only be transiently activated at the time of intention (e.g. earlier in the day), and then be reactivated again by an appropriate trigger event (e.g. noticing the shopping list left on the car seat). In this example, a situational factor, such as the expected duration over which the intention would need to be actively maintained, might be important in determining which is the most useful control strategy. If the duration is short (e.g. the intention is formed close to the end of the day), continuous maintenance of the cognitive goal could be achieved and might be used to strongly constrain behavior during that period (e.g. not scheduling a late meeting; ensuring that the route to the store, rather than home, is followed). By contrast, if the delay is long, continuous goal maintenance may be impractical and too consuming of cognitive resources that could be deployed elsewhere. Because of the complementary computational tradeoffs between proactive and reactive control, a range of variables and factors could bias which strategy is preferred in different task situations, and for different individuals.

Author's personal copy

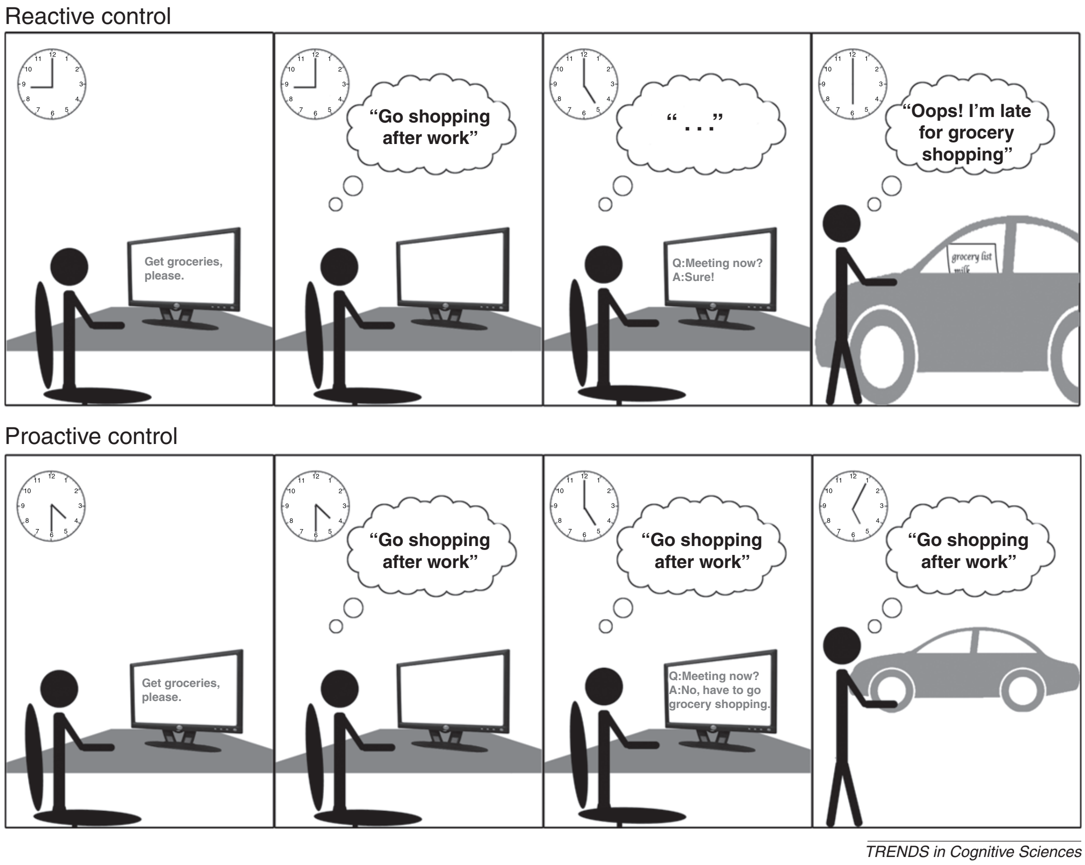

Figure I. Tradeoffs between reactive and proactive control in everyday situations. Illustration of a prospective memory situation in which an individual forms an intention to go grocery shopping after work. Top panel indicates a reactive control strategy that involves transient representation and then episodic storage of the intention after it is first formed (here, in the morning). As a consequence, the intention may not be accessible when scheduling other activities (e.g. a late meeting), and would only be retrieved by a salient trigger event (e.g. when the grocery list is noticed in the car). Lower panel indicates a proactive control strategy, which may only be feasible when there is a short delay between intention formation and implementation (i.e. the intention is formed in the late afternoon). However, the advantage of proactive control is that continuous access to task goals may bias the scheduling of activities (i.e. avoiding late meetings), so as to facilitate successful task completion.

regions compared to intermixed trials associated with slow performance [26]. In all of these studies, the DMC framework helps provide a unifying explanation by interpreting the effects of subtle experimental manipulations on brain activation dynamics in terms of a shift in the relative utilization of proactive versus reactive control mechanisms.

Inter-individual variation

A second assumption of the DMC framework is that there may be stable individual difference factors that lead to biases in whether proactive or reactive control is the preferred mode in performing tasks with high cognitive control demands. The key insight underlying this assumption is that the utilization of proactive control will be related to cost/benefit tradeoffs that relate both to the efficacy or ease of actively maintaining goal representations in advance of their utilization, as well as to internal estimates of how beneficial or valuable are the consequences of such a control strategy for task performance. Thus, cognitive individual differences such as working memory capacity and fluid intelligence should impact the utilization of proactive control, potentially because they reflect the ease or efficacy of active goal maintenance in working memory, as has been suggested by previous investigators [27,28]. Consistent with this hypothesis, in the recent probes study described above [21], individuals with higher fluid intelligence showed increased evidence of PFC activation dynamics associated with proactive control (i.e. delay-related activation), whereas individuals with low fluid intelligence showed a contrasting pattern of increased reactive control (i.e. probe-triggered activation on interference trials).

Perhaps more surprisingly, the DMC framework suggests that affect-related traits (e.g. personality factors) could also influence which cognitive control mode is preferred. These traits are not postulated to impact the efficacy of goal maintenance but rather may impact value estimates of the relative costs and benefits that proactive versus reactive strategies have for ongoing behavioral performance. To investigate this hypothesis, we have also directly examined the role of personality-related individual differences in explaining between-subject variation in neural and behavioral signatures of proactive versus reactive control. As an example, Jimura *et al.* [29] recently examined whether the personality trait of reward sensitivity [30] might explain individual differences in the utilization of proactive control, when performing difficult cognitive tasks in rewarding motivational contexts. The

Author's personal copy

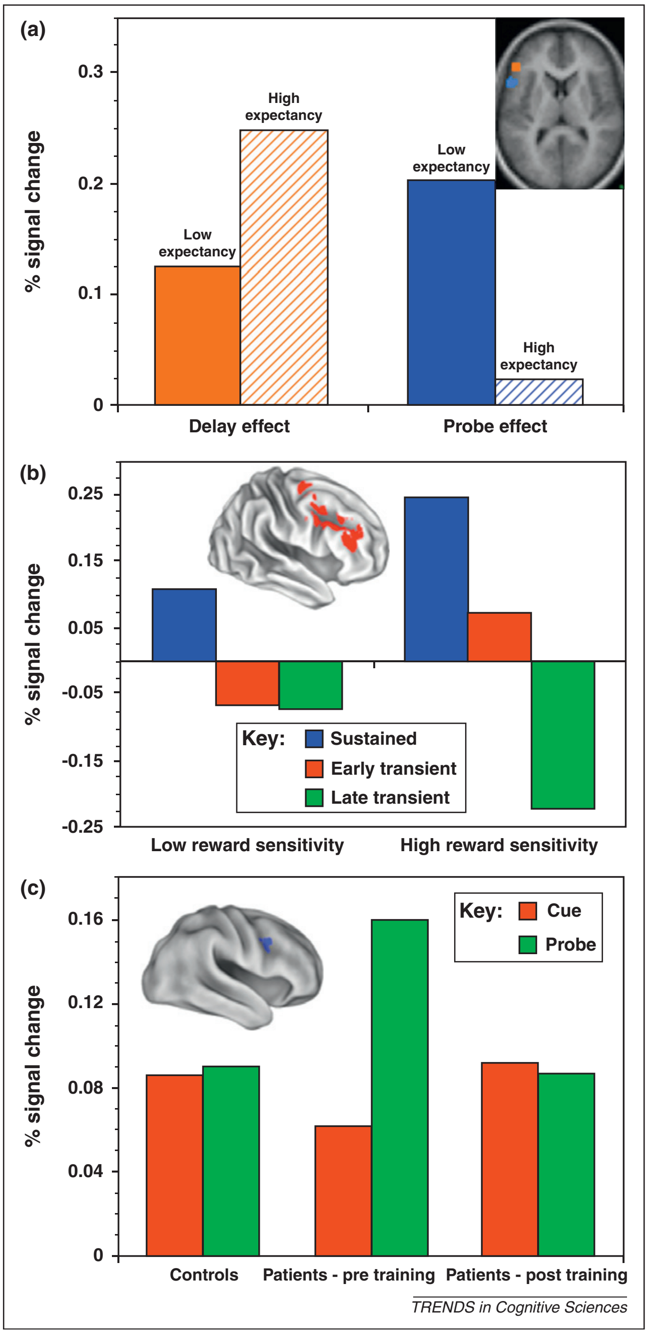

Figure 2. Temporal dynamics of lateral PFC activity reflects cognitive control mode shifts associated with different sources of variation. **(a)** Intra-individual (state related) variation due to manipulation of interference expectancy during the recent probes working memory interference task. Low interference expectancy conditions were primarily associated with interference effects at the time of the probe (i.e., recent negative activity greater than novel negative; blue region and blue filled bar), reflecting reactive control. However, in high expectancy conditions, probe-related activation was decreased (blue hatched bar), whereas in adjacent regions delay-related activation increased (orange region and bars) indicating an anticipatory and global (i.e. present on all trials) proactive control effect. Adapted from [21]. **(b)** Inter-individual variation due to trait reward sensitivity during working memory. Task performance under reward motivation conditions was associated with an increase in sustained and early-trial transient activity (potentially reflecting across-trial maintenance of task goals and encoding/updating of working memory information; blue and red bars) but a decrease in late-trial transient activity (potentially reflecting probe-related processing; green bars), consistent with a shift towards proactive control. The effects were observed much more prominently in highly reward-sensitive individuals. Adapted from [29]. **(c)** Between-groups variation and training effects observed in schizophrenia patients on the AX-CPT context processing task. Prior to cognitive training, schizophrenia patients showed reduced cue-related activity but increased probe-related activity, indicating a differential reliance on reactive control (shown here in a representative lateral PFC region). However, following extensive strategy training with the task, normalization of activation dynamics (and task performance) was observed. Adapted from [39].

authors hypothesized that highly reward-sensitive individuals might estimate successful behavioral performance to be especially valuable in contexts in which it is associated with reward attainment. Thus in these contexts they would be expected to be preferentially motivated to adopt a proactive cognitive control strategy to optimize their performance.

Participants were asked to perform a high-load working memory task under baseline conditions and conditions in which performance-contingent monetary rewards were offered on a subset of trials [29]. The task performance of all participants was improved in the reward context (even on the nonrewarded trials) relative to baseline, but the largest effects were observed in individuals showing high reward sensitivity. These behavioral effects were also reflected in terms of context-related shifts in lateral PFC activation dynamics. Consistent with the hypothesis that the reward context was associated with a shift towards proactive control, there was an increase in both sustained (i.e. persisting across trials) and anticipatory (encoding-related and delay-related) activation within right dorsolateral PFC in this condition, but a decrease in activity during the probe period when reactive control processes might occur (Figure 2b). More importantly, this PFC activation shift was most prominent in highly reward-sensitive individuals (Figure 2b), and was found to statistically mediate the relation between trait reward sensitivity and reward-related improvements in performance. Interestingly, trait reward sensitivity has been found to be associated with behavioral and neural signatures of proactive control in similar studies manipulating reward contexts but involving different tasks and domains, such as the AX-CPT [31] and cued task-switching [32]. Together, the results suggest that individual differences in trait reward sensitivity help explain between-individual variation in the tendency to adopt a proactive control strategy but particularly under cognitive task conditions having high reward motivational value.

Trait reward sensitivity is not the only affect-related individual difference factor that has been found to explain between-individual variation in reactive versus proactive control. For example, threat sensitivity also seems to predict behavioral signatures of proactive control in punishment-oriented motivational contexts [32]. By contrast, trait (and state) anxiety was associated with a neural signature of increased reactive control during the n-back working memory task (i.e. reduced sustained but increased transient activity particularly on high interference lure trials) in lateral PFC and the rest of the brain cognitive control network [33]. If anxiety is associated with a reduction in the capacity to actively maintain cognitive task goals in working memory because this capacity is taken up with a sustained internal attentional focus towards task-unrelated thoughts (i.e. worries and rumination) or an external focus towards unpredictable threats in the environment, then the relation between anxiety and reactive control makes sense from the DMC perspective.

Author's personal copy

Between-group variation

A final assumption of the DMC framework is that the differences between proactive and reactive control modes might be important for understanding the variation in cognitive control functions observed in different clinical and developmental populations or groups (e.g. individuals with schizophrenia, older adults, etc.). In particular, rather than making the simpler hypothesis that these populations have global impairments in cognitive control, we instead suggest that they might show differential reliance on reactive versus proactive control. This hypothesis motivates a more nuanced and fine-grained analysis of cognitive control function in these different groups and, further, may provide more appropriate targets for cognitive intervention.

The AX-CPT context processing task has become a popular paradigm for examining changes in the use of proactive and reactive control in different populations. In the AX-CPT, certain probe trials (termed BX) evoke dominant but inappropriate response tendencies that may require reactive control to override them. Alternatively, preceding contextual cues produce expectancies regarding the upcoming probes that can be used for proactive control. Proactive control is beneficial for BX probes but is actually detrimental to performance on another probe type (AY) because on these the cue-triggered expectancy is invalid. In studies conducted in a variety of populations, including older adults, young children, and individuals with schizophrenia, a similar pattern of impaired BX performance but relative sparing on AY trials is observed [34–36]. This suggests a reduction in the use of proactive control in these groups. Interestingly, however, in some groups (e.g. older adults) the BX impairment is expressed primarily in terms of response slowing rather than elevated errors [37], suggesting that reactive control may be relatively intact. This hypothesis has been supported by findings from brain imaging studies in both older adults and individuals with schizophrenia: reduced cue-related activation of lateral PFC but at the same time increased probe-related activation was observed particularly for BX probes [38,39] (Figure 2c). These changes in both cue- and probe-related activity have been observed within the same lateral PFC regions and are consistent with a shift towards more reactive control. The within-region shift in activation dynamics is also crucial because it rules out a simple hypothesis that cognitive control is generically impaired, as well as alternative methodologically based interpretations (e.g. reduced hemodynamic response, increased variability in neural activity, or other sources).

The DMC framework has proved useful for exploring cognitive control changes, not just in older adults and individuals with schizophrenia but in a range of other populations, including children [35,40] and adolescents [41,42], expert video game players [43], individuals with attention deficit hyperactivity disorder [44] and individuals with depressed mood [45]. Although many of these studies have also used AX-CPT to investigate proactive and reactive control, other studies have employed different tasks and paradigms, including Stroop and n-back [33,44,45], and have used event-related potentials in addition to behavioral or functional magnetic resonance imaging methods [43,46]. The range of populations and research approaches used in conjunction with the DMC framework suggests that it may have wide applicability for understanding the diversity of cognitive control processes. Moreover, the more nuanced conceptualization of cognitive control provided by the DMC framework may provide a clearer target for intervention strategies. Specifically, it suggests that proactive control will only be utilized if the cost/benefit tradeoff is favorable, and if the salience and efficacy of this control mode is appreciated. Likewise, the DMC framework makes clear that increased utilization of proactive control will not only result in performance enhancements but could also result in some types of decrements (e.g. when preparation is based on misleading contextual expectancies, such as on AY trials in the AX-CPT). Finally, a shift towards proactive control might result in a reduced need to utilize reactive control processes, suggesting that interventions aimed at enhancing proactive control might find otherwise counterintuitive evidence of reduced control engagement in situations typically dominated by high reactive control.

These intervention-related components of the DMC framework have recently been tested in studies aimed at increasing proactive control in the AX-CPT task [17,39]. Here, proactive control was explicitly trained by calling attention to the importance of contextual cue information, and by highlighting how such information could be used to generate proactive expectancies regarding the responses to upcoming probes. In one study with older adults, progressive training and practice with these strategies led to a shift in AX-CPT performance with performance improvements observed on BX trials but actually worse (yet theoretically predicted) performance on AY trials [47]. This behavioral shift was accompanied by (and statistically associated with) a shift in lateral PFC activity dynamics, in which cue-related activation was increased following training, whereas probe-related activity actually decreased. A very similar pattern of results was also observed in a study conducted in individuals with schizophrenia [39] (Figure 2c). The findings from this work can be easily interpreted within the DMC framework as reflecting a shift from reactive to proactive control. However, without the benefit of the framework, the results might have otherwise been puzzling and hard to interpret.

Concluding remarks

In this article, I have attempted to lay out a potentially useful framework for understanding the variable nature of cognitive control mechanisms. The crucial insight of the framework is an appreciation of the fact that variability might be an intrinsic component of cognitive control mechanisms that increases their effectiveness and applicability in dealing with the fluctuating and dynamic nature of both internal physiological states and external environmental constraints. The DMC framework may provide a unifying explanation of how even subtle experimental manipulations can have potentially strong influences on the deployment of cognitive control, and the dynamics of brain regions engaged. In addition, I have suggested that the framework generates specific intuitions and predictions regarding the central nature of trait-like individual differences in modulating cognitive control function, not only standardly

Author's personal copy

Box 2. Unresolved issues and future directions

As the prior sections illustrate, the DMC framework has proved to be a promising one for understanding intraindividual, interindividual and between-groups variation in the mechanisms of cognitive control. Nevertheless, there are a number of unresolved questions and issues regarding the framework that remain to be addressed:

Independent mechanisms? The DMC framework postulates that proactive and reactive control may involve potentially independent mechanisms, although this has not been directly confirmed. A key question is whether there are experimental factors (or individual difference factors) associated with an increased utilization of reactive control, without finding a linked decrease in proactive control. Examination of the Stroop task to address this theoretical question might be useful because recent studies have found evidence of experimental manipulations that seem to selectively engage reactive control [52].

Neural architecture A primary claim of the DMC framework is that many PFC regions can show both proactive (sustained/anticipatory) and reactive (transient) dynamics depending on the specifics of task demands. Nevertheless, there may be anatomical constraints, given prior findings and theoretical models of functional specialization within lateral PFC [14,15,53], including accounts that postulate a posterior–anterior gradient that seems to align well with reactive–proactive distinctions (i.e. temporally extended and sustained representation in anterior PFC, more transient engagement in posterior PFC, [7]). Regions outside lateral PFC may also play key roles that will need to be further clarified, such as that postulated for ACC in conflict detection processes that initiate reactive control but could also facilitate a reactive-to-proactive shift [54,55], or for associative and episodic retrieval mechanisms in cortical (e.g. parietal) and subcortical (e.g. hippocampal) brain regions that may provide another route for bottom-up triggering of reactive control [24].

Formal mechanistic models There is a strong need to formalize the DMC account within explicit computational models. A key question is to understand the mechanisms by which various task factors and individual difference factors can lead to shifts or fluctuations in control state, without recourse to a homunculus that mysteriously 'detects' demands for reactive or proactive control. We have made initial attempts in this regard but these have been limited to specific task domains (e.g. task-switching; [56]) and experimental effects (e.g. Stroop proportion congruence; [55]); thus, more comprehensive and rigorous modeling efforts are needed.

Behavioral markers A key goal for future research will be to establish behavioral markers that provide robust and independent indices of both proactive and reactive control. In prior work we have used a variety of markers including: AY versus BX trials in the AX-CPT [17,37], switch-costs in cued task-switching [26,32], proportion congruence and related effects in the Stroop [55,57], and 'recent negative' interference in item recognition working memory [21]. However, given that no task or measure is 'process pure', a latent variable approach might be the most fruitful, involving multiple behavioral indices, along with correlational or more advanced statistical techniques (e.g. structural equation modeling; e.g. [9]) to establish that these indices tap into shared and dissociable variance components associated with proactive and reactive control.

Sources of individual difference A tantalizing possibility, hinted at by the DMC framework, is that there may be an individual difference dimension that reflects a stable trait-like tendency to prefer reactive or proactive control. One promising route may be to look for this individual difference factor in terms of normal genetic variation, reflecting the fact that the cost-benefit tradeoffs associated with proactive and reactive control might be adaptively optimized to certain environmental niches or have other selection advantages [58]. The COMT allele is a promising candidate genetic mechanism of this sort because prior work suggests COMT variation might relate to variation in phasic versus tonic dopamine actions in PFC that align well to computational distinctions we have posited between proactive and reactive control [59].

accepted cognitive traits, such as working memory capacity and fluid intelligence but also personality traits that are typically thought of as 'noncognitive', such as reward and threat sensitivity. Finally, the framework has also proved to be useful in reconceptualizing the nature of cognitive impairment found in different populations, such as older adults and individuals with schizophrenia, not only as generic deficit in control function but as a more specific shift from proactive to reactive control. This insight provides greater interpretational leverage regarding existing behavioral and neuroimaging findings but also creates new targets for intervention efforts to enhance cognitive control. Of course, there are currently limitations and central unresolved issues associated with the DMC framework that will need to be addressed in future investigations (Box 2). I hope that other investigators interested in cognitive control will join in these research efforts.

Acknowledgments

This work was supported by NIH R01 MH66078. Thanks to Greg Burgess, Koji Jimura and Bethany Edwards for their contributions to the work described here, and to the rest of the Cognitive Control and Psychopathology laboratory for many fruitful discussions. Thanks to Carol Cox for assistance with figure preparation.

References

1 Miller, E.K. and Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 21, 167–202
2 Engle, R.W. and Kane, M.J. (2003) Executive attention, working memory capacity, and a two-factor theory of cognitive control. *Psychol. Learn. Motiv.* 44, 145–199
3 Goldman-Rakic, P.S. (1996) The prefrontal landscape: implications of functional architecture for understanding human mentation and the central executive. In *The Prefrontal Cortex: Executive and Cognitive Functions* (Roberts, A.C. *et al.*, eds), pp. 87–103, Oxford University Press
4 O'Reilly, R.C. (2006) Biologically based computational models of high-level cognition. *Science* 314, 91–94
5 Botvinick, M.M. *et al.* (2001) Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652
6 Monsell, S. and Driver, J. (2000) In *Control of Cognitive Processes: Attention and Performance* (Vol. XVIII), MIT Press
7 Koechlin, E. and Summerfield, C. (2007) An information theoretical approach to prefrontal executive function. *Trends Cogn. Sci.* 11, 229–235
8 Smith, E.E. and Jonides, J. (1999) Storage and executive processes in the frontal lobes. *Science* 283, 1657–1661
9 Miyake, A. *et al.* (2000) The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: a latent variable analysis. *Cognit. Psychol.* 41, 49–100
10 Koechlin, E. *et al.* (2003) The architecture of cognitive control in the human prefrontal cortex. *Science* 302, 1181–1185
11 Stuss, D.T. and Alexander, M.P. (2007) Is there a dysexecutive syndrome? *Philos. Trans. R. Soc. B: Biol. Sci.* 362, 901–915
12 Petrides, M. (2005) Lateral prefrontal cortex: architectonic and functional organization. *Philos. Trans. R. Soc. B: Biol. Sci.* 360, 781–795
13 Banich, M.T. (2009) Executive function: the search for an integrated account. *Curr. Dir. Psychol. Sci.* 18, 89–94
14 Badre, D. (2008) Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends Cogn. Sci.* 12, 193–200
15 Braver, T.S. and Ruge, H. (2006) Functional neuroimaging of executive functions. In *Functional Neuroimaging of Cognition* (Cabeza, R. and Kingstone, A., eds), pp. 307–347, MIT Press
16 Braver, T.S. *et al.* (2007) Explaining the many varieties of working memory variation: dual mechanisms of cognitive control. In *Variation*

Author's personal copy

in Working Memory (Conway, A. *et al.*, eds), pp. 76–106, Oxford University Press

17 Braver, T.S. *et al.* (2009) Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proc. Natl. Acad. Sci. U.S.A.* 106, 7351–7356

18 Jacoby, L.L. *et al.* (1999) The role of cognitive control: early selection versus late correction. In *Dual Process Theories in Social Psychology* (Chaiken, S. and Trope, E., eds), pp. 383–400, Guilford Press

19 Braver, T.S. and Cohen, J.D. (1999) Dopamine, cognitive control, and schizophrenia: the gating model. *Prog. Brain Res.* 121, 327–349

20 Braver, T.S. and Cohen, J.D. (2000) On the control of control: the role of dopamine in regulating prefrontal function and working memory. In *Attention and Performance* (Vol. XVIII) (Monsell, S.and Driver, J., eds), pp. 713-738, MIT Press

21 Burgess, G.C. and Braver, T.S. (2010) Neural mechanisms of interference control in working memory: effects of interference expectancy and fluid intelligence. *PLoS ONE* 5, e12861

22 Jonides, J. and Nee, D.E. (2006) Brain mechanisms of proactive interference in working memory. *Neuroscience* 139, 181–193

23 D'Esposito, M. *et al.* (1999) The neural substrate and temporal dynamics of interference effects in working memory as revealed by event-related functional MRI. *Proc. Natl. Acad. Sci. U.S.A.* 96, 7514–7519

24 Speer, N.K. *et al.* (2003) Strategy-dependent changes in memory: effects on brain activity and behavior. *Cogn. Affect. Behav. Neurosci.* 3, 155–167

25 Savine, A.C. and Braver, T.S. (2010) Motivated cognitive control: reward incentives modulate preparatory neural activity during task-switching. *J. Neurosci.* 30, 10294

26 Braver, T.S. *et al.* (2003) Neural mechanisms of transient and sustained cognitive control during task switching. *Neuron* 39, 713–726

27 Duncan, J. *et al.* (1996) Intelligence and the frontal lobe: the organization of goal-directed behavior. *Cogn. Psychol.* 30, 257–303

28 Kane, M.J. and Engle, R.W. (2002) The role of prefrontal cortex in working-memory capacity, executive attention and general fluid intelligence: an individual-differences perspective. *Psychon. Bull. Rev.* 9, 637–671

29 Jimura, K. *et al.* (2010) Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8871–8876

30 Depue, R.A. and Collins, P.F. (1999) Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. *Behav. Brain Sci.* 22, 491–569

31 Locke, H.S. and Braver, T.S. (2008) Motivational influences on cognitive control: behavior, brain activation, and individual differences. *Cogn. Affect. Behav. Neurosci.* 8, 99–112

32 Savine, A.C. *et al.* (2010) Enhancement of cognitive control by approach and avoidance motivational states. *Cogn. Emot.* 24, 338–356

33 Fales, C.L. *et al.* (2008) Anxiety and cognitive efficiency: differential modulation of transient and sustained neural activity during a working memory task. *Cogn. Affect. Behav. Neurosci.* 8, 239–253

34 Braver, T.S. *et al.* (2001) Context processing in older adults: evidence for a theory relating cognitive control to neurobiology in healthy aging. *J. Exp. Psychol. Gen.* 130, 746–763

35 Chatham, C.H. *et al.* (2009) Pupillometric and behavioral markers of a developmental shift in the temporal dynamics of cognitive control. *Proc. Natl. Acad. Sci. U.S.A.* 106, 5529–5533

36 Barch, D.M. *et al.* (2001) Selective deficits in prefrontal cortex function in medication-naive patients with schizophrenia. *Arch. Gen. Psychiatry* 58, 280–288

37 Braver, T.S. *et al.* (2005) Context processing and context maintenance in healthy aging and early-stage dementia of the Alzheimer's type. *Psychol. Aging* 20, 33–46

38 Paxton, J.L. *et al.* (2008) Cognitive control, goal maintenance, and prefrontal function in healthy aging. *Cereb. Cortex* 18, 1010–1028

39 Edwards, B.G. *et al.* (2010) Improving prefrontal cortex function in schizophrenia through focused training of cognitive control. *Front. Hum. Neurosci.* 4, 1–12

40 Lorsbach, T.C. and Reimer, J.F. (2010) Developmental differences in cognitive control: goal representation and maintenance during a continuous performance task. *J. Cogn. Dev.* 11, 185–216

41 Iselin, A.M.R. and DeCoster, J. (2009) Reactive and proactive control in incarcerated and community adolescents and young adults. *Cogn. Dev.* 24, 192–206

42 Andrews-Hanna, J.R. *et al.* (2011) Cognitive control in adolescence: neural underpinnings and relation to self-report behaviors. *PLoS ONE* 6, e21598

43 Bailey, K. *et al.* (2010) A negative association between video game experience and proactive cognitive control. *Psychophysiology* 47, 34–42

44 Burgess, G.C. *et al.* (2010) Attentional control activation relates to working memory in attention-deficit/hyperactivity disorder. *Biol. Psychiatry* 67, 632–640

45 West, R. *et al.* (2010) The influence of negative affect on the neural correlates of cognitive control. *Int. J. Psychophysiol.* 76, 107–117

46 Czernochowski, D. *et al.* (2010) On why not to rush older adults: relying on reactive cognitive control can effectively reduce errors at the expense of slowed responses. *Psychophysiology* 47, 637–646

47 Paxton, J.L. *et al.* (2006) Effects of environmental support and strategy training on older adults' use of context. *Psychol. Aging* 21, 499–509

48 Cowan, N. (2001) The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav. Brain Sci.* 24, 87–185

49 McElree, B. (2001) Working memory and focal attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 27, 817–835

50 Oberauer, K. (2002) Access to information in working memory: exploring the focus of attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 28, 411–421

51 Kliegel, M. and McDaniel, M.A. (2008) *Prospective Memory: Cognitive, Neuroscience, Developmental, and Applied Perspectives*, Lawrence Erlbaum

52 Bugg, J.M. *et al.* (2011) Why it is too early to lose control in accounts of item-specific proportion congruency effects. *J. Exp. Psychol. Hum. Percept. Perform.* 37, 844–859

53 De Pisapia, N. *et al.* (2007) Functional specializations in lateral prefrontal cortex associated with the integration and segregation of information in working memory. *Cereb. Cortex* 17, 993–1006

54 Ullsperger, M. and King, J.A. (2010) Proactive and reactive recruitment of cognitive control: comment on Hikosaka and Isoda. *Trends Cogn. Sci.* 14, 191

55 De Pisapia, N. and Braver, T.S. (2006) A model of dual control mechanisms through anterior cingulate and prefrontal cortex interactions. *Neurocomputing* 69, 1322–1326

56 Reynolds, J.R. *et al.* (2006) Computational and neural mechanisms of task switching. *Neurocomputing* 69, 1332–1336

57 Bugg, J.M. *et al.* (2011) Revealing list-level control in the Stroop task by uncovering its benefits and a cost. *J. Exp. Psychol. Hum. Percept. Perform.* 37, 1595–1606

58 Braver, T.S. *et al.* (2010) Vive les differences! Individual variation in neural mechanisms of executive control. *Curr. Opin. Neurobiol.* 20, 242–250

59 Bilder, R.M. *et al.* (2004) The catechol-O-methyltransferase polymorphism: Relations to the tonic-phasic dopamine hypothesis and neuropsychiatric phenotypes. *Neuropsychopharmacology* 29, 1943–1961