

Abstract

A hallmark of adaptation in humans and other animals is our ability to control how we think and behave across different settings. Research has characterized the various forms cognitive control can take – including enhancement of goal-relevant information, suppression of goal-irrelevant information, and overall inhibition of potential responses – and has identified computations and neural circuits that underpin this multitude of control types. Studies have also identified a wide range of situations that elicit adjustments in control allocation (e.g., those eliciting signals indicating an error or increased processing conflict), but the rules governing when a given situation will give rise to a given control adjustment remain poorly understood. Significant progress has recently been made on this front by casting the allocation of control as a decisionmaking problem, and developing unifying and normative models that prescribe when and how a change in incentives and task demands will result in changes in a given form of control. Despite their successes, these models, and the experiments that have been developed to test them, have yet to face their greatest challenge: deciding how to allocate control across the multiplicity of control signals that one could engage at any given time. Here, we will lay out the complexities of the inverse problem inherent to cognitive control allocation, and their close parallels to inverse problems within *motor* control (e.g., choosing between redundant limb movements). We discuss existing solutions to motor control's inverse problems drawn from optimal control theory, which have proposed that effort costs act to regularize actions and transform motor planning into a well-posed problem. These same principles may help shed light on how our brains optimize over complex control configuration, while providing a new normative perspective on the origins of mental effort.

Keywords: Cognitive control; Motor control; Decision making; Inverse problem

"There are many paths up the mountain, but the view from the top is always the same"
- Chinese Proverb

Over the past half-century, our understanding of the human brain's capacity for cognitive control has grown tremendously (Abrahamse et al., 2016; Botvinick and Cohen, 2014; Fortenbaugh et al., 2017; Friedman and Robbins, 2021; Koch et al., 2018; Menon and D'Esposito, 2021; von Bastian et al., 2020; Westbrook and Braver, 2015). The field has developed consistent ways of defining and operationalizing control, such as in terms of its functions and what distinguishes different degrees of automaticity (Cohen et al., 1992; Posner and Snyder, 1975; Shiffrin and Schneider, 1977). It has developed consistent methods for eliciting control and measuring the extent to which control is engaged by a given task (Danielmeier and Ullsperger, 2011; Egner, 2007; Gonthier et al., 2016; Koch et al., 2018; von Bastian et al., 2020; Weichart et al., 2020). It has demonstrated how such control engagement varies across individuals (Friedman and Miyake, 2017; von Bastian et al., 2020) and over the lifespan (Braver and Barch, 2002; Luna, 2009). Finally, research in this area has made substantial progress towards mapping the neural circuitry that underpins the execution of different forms of cognitive control (Friedman and Robbins, 2021; Menon and D'Esposito, 2021; Parro et al., 2018; Shenhav et al., 2013). The factors that determine when control is engaged and how it is configured have, on the other hand, remained mysterious and heavily debated (Shenhav et al., 2017).

Studies have uncovered reliable antecedents for control adjustments, including the commission of an error (Danielmeier and Ullsperger, 2011; Rabbitt, 1966) or changes in task demands (Gratton et al., 1992; Logan and Zbrodoff, 1979). However, it has been a longstanding goal for the field to develop a comprehensive model of how people use the broader array of information they monitor to configure the broader array of control signals they can adjust. To address this question, models proposed that the problem of determining control allocation can be solved through a general decision-making process that involves weighing the costs and benefits of potential control allocations (Lieder et al., 2018; Shenhav et al., 2013; Verguts et al., 2015; Westbrook and Braver, 2015). These models have already shown promise in accounting for how people adjust individual control signals (e.g., how much they attend to a particular task) based on the incentives and demands of a given task environment (Bustamante et al., 2021; Lieder et al., 2018; Musslick et al., 2015; Verguts et al., 2015). Here, we focus on a different aspect of this problem: how it is that people navigate the *multitude* of solutions that can match the demands of their environment? How can cognitive control scale to configuring the complex information processing we deploy throughout our daily life? What is the relationship of mental effort to the complexity of this control? Building off well-characterized computational models from motor planning, we examine how multiplicity presents a critical challenge to cognitive control configuration, and how algorithmic principles from motor control can help to overcome these challenges and refine our understanding of goal-directed cognition.

The multiplicity of cognitive control

To study the mechanisms that govern the allocation of cognitive control, researchers have sought to identify reliable predictors of *changes* in control allocation within and across experiments. These triggers for control adjustment have in turn provided insight into signals – such as errors and processing conflict – that the brain could monitor to increase or decrease control. Research has shown that control adjustments induced by these signals, even within the same setting, vary not only in degree but also kind (see Table 1).

Error-related control adjustments

In common cognitive control tasks such as the Stroop, Simon, and Eriksen flanker task (Egner, 2007; von Bastian et al., 2020), participants have prepotent biases that often lead to incorrect responses (e.g., responding based on the salient flanking arrows rather than the goal-relevant central arrow). Errors thus serve a useful indicator that the participant was likely under-exerting control and should adjust their control accordingly. The best-studied instantiation of error-related control adjustments manifests in a participant's tendency to respond more slowly and more accurately after an error (Danielmeier and Ullsperger, 2011; Laming, 1979a; Rabbitt, 1966; Figure 1A), which can be understood as together reflecting post-error adjustments in caution. Indeed, work has shown that in a model like the drift diffusion model (DDM; (Ratcliff, 1978; Ratcliff and McKoon, 2008), post-error slowing and post-error increases in accuracy can be jointly accounted for by an increase in one's *response threshold*, the criterion they set for how much evidence to accumulate about the task stimuli before deciding how to respond (Dutilh et al., 2012; Fischer et al., 2018; Figure 1B).

Experiments investigating the neural implementation of these post-error adjustments have found that threshold adjustments are associated with the suppression of motor-related activity (Danielmeier et al., 2011; Fischer et al., 2018; Figure 1C). For instance, Danielmeier and colleagues (2011) had participants perform a Simon-like task that required them to respond based on the color of an array of dots that were moving in a direction compatible or incompatible with the correct color response. When participants responded incorrectly, they tended to be slower and more accurate on the following trial. This increased caution was coupled with decreased BOLD activity in motor cortex on that subsequent trial, consistent with the possibility that errors led to controlled adjustments of decision threshold (in this case by putatively lowering the baseline activity to require more evidence before responding).

In addition to changing overall caution, errors can also influence how specific stimuli are processed. Studies have shown that error trials can be followed by selective enhancement of task-relevant (target) processing (Danielmeier et al., 2015, 2011; King et al., 2010; Maier et al., 2011; Steinhauser and Andersen, 2019) and/or suppression of task-irrelevant (distractor)

processing (Danielmeier et al., 2015, 2011; Fischer et al., 2018; Figure 1A-B). For instance, in the same study by Danielmeier and colleagues (2011), errors tended to be followed by increased activity in regions encoding the target stimulus dimension and decreased activity in regions encoding the distractor dimension (Figure 1C; see also Fischer et al., 2018; King et al., 2010). Thus, whereas post-error slowing effects reflect control over one's decision threshold, such post-error reductions of interference likely reflect a different form of control, one that adjusts the rate at which target- and distractor-related information is accumulated before reaching that threshold (referred to as *drift rate* in the DDM).

Conflict-related control adjustments

In addition to error commission, another potential indicator of insufficient control is the presence of processing conflict (Berlyne, 1957; Botvinick et al., 2001), such as when a person feels simultaneously drawn to respond left (e.g., based on target information) and right (e.g., based on a distractor). One of the best-studied forms of conflict-related control adjustment is the *conflict adaptation* or *congruency sequence effect*, which manifests as reduced sensitivity to response (in)congruency after a person has previously performed one or more high-conflict (e.g., incongruent) trials (Egner et al., 2007; Egner and Hirsch, 2005; Funes et al., 2010; Gratton et al., 1992; Jiang and Egner, 2013). These adaptations are analogous to examples of post-error reductions of interference described above, and have the same candidate computational underpinnings in adjustments to the rate of evidence accumulation (Kerns et al., 2004; Musslick et al., 2019b, 2015) These control adjustments have likewise been found to be associated with changes in neural activity in goal-relevant perceptual processing pathways. For example, Egner & Hirsch (2005) showed that participants were less sensitive to Stroop incongruence after higher-conflict trials, and that this was coupled with increased activity in the target-associated cortical areas (fusiform face area for face targets).

Another body of work has shown that conflict can trigger changes to response threshold, particularly within a trial, for instance when selecting between two similarly-valued options (Aron, 2007; Cavanagh et al., 2011; Fontanesi et al., 2019; Frank et al., 2015; Ratcliff and Frank, 2012; Verguts et al., 2011; Wiecki and Frank, 2013). These adjustments have been linked to interactions between dorsal anterior cingulate cortex (dACC) and the subthalamic nucleus (Brittain et al., 2012; Cavanagh et al., 2011; Frank et al., 2015; Schroeder et al., 2002; Wessel et al., 2019). For instance, simultaneous EEG-fMRI has revealed that BOLD in dACC and mediofrontal EEG theta power moderates the relationship between decision conflict and adjustments to response threshold (Frank et al., 2015).

Incentive-related control adjustments

In addition to signals like error and conflict that reflect dips in performance, the need for control can also be signaled by the presence of performance-based incentives (e.g., monetary rewards for

good performance). Incentives can influence overall performance, for instance often leading participants to perform tasks faster and more accurately across trials (Parro et al., 2018; Yee and Braver, 2018). Incentives can also trigger task-specific adjustments of cognitive control, enhancing the processing of goal-relevant information (Etzel et al., 2016; Krebs et al., 2010; Soutschek et al., 2014) and/or suppressing the processing of distractor information (Padmala and Pessoa, 2011), likely reflecting changes in associated drift rates similar to error-related adjustments discussed above (cf. Ritz & Shenhav, 2021, discussed further below). Also similar to error-related findings, there is evidence that incentive-related control adjustments are mediated by changes in processing within stimulus-selective circuits (Esterman et al., 2017; Etzel et al., 2016; Hall-McMaster et al., 2019; Padmala and Pessoa, 2011; Soutschek et al., 2015). For example, Padmala and Pessoa (2011) used a Stroop task to show that participants are less sensitive to distractor information when under performance-contingent rewards. They found that this distractor inhibition was mediated by reduced activation in cortical areas sensitive to the distracting stimuli (visual word form areas for text distractors).

Performance incentives have been shown to influence not only how well one performs on a given trial but also how *consistently* they perform within and across trials. When performing sustained attention tasks that require participants to repeat the same response on most trials (e.g., frequent go trials) but respond differently on rare occurrences of a different trial type (e.g., infrequent no-go trials), attentional lapses can manifest as increased variability in response times across trials (Fortenbaugh et al., 2017). When performance is incentivized, participants demonstrate both higher accuracy and lower response time variability (Esterman et al., 2014, 2016, 2017). These performance improvements can be accounted for by assuming that incentives influence control over how noisily evidence is accumulated within each trial (e.g., due to mindwandering; Ritz et al., 2020; Manohar et al., 2015). Neuroimaging studies suggest that enacting the control required to achieve more consistent (less variable) performance is associated with increases in both sustained and evoked responses in domain-general attentional networks and stimulus-specific regions (Esterman et al., 2017).

| | Behavior | Cognitive process (DDM) | Neuroscience |
|--------|---------------------------------|---------------------------------------|------------------------------------|
| | RT↑ | Threshold ↑ | Motor cortex activation ↓ |
| | (Danielmeier et al., 2011; | | |
| | Debener et al., 2005; Gehring | | |
| Errors | and Fencsik, 2001; Jentzsch and | | |
| | Dudschig, 2009; King et al., | (Dutilh et al., 2012; Fischer et al., | (Danielmeier et al., 2011; King et |
| | 2010; Rabbitt, 1966) | 2018) | al., 2010) |
| | Error Rate ↓ | | |

| | (Danielmeier et al., 2011; | | |
|------------|--|--|---|
| | Laming, 1979b, 1968; Maier et al., 2011; Marco-Pallarés et al., 2008) | | |
| | Interference ↓ | Distractor Drift Rate ↓ | Target-related activation ↑ |
| | (King et al., 2010; Maier et al., 2011; Ridderinkhof, 2002; Steinhauser and Andersen, 2019) | (Fischer et al., 2018) | (Danielmeier et al., 2011; King et al., 2010; Maier et al., 2011; Steinhauser and Andersen, 2019) |
| | | | Distractor-related activation \downarrow |
| | | | (Danielmeier et al., 2011; Fischer et al., 2018; King et al., 2010) |
| | RT↑ | Threshold ↑ | STN activation ↑ |
| Conflict | (Herz et al., 2016; Verguts et al., 2011) | (Fontanesi et al., 2019; Herz et al., 2016) | |
| | Interference ↓ | Distractor Drift Rate ↓ | Target-related activation ↑ |
| | (Braem et al., 2012; Danielmeier et al., 2011; Funes et al., 2010; Gratton et al., 1992; Kerns et al., 2004; Kerns, 2006; Ullsperger et al., 2005) | (Ritz and Shenhav, 2021) | (Egner et al., 2007; Egner and Hirsch, 2005) |
| | RT ↓ Accuracy ↑ | Threshold ↑ | |
| Incentives | (Chiew and Braver, 2016; Fröber and Dreisbach, 2014; Frömer et al., 2021; Ličen et al., 2016; Soutschek et al., 2014; Yee et al., 2016) | (Dix and Li, 2020; Leng et al., 2020; Thurm et al., 2018) | |
| | | Threshold ↓ | |
| | | (Leng et al., 2020) | |
| | Target effect ↑ | Drift rate ↑ | Target-related activation ↑ |
| | (Adkins and Lee, 2021; Krebs et al., 2010) | (Dix and Li, 2020; Jang et al., 2021; Leng et al., 2020) | (Etzel et al., 2016; Grahek et al., 2021; Soutschek et al., 2015) |
| | Distractor effect ↓ | Target Drift Rate ↑ | Distractor-related activation ↓ |
| | (Chiew and Braver, 2016; Padmala and Pessoa, 2011; Soutschek et al., 2014) | (Ritz and Shenhav, 2021) | (Padmala and Pessoa, 2011) |

| RT variability ↓ | Accumulation noise 4 | Sustained task-relevant activation ↑ |
|-------------------------------|---|--------------------------------------|
| (Esterman et al., 2016, 2014) | (Manohar et al., 2015; Ritz et al., 2020) | |

Table 1. Multiplicity of control adaptations in response to errors, conflict, and incentives.

Multidimensional configuration of cognitive control

Previous research has uncovered a multiplicity of adjustments that occur in response to changes in the demands or incentives for control. Importantly, they show that a monitored signal (e.g., an error) can produce several different control adjustments, and that a control adjustment (e.g., increased caution) can be elicited by several different monitored signals. Rather than a strict one-to-one relationship between monitored signals and control adjustments, this diversity suggests that participants make simultaneous decisions across multiple control effectors.

This control multiplicity is evident in studies of post-error adjustments discussed above (Danielmeier and Ullsperger, 2011), in which errors can result in both increased caution (i.e., more conservative response thresholds) and a change in attentional focus to favor target over distractor information (putatively underpinned by adjustments in drift rate). Experiments have found that both adjustments appear to occur simultaneously (Danielmeier et al., 2015, 2011; Fischer et al., 2018; King et al., 2010), reflecting a multi-faceted response to the error event.

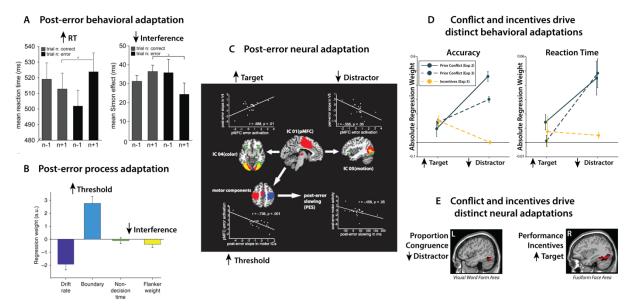


Figure 1. Examples of the multiplicity of cognitive control adaptation. Examples of control adjustments induced by error commission (A-C) and the presence of conflict or performance incentives (D-E). For a more comprehensive list, see Table 1. A) Performance errors elicit post-error slowing (left) and post-error reduction in interference (right). RTs are plotted before and after correct trials (grey) and error trials (black). Adapted from (King et al., 2010). B) Fischer and colleagues (Fischer et al., 2018)) showed that post-error control

adjustments like these can be accounted for by a combination of increases in decision thresholds and decreased distractor influence over drift rate within a DDM. C) These post-error adaptations are associated with decreases in motor activity (which predict slowing effects), enhanced activity in target-localized areas, and suppressed activity in distractor-localized areas (Danielmeier et al., 2011; see also Fischer et al., 2018). These neural adaptations are linked to error-related responses in dACC on the previous trial. D) Conflict and incentives reconfigure the relative allocation of control towards target versus distractor processing (Ritz and Shenhav, 2021). In this study, previous conflict (navy) primarily suppressed distractor sensitivity, whereas incentives (gold) primarily enhanced target sensitivity. E) At the neural level, a related study found that expecting a trial to be more likely to be high-conflict suppressed activity in distractor-related areas, whereas larger incentives enhanced activity in target-related areas. Adapted from (Soutschek et al., 2015).

In a recent study, we showed that people can also exert separate control over their processing of targets and distractors within a given setting (Ritz and Shenhav, 2021; Figure 1D). Similar to Danielmeier and colleagues (2011), we had participants perform a random dot kinematogram that required responding to dot color while ignoring dot motion. Across trials, we parametrically varied both the target coherence (how easily the correct color could be identified), and distractor interference (how coherently dots were moving in the same or opposite direction as the target response). We found that participants exerted control over their processing of both target and distractor information, but that they did so independently and differentially depending on the relevant task demands. Under performance incentives, participants preferentially enhanced their target sensitivity, whereas after high-conflict trials, participants preferentially suppressed their distractor sensitivity (and, to a lesser extent, also enhanced target sensitivity). A similar pattern has been observed at the neural level while participants perform a Stroop task (Soutschek et al., 2015; Figure 1E). Whereas performance incentives preferentially enhanced sensitivity in targetrelated areas (visual word form area for text targets), conflict expectations preferentially suppressed sensitivity in distractor-related areas (fusiform face area for face distractors). These findings demonstrate that control can be flexibly reconfigured across multiple independent control signals to address relevant incentives and task demands.

There is also evidence that different people prioritize different control signals within the same setting. For instance, Boksem and colleagues (2006) had participants perform the Simon task over an extended experimental session, and observed performance fatigue in the form of slower and less accurate responding over time. Towards the end of the session, the experimenters introduced monetary incentives and found that this counteracted the effects of fatigue, but did so heterogeneously across the group. When making an error during this incentivized period, some participants responded by focusing more on responding *quickly* while others focused on responding *accurately*. The engagement of these differential control strategies were associated with changes in distinct event-related potentials (error-related negativity vs. contingent negative variation). Similar variability in reliance on different control strategies has been seen across the lifespan (Braver and Barch, 2002; Fortenbaugh et al., 2015; Luna, 2009; Ritz et al., 2020) and between clinical and healthy populations (Casey et al., 2007; Grahek et al., 2019; Lesh et al., 2011).

Collectively, previous research suggests that there is a many-to-many mapping between the signals that participants monitor related to task demands, performance, and incentives, and the multitude of control signals that participants can deploy. Recent theoretical models have explained this heterogeneity in terms of the flexible deployment of control, proposing that there is an intervening *decision* process that integrates monitored information, determining which control signals to engage, and to what extent, based on the current situation (Lieder et al., 2018; Shenhav et al., 2013; Verguts et al., 2015).

Selection and configuration of multivariate control

Casting control allocation as a decision process provides a path toward addressing how people integrate information from their environment to select the optimal control allocation. This process of *optimization* entails finding the best solution for an objective function and set of constraints. Objective functions define the costs of benefits of different solutions, whereas constraints limit the space of possible solutions. Optimization has long played a central and productive role in building computational accounts of multivariate planning in the domain of *motor* control (Shadmehr and Ahmed, 2020; Wolpert and Landy, 2012), suggesting that this research into how the brain coordinates actions may thus offer general principles for how the brain coordinates cognition.

The starting point for solving any optimization problem is identifying the objective function. Researchers in decision making and motor control have suggested that participants maximize the amount of reward harvested per unit time (*reward rate*; Harris and Wolpert, 2006; Manohar et al., 2015; Niv et al., 2007; Shadmehr et al., 2010). Studies have found that people's motor actions are sensitive to incentives, with faster and/or more accurate movement during periods when they can earn more rewards (Codol et al., 2021, 2020; Manohar et al., 2019, 2017, 2015; Pekny et al., 2015; Sukumar et al., 2021; Trommershäuser et al., 2003a, 2003b; Yoon et al., 2020). For example, participants will saccade toward a target location more quickly and more precisely on trials that are worth more money (Manohar et al., 2019, 2017, 2015). Responding faster and more precisely breaks the traditional speed-accuracy trade-off (Bogacz et al., 2006; Manohar et al., 2015), and is thought to reflect the use of control to optimize both reward and duration (Shadmehr and Ahmed, 2020).

It has been similarly proposed that a core objective of cognitive control allocation is also the maximization of reward rate (Bogacz et al., 2006; Boureau et al., 2015; Lieder et al., 2018; Manohar et al., 2015; Shenhav et al., 2013). That is, that people select how much and what kinds of control to engage at a given time based on how control will maximize expected payoff (e.g., performance-based incentives like money or social capital) while minimizing the time it takes to achieve that payoff. Consistent with this proposal, studies have shown that people configure information processing (e.g., adjust their response thresholds) in ways that maximize reward rate

(Balci et al., 2011; Simen et al., 2009; Starns and Ratcliff, 2010), and that they adjust this configuration over time based on local fluctuations in reward rate (Guitart-Masip et al., 2011; Otto and Daw, 2019).

We recently used a reward-rate optimization framework to make model-based predictions for how people coordinate *multiple* types of control (Leng et al., 2020). Participants performed a Stroop task that was self-paced, enabling them to dynamically adjust at least two forms of control: their overall drift rate (governing both how fast and accurate they are) and their response threshold (governing the extent to which they trade off speed for accuracy; Figure 2A). We varied the amount of money participants could gain with each correct response and the amount they could lose with each incorrect response. Participants could increase their response threshold to guarantee that every response was correct, but this came at the cost of completing fewer trials and therefore earning fewer rewards over the course of the. Increasing their drift rate can achieve higher reward rates, but is subject to effort costs, that we will return to later. The reward-rate optimal configuration across both drift and threshold would be to increase drift rate and decrease threshold for larger rewards, and increase thresholds for larger penalties (Figure 2B). Critically, we found that participants' DDM configuration matched the predictions of this optimal model (Figure 2C). These results provide evidence that participants' performance can align with the optimal joint configuration across multiple control parameters.

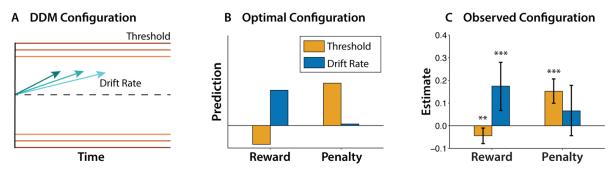


Figure 2. Multivariate configurations of control adapt to changes in reward rate. A) Leng et al. (2020) tested how participants adjusted their rate of evidence accumulation (drift rate in a DDM; blue) and speed accuracy trade-off (response threshold in a DDM; red) while performing a self-paced Stroop task with varying levels of reward for correct responses and penalties for errors. B) A reward-rate optimal model predicted that higher rewards should bias their control configuration towards higher drift rates and lower thresholds, whereas larger penalties should bias these configurations towards higher thresholds and have little impact on drift rate. C) DDM fits to task performance confirmed these predictions, demonstrating that participants adjusted their control configuration in a multivariate and reward-rate-optimal manner.

These studies validate the proposal that control allocation can be framed as decision-making over multidimensional configurations of control (i.e., combination of different control types engaged to different degrees) and that these decisions seek to optimize an objective function such as expected reward rate. However, for all the algorithmic tools it provides, this decision-making framework also presents an entirely new set of challenges. Most notably, the many possible

control signals often means that there will be multiple equivalent solutions to this decision. Here, again, valuable insights can be gained from research on motor control, where these challenges and their potential solutions have been extensively explored.

Inverse problems in motor and cognitive control

Inverse problems in motor control

Some of the most influential computational modelling of motor planning was founded at the Central Labor Institute in Moscow in the early 20th century. This group formalized for the first time a fundamental problem for motor control: how does the motor system choose among the many similar actions that could be taken to achieve a goal (Bernstein, 1935; Whiting, 1983)? This problem is centered around the fact that motor control is inherently *ill-posed*, with more degrees of freedom in the body than in the task space, making it difficult to select between equivalent motor actions.

These motor redundancies can occur in several domains of motor planning (Kawato et al., 1990). At the task level, there may be many trajectories through the task space that achieve the same goals, such as the paths a hand could take on its way to picking up a cup (*Task Degeneracy*; Figure 3A). At the effector level, there are often more degrees of freedom in the skeletomotor system than in the task space, creating an 'inverse kinematics' problem for mapping from goals on to actions (*Effector Degeneracy*; Figure 3B). For example, there are many ways you could move your arm to trace a line with the tip of your finger. A related problem arises when there is redundancy across effectors, such as in agonist and antagonistic muscles (*Effector Antagonism*; Figure 3C). Due to their opponency, the same action can occur by trading off the contraction of one muscle against the relaxation of the other. These inverse problems have been a major challenge for theoretical motor control, and to the extent that a similar problem occurs in cognitive control, solutions from the motor domain may help guide our understanding of ill-posed cognitive control.

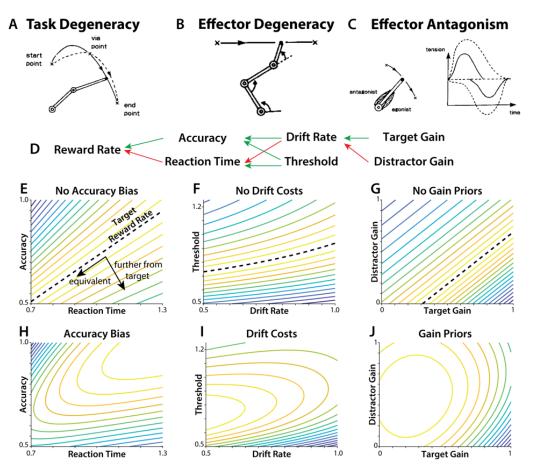


Figure 3. Degeneracies in motor and cognitive control. A) Task degeneracy. There are an infinite number of trajectories that achieve the goal of moving from a start point to an endpoint through an intermediate via point. B) Effector Degeneracy. Because there are more degrees of free in the effector (arm joints) than in the task (1D movement), there are an infinite number of configurations that can produce the same movement. C) Effector Antagonism. Because effectors have an opposite influence over action (e.g., agonist and antagonist muscles), there are an infinite number of configurations that will produce the same movement, resulting in another form of degeneracy. D) Reward rate optimization in the drift diffusion model provides an example of an analogous control problem in the cognitive domain. Participants could have a goal of achieving a specific reward rate (e.g., to match the rate of replenishment in their environment). Their reward rate is determined by their performance, namely accuracy and reaction time (as well as non-decision time). Their performance depends on their drift rate and threshold (as well as other factors like noise and bias). Their drift rate depends on the priority of different information sources. Degeneracies along this processing pathway make it difficult for cognitive control to optimize reward rate. E) Task degeneracy can result from the combinations of accuracies and reaction times that produce an equivalent reward rate F) 'Effector' degeneracy can result from the combinations of drift rate and threshold that produce the same reward rate. G) 'Effector' antagonism can result from opposing contributions of target gains (positive effect on drift rate) and distractor gains (negative effect on drift rate) on reward rate. (H) A solution to task degeneracy is to bias performance towards higher accuracy, creating a globally optimal solution. I) A solution to effector degeneracy is to place a cost on higher drift rates, biasing parameter configurations towards lower drift rates and creating a globally optimal solution. J) A solution to effector antagonism is to set a prior on control gains, biasing these gains towards the prior configuration (e.g., high distractor sensitivity and low target sensitivity) and creating a globally optimal solution. Panels A-C adapted from (Kawato et al., 1990).

Inverse problems in cognitive control: the algorithmic level

Considering the massive degrees of freedom that exist in neural information processing systems, cognitive control is a prime candidate for inverse problems of its own. To illustrate this, we can return to the example of how people decide to allocate control across parameters of the drift diffusion model (Figure 3D). As reviewed above, participants can separately control individual parameters of evidence accumulation, specifically drift rate (e.g., Ritz and Shenhav, 2021; White et al., 2011), threshold (e.g., Cavanagh and Frank, 2014; Fischer et al., 2018), and accumulation noise (e.g., Nakajima et al., 2019; Ritz et al., 2020). This example case of finding a reward-rate optimal configuration of DDM parameters faces the same set of challenges as those outlined above from motor control.

First, just as there are many hand trajectories that can produce a desired outcome, there are also many ways to produce good decision-making performance (Figure 3E). Different combinations of accuracy (numerator) and reaction time (denominator) can trade-off to produce the same reward rate. This creates an equivalence in the task space between different performance outcomes with regards to the goals of the system.

Second, just as there are more degrees of freedom in the arm than in many motor tasks, there is more flexibility in information processing than in many cognitive tasks. For example, the same patterns of behavior (and therefore expected reward rates) can result from different configurations of DDM parameters (Bogacz et al., 2006; Figure 3F). From a model-fitting perspective, this forces researchers to limit the parameters they attempt to infer from behavior, fixing at least one parameter value (often accumulation noise), while estimating the others (Bogacz et al., 2006; Ratcliff and Rouder, 1998). This degeneracy similarly limits a person's ability to perform the "mental model-fitting" required to optimize across all these control signals when deciding how to allocate control. These difficulties are exacerbated in more biologically plausible models of evidence accumulation like the leaky competing accumulator (Usher and McClelland, 2001), which introduce additional parameters (e.g., related to memory decay and levels of inhibition across competing response units), resulting in even greater parameter degeneracy (Miletić et al., 2017). A similar trade-off exists in the classic debate between early and late attentional selection, namely whether attention operates closer to sensation or closer to response selection (Driver, 2001). Given that attention appears to operate at multiple processing stages (Lavie, 1995), degeneracies will arise if early or late attentional control will similarly influence task performance.

Third, just as there is antagonism across motor effectors, there is also antagonism across cognitive processes. That is, even when the algorithmic goal is clear, there are degenerate control signals that can achieve this goal. For instance, in typical interference-based paradigms (e.g., flanker or Stroop), participants must respond to one element of a stimulus while ignoring information that is irrelevant and/or distracting. To increase the overall rate of accumulation of goal-related information, the person can engage two different forms of attentional control:

enhance targets or suppress distractors. Utilizing either of these strategies will improve performance, meaning that cognitive controller could trade off enhancing targets or suppressing distractors to reach the same level of performance (Figure 3G). Recent work has shown that target and distractor processing can be controlled independently in conflict tasks (Adkins and Lee, 2021; Evans and Servant, 2020; Ritz and Shenhav, 2021), creating an ill-posed problem of coordinating across these strategies.

Inverse problems in cognitive control: the implementational level

It is difficult to optimally configure decision-making, and this control faces several equivalent problems to those faced in motor control. In the case of algorithmic cognitive models, we find that parameter degeneracy (e.g., DDM) and process degeneracy (e.g., target-distractor trade-off) make it difficult to optimally configure information processing. However, problems at this level of analysis reflect the best-case scenario, as these cognitive models are themselves often intended to be lower-dimensional representations of the underlying neural processes (Bogacz, 2007). At the implementational level, cognitive control occurs over the complex neural instantiation of these algorithms, further exacerbating the ill-posed nature of the control problem.

One domain in which there can be redundancy in neural control is at the stage of processing at which control is applied, mirroring debates about early and late attentional selection highlighted above. Previous work has suggested that control can influence 'early' sensory processing (Adam and Serences, 2021; Egner and Hirsch, 2005) and 'late' processing in PFC (Mante et al., 2013; Stokes et al., 2013). To the extent that interventions along processing pathways have a similar influence on performance in a given task, there is a dilemma for where to allocate control.

The difficulty in deciding 'where' to allocate control is magnified as the control targets move from macro-scale processing pathways to local configurations of neural populations. For example, a controller could need to configure a small neural network to produce a specific spiking profile in response to inputs. Confounding this goal, it has been shown that a broad range of cellular and synaptic parameters produce very similar neuron- and network-level dynamics at the scale of only a few units (Alonso and Marder, 2019; Goaillard and Marder, 2021; Marder and Goaillard, 2006; Prinz et al., 2004). For example, very different configuration of sodium and potassium conductance can produce very similar bursting profiles, analogously to the redundancy of antagonistic muscles (Golowasch et al., 2002). These findings demonstrates that even simple neural networks face an ill-posed configuration problem, highlighting additional challenges to the biological implementation of cognitive control. Despite this degeneracy, research on brain-computer interfaces has shown that animals can exert fine-grained control over neural populations. Animals are capable of evoking arbitrary activity patterns to maximize reward (Athalye et al., 2019), even at the level of controlling single neurons (Prsa et al., 2017).

Across these different scales of implementation, the optimization of neural systems faces a core set of inverse problems. There are many macro-scale configurations that map similarly onto task

goals, and there are many micro-scale configurations that map similarly on to local dynamics. This problem is closely related to the long-debated issue of *multiple realizability* in philosophy of science, which explores the lack of one-to-one mapping between neural and mental phenomena (e.g., whether pain is identical to 'C fiber' activity; Putnam, 1967). The lack of one-to-one mappings between structure and function poses not only an inferential problem to scientists and philosophers, but also an optimization problem to a brain's control system.

The problem with inversion

As we've outlined above, the core difficulty in planning cognitive control comes from situations in which the brain needs to map a higher-dimensional control configuration on to a lower-dimensional task space, particularly when there is redundancy in this mapping (Figure 4). This class of problems has been carefully explored in applied mathematics (Calvetti and Somersalo, 2018; Engl et al., 1996; Evans and Stark, 2002; Willcox et al., 2021), and this field has developed helpful formalisms and solutions to the problems faced by the brain. We can first consider the *forward problem*, where a brain forecasts what would happen if it adopted a specific control configuration. For example, the controller may predict how performance will change if it raises its decision threshold. This problem generally has a unique solution, as a specific configuration will usually produce a specific result even if there is redundancy. Furthermore, projecting from a higher-dimensional configuration to a lower-dimensional outcome will compress the output, resulting in a stable solution.

However, the goal in optimization is to solve the *inverse problem*, in this case inferring which control configurations will produce a desired task state. As discussed earlier, this problem is generally ill-posed (Hadamard, 1902) because there are multiple redundant solutions for implementing cognitive control. Another reason this is an ill-posed problem is that this projects a lower-dimensional outcome into a higher-dimensional configuration (Calvetti and Somersalo, 2018; Engl et al., 1996). For example, the controller may optimize reward rate, but to do so must configure many potential neural targets. Since outcomes are noisy (e.g., noisy estimates of values due to sampling error or an imperfect forecasting), projection into a higher dimensional control space will amplify this noise. In this regime, small changes in values or goals can produce dramatically different control configurations, leading the optimization process to be unstable. Together, these features impede the brain's ability to optimize cognitive control in the service of goals.

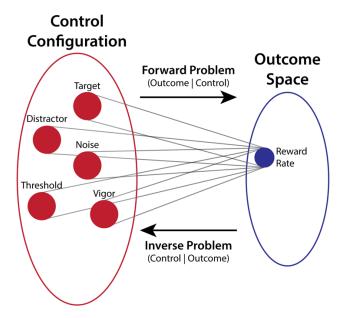


Figure 4. Forward and inverse problems in cognitive control. The forward problem in cognitive control entails predicting how a control configuration (left) would lead to a task state (right). This problem is stable because it maps from a high-dimensional control space into a lower-dimensional task space. Specification of cognitive control requires solving the inverse problem, inferring the optimal control configuration to achieve a goal. This problem is unstable because it (redundantly) maps from a lower-dimensional task space into a higher-dimensional control space. Schematic adapted from (Krakauer et al., 2017).

This fundamental challenge of inferring the actions that will achieve goals has long been a central one within research on computational motor control (McNamee and Wolpert, 2019). Thankfully, these inverse problems can be made tractable though well-established modifications to the optimization process (Engl et al., 1996; Tikhonov, 1963). Motor theorists have leveraged these solutions to help explain action planning, and in doing so providing insight into the nature of effort costs.

Solving the inverse problem

Motor solutions to the inverse problem

A major innovation in theoretical motor control was to reframe the motor control problem as an optimization problem. Under this perspective, actions optimize an objective function over the duration of the motor action (similarly to the reward rate used for decision optimization). For scientists who took this approach, a primary focus was to understand people's objective functions, and in particular the costs that constrain people's actions. Researchers proposed that people place a cost on jerky movements (Flash and Hogan, 1985), muscle force (Chow and Jacobson, 1971; Nelson, 1983; Uno et al., 1989), or action-dependent noise (Harris and Wolpert, 1998), and therefore try to minimize one or more of these while pursuing their goals. A core

difference between these accounts was whether costs depended on movement trajectories (Flash and Hogan, 1985) or muscle force (Uno et al., 1989), with the latter better explaining bodily constraints on actions (e.g., constraints due to range of movement).

It now appears that actions are constrained by a muscle-force-dependent cost (Diedrichsen et al., 2010; Morel et al., 2017; O'Sullivan et al., 2009; Uno et al., 1989), though see also endpoint noise (Harris and Wolpert, 1998; O'Sullivan et al., 2009; Todorov, 2005)). However, it remains unclear whether these effort costs are due to physiological factors like metabolism, or whether they reflect a more general property of the decision process. While metabolism would be an obvious candidate for these effort costs, researchers have found that subjective effort appraisals are largely uncorrelated with information being signaled by bodily afferents (Marcora, 2009). Furthermore, whereas metabolic demands should increase linearly with muscle force, effort costs are better accounted for by a quadratic relationship (Diedrichsen et al., 2010; Shadmehr and Ahmed, 2020).

These discrepancies suggest that motor effort may not depend solely on energy expenditure, but also on properties of the optimization process (e.g., related to the anticipated control investment). A promising explanation for these effort costs may arise from the solution to motor control's ill-posed inverse problem. A central method for solving ill-posed problems is to constrain the solution space through regularization (i.e., placing costs on higher intensities of motor control), a role that motor control theorists have proposed for effort costs (Jordan, 1989; Kawato et al., 1990). For example, across all motor plans that would produce equivalent performance outcomes, there is only one solution that also expends the least effort. From this perspective, motor effort enables better planning by creating global solutions to degenerate planning problems.

Regularization as a solution to ill-posed cognitive control selection

Much like motor control, cognitive control must also solve a degenerate inverse problem. Like motor control, cognitive control is subjectively costly (Shenhav et al., 2017). For example, participants will forego money (Westbrook et al., 2013) and even accept pain (Vogel et al., 2020) to avoid more cognitively demanding tasks. If physical effort regularizes degenerate motor planning, then it is plausible that cognitive effort similarly regularizes degenerate cognitive planning. Re-casting physical and mental effort as a regularization cost brings these domains in line with a wide range of related psychological phenomena. For example, inferring depth from visual inputs is also an ill-posed problem, and this inference has been argued to depend on regularization (Bertero et al., 1988; Poggio et al., 1985b, 1985a).

Recent proposals have drawn connections between cognitive effort and regularization under a variety of theoretical motivations. For instance, it has been proposed that cognitive effort enhances multi-task learning (Kool and Botvinick, 2018; Musslick et al., 2020), where effort

costs regularize towards task-general policies ('habits') that enable better transfer learning. It has been also been proposed, based on principles of efficient coding (Zénon et al., 2019), that effort costs enable compressed and more metabolically efficient stimulus-action representations. Finally, effort costs have been motivated from the perspective of model-based control (Piray and Daw, 2021), where regularization towards a default policy allows for more efficient long-range planning. These accounts offer different perspectives on the benefits of regularized control, complementing motor control's emphasis on solving ill-posed inverse problems.

Regularization in inverse problems has a normative Bayesian interpretation, in which constraints come from prior knowledge about the solution space (Calvetti and Somersalo, 2018). This Bayesian perspective has been influential in modelling ill-posed problems like inferring knowledge from limited exemplars (Tenenbaum et al., 2011, 2006) and planning sequential actions (Botvinick and Toussaint, 2012; Friston et al., 2012; Solway and Botvinick, 2012). Regularization and Bayesian inference have been a productive approach for understanding how people solve ill-posed problems in cognition and action. Within the Bayesian frameworks, effort costs can be re-cast in terms of shrinkage towards a prior, providing further insight into how a regularization perspective could inform cognitive control. If there are priors on cognitive or neural configurations, such as automatic processes like habits, then regularized control would penalize deviations from those defaults.

A Bayesian perspective on the relationship between automaticity and control costs makes an interesting and counterintuitive prediction: when people's priors are to exert high levels of control, they will find it difficult to relax their control intensity. Research on control learning supports these predictions. A large body of work has found that participants learn to exert more control when they expect a task to be difficult (Bugg and Chanani, 2011; Jiang et al., 2015; Logan and Zbrodoff, 1979; Yu et al., 2009), or when stimuli are associated with conflict (Bugg and Crump, 2012; Bugg and Hutchison, 2013). This results in an allocation of excessive and maladaptive levels of control when a trial turns out to be easy (Logan and Zbrodoff, 1979). A recent experiment by Bustamante and colleagues (2021) extended these findings by showing how biases in control exertion can emerge over the course of reward learning in a featurespecific manner. Participants performed a color-word Stroop task where they could choose to either name the color (more control-demanding) or read the word (less control-demanding). They learned that certain stimulus features would yield greater reward for color-naming and others for word-reading. Critically, during a subsequent transfer phase, participants had trouble learning to adaptively disengage control when faced with a combination of stimulus features that had each previously predicted greater reward for greater effort. That is, they had learned to over-exert control. Further work is needed to understand whether this over-exertion is due to control mobilization, or control priors that make color-naming less effortful (Yu et al., 2009).

Algorithms for motor and cognitive control

Motor and cognitive control appear to solve similar problems (action-outcome inversion), and plausibly through similar computational principles (regularized optimization). The next logical step is to ask whether cognitive control has developed similar algorithmic solutions to this inversion as the motor control system. A longstanding gold-standard algorithm for modelling motor actions is the Linear Quadratic Regulator (LQR; Haar and Donchin, 2020; Shadmehr and Krakauer, 2008; Todorov and Jordan, 2002), and this algorithms serves as a promising candidate for understanding the regulation of cognitive actions.

LQR can provide the optimal solution to sequential control problems when two specific criteria are met. First, the system under control must have linear dynamics, such as a cruise controller that adjusts the speed of a car. Second, the control must be optimizing quadratic objectives. This usually involves minimizing both the squared goal error (e.g., the squared deviation from the desired speed) and the squared control intensity (e.g., the squared motor torque). Under these conditions, LQR provides an analytic (i.e., closed-form) solution to the optimal sequential policy, avoiding the curse of dimensionality (Van Rooij, 2008).

In the domain of motor control, this model empirically captures participants' motor trajectories (Stevenson et al., 2009; Todorov and Jordan, 2002; Yeo et al., 2016), particularly in the case where there are mid-trajectory perturbations to goals or effectors (Diedrichsen, 2007; Knill et al., 2011; Liu and Todorov, 2007; Nashed et al., 2012; Takei et al., 2021). A striking example of the power of this model to capture behavior was observed in an experiment on motor coordination (Diedrichsen, 2007). Participants performed a reaching task in which the goal either depended on both arms (e.g., rowing), or where each arm had a separate goal (e.g., juggling). During the reach, the experimenters perturbed one of the arms, and found that participants compensated with both arms only when they were both involved in the same goal. In LQR, this goal-dependent coordination arises due to the algorithm's model-based feedback control, with squared effort costs favoring distributing the work across goal-relevant effectors. Accordingly, this study found that LQR simulations accurately captured participants' reach trajectories. Furthermore, participants' behavior also confirmed a key prediction of LQR, namely that noise correlations between arms will be task-specific, constraining control to the goal-relevant dimensions of the task manifold (cf. 'minimal intervention principle'; Todorov and Jordan, 2002).

A starting point for developing algorithmic links between cognitive and motor control is to consider whether cognitive control is a problem that is well-suited for LQR. The first prediction from LQR is that the dynamics between cognitive states are approximately linear. One measure of these dynamics comes from task switching, in which participants switch between multiple stimulus-response rules ('task sets'; (Monsell, 2003)). Researchers have found that these transitions between task sets are well-captured by linear dynamics (Musslick et al., 2019a;

Musslick and Cohen, 2021; Steyvers et al., 2019). For example, when participants are given a variable amount of time to prepare for a transition between two tasks (e.g., responding based on letters vs digits), the stereotypical switch cost of slower responding after a task switch compared to a task repetition decreases with greater preparation time (Rogers and Monsell, 1995). A simple re-analysis of this pattern shows that switch costs can be well-captured by a linear dynamical model (Figure 5A). Whereas switching to the 'letter' or 'digit' task had different initial and asymptotic performance costs, they appear to exhibit a similar rate of change.

Linear dynamics have also been observed in attentional adjustments that occur within a trial of a given task. For instance, recent work has shown that performance on an Eriksen flanker task can be accounted for by a DDM variant in which initially-broad attention narrows within a trial to primarily focus only the central target, resulting in a shift from the drift rate being initially dominated by the flankers to being primarily dominated by the target (Servant et al., 2014; Weichart et al., 2020; White et al., 2011). Using the dot motion task described earlier, we recently showed that these within-trial dynamics can be further teased apart into target-enhancing and distractor-suppressing elements of feature-based attention, each with its own independent dynamics (Ritz and Shenhav, 2021). These dynamics were well-captured by an accumulation model that regulated feature gains with a linear feedback control law (Figure 5B).

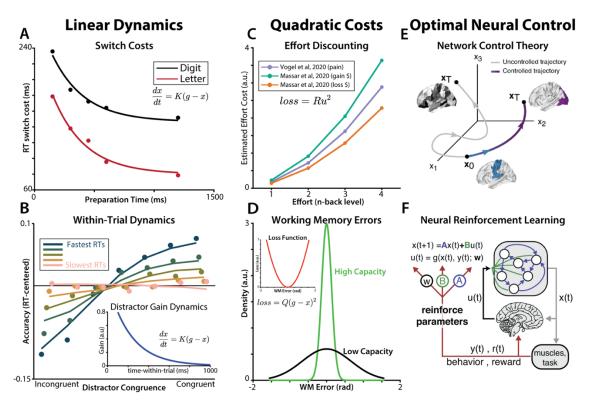


Figure 5. Linear-Quadratic properties of cognitive control. A-B) There is evidence of linear cognitive control reconfiguration dynamics both between trials and within a given trial. (A) In task-switching experiments, participants' switch costs exponentially decay with longer preparation time, consistent with linear dynamics. Lines show a maximum likelihood fit to data from (Rogers and Monsell, 1995) in which participants

switched between letter and digit tasks. We estimated a shared speed (K) across tasks, with separate initial conditions and asymptote fit to average switch costs in each task. (B) Similar dynamics are found in within-trial dynamics of target and distractor processing (Ritz and Shenhav, 2021). Participants' sensitivity to distractors exponentially decayed over time within the trial, consistent with linear dynamics. C-D) Quadratic cost functions are evident in studies of effort discounting and working memory. (C) In effort-discounting tasks, participants' subjective cost of n-back tasks quadratically increases with their working memory load. Estimated cost functions are plotted from (Massar et al., 2020; Vogel et al., 2020). (D) Errors on working memory tasks are approximately Gaussian, consistent with a quadratic loss function on accuracy (Sims et al., 2012). E-F) Neural models of optimal control. (E) Network Control Theory is a framework for characterizing macro-scale connectivity (Tang and Bassett, 2018). It uses LQR to interprets connectivity graphs in terms of how they facilitate goal-directed configuration of large-scale brain states. (F) Neural Reinforcement Learning is a framework for meso-scale control and connectivity (Athalye et al., 2019). It describes the transition from early effortful control to gradual alterations of connectivity to facilitate task goals (cf. automaticity). A recent implementation of this framework explicitly uses LQR (Athalye et al., 2021).

A second prediction from LQR is that cognitive effort costs are quadratic. There are two lines of evidence that support this prediction. One line of evidence comes from studies of *cognitive effort discounting*, which examine how people explicitly trade off different amounts reward (e.g., money) against different levels of cognitive effort (e.g., n-back load). These studies quantify the extent to which different levels of effort are treated as a cost when making those decisions (i.e., how much reward is discounted by this effort), and many of them find that quadratic effort discounting captures choice the best among their tested models (Figure 5C; Białaszek et al., 2017; Massar et al., 2020; Petitet et al., 2021; Soutschek et al., 2014; Vogel et al., 2020; though see also Chong et al., 2017; Hess et al., 2021; McGuigan et al., 2019)¹. A second line of evidence supporting quadratic costs is found in tasks that require participants to hold a stimulus in working memory (e.g., a Gabor patch of a given orientation) and then reproduce that stimulus after a delay period. Errors on this task tend to be approximately Gaussian (Bays and Husain, 2008; Ma et al., 2014; Sprague et al., 2016; van den Berg et al., 2012; Wilken and Ma, 2004), consistent with the predictions of ideal observer models that incorporate quadratic loss function (Sims, 2015; Sims et al., 2012; Figure 5D).

Recent work has begun to make explicit links between LQR and the neural implementation of cognitive control. Most notably, Bassett and colleagues have used LQR to model the large-scale control of brain networks (Tang and Bassett, 2018; Figure 5E). This approach uses LQR modelling of whole-brain network dynamics to understand the ability of sub-networks to reconfigure macro-scale brain states (Betzel et al., 2016; Braun et al., 2021; Gu et al., 2021, 2015), see also (Yan et al., 2017). For instance, in an fMRI experiment using the n-back task, Braun and colleagues (2021) found that their LQR model inferred that the brain requires more control to maintain a stable 2-back state than a 0-back state, as well as more control to transition

¹ A concern about effort discounting is that it ought to be estimated based on cognitive demands rather than task demands. Notably, participants consistently show quadratic effort discounting in the n-back task, one domain where there is at least a well-characterized linear relationship between these levels of task load and PFC activity (Braver et al., 1997).

from a 0-back state into a 2-back state than vice versa. Interestingly, individual differences in these model-derived estimates of stability and flexibility were associated with differences in dopamine genotype, dopaminergic receptor blockade, and schizophrenia diagnosis (Braun et al., 2021). An LQR modelling approach has been similarly used to model dynamics in directly-recorded neural activity to understand how local connectivity influences control demands (Athalye et al., 2021; Stiso et al., 2019; Figure 5F), with accompanying theories of how these configuration processes are learned through experience and reward (Athalye et al., 2019).

Conclusions and future directions

The second half of the twentieth century saw a wave of progress on mathematical models for optimal control problems in applied mathematics. A second wave of computational motor control followed closely, combining rigorous measurement of motor actions with normative models from this new optimal control theory (Chow and Jacobson, 1971; Flash and Hogan, 1985; Nelson, 1983; Todorov and Jordan, 2002; Uno et al., 1989). Recently, a third wave of cognitive control research has extended optimal control principles to goal-directed cognition (Bogacz et al., 2006; Lieder et al., 2018; Musslick and Cohen, 2021; Piray and Daw, 2021; Shenhav et al., 2013, 2017; Tang and Bassett, 2018; Yu et al., 2009). This work tries to formalize the principles that tie these different frameworks together, highlighting how cognitive control can learn from decades of computational motor control research. These principles have the potential to inform the theoretical development and focused empirical investigation into the architecture of goal-directed cognition. As behavioral tasks, statistical techniques, and neuroimaging methods improve our measurements of how the brain configures information processing, theoretical constraints will be essential for asking the right questions.

One insight from casting cognitive control as regularized optimization is that the sources of the control costs that can enable 'failures' of control are not necessarily due to cognitive *limitations* (e.g., limited capacity to engage multiple control signals). Instead, these costs can arise due to the *flexibility* of cognition, enabling a complex brain to optimize over degenerate control actions. Under this framework, effort helps *solve* the decision problem of how to configure control. One productive application of this perspective may be to help shed light on why people differ in how they configure these multivariate control signals, for instance prioritizing some forms of control over others. A regularization perspective would emphasize understanding different people's priors (such as judgements of ability, (Bandura, 1977; Shenhav et al., 2021)) and configural redundancy when accounting for people's mental effort costs.

There are several important avenues for building further on the promising theoretical and empirical foundations that have been recently established in the study of multivariate control optimization. For instance, it will be important to understand how effort's role in solving the inverse problem trades off against other proposed benefits like generalization (Kool and

Botvinick, 2018; Musslick et al., 2020) and efficiency (Zénon et al., 2019). It will also be important to develop finer-grained connections between computational theories of regularized cognitive control and the algorithmic and implementational theories of how the brain performs control optimization and execution. For instance, to what extent can specific regularized control algorithms such as LQR explain the dynamics of cognitive control optimization and deployment? While LQR modelling has been a powerful approach for understanding the role of neural connectivity in goal-driven brain dynamics, more work is needed to bridge these findings to cognitive models of control optimization and specification.

Progress on these questions will in turn require more precise estimates of the underlying control processes. The study of motor control has benefited immensely from high resolution measurements of motor effectors, for instance tracking hand position during reaching. Analogous measures of cognitive control are much more difficult to acquire, in part because they require inference from motor movements (e.g., response time) and/or patterns of activity within neural populations whose properties are still poorly understood and are typically measured with limited spatiotemporal resolution. Future experiments should combine computational modelling with spatiotemporally resolved neuroimaging to understand the implementation of different types of control. In addition to addressing core questions at the heart of multivariate control optimization, such methodological improvements will also help us better understand the heterogeneity of multivariate effort. For instance, an untested assumption implied by existing theoretical frameworks is that all forms of cognitive control will incur subjective costs in a similar fashion, for instance that higher levels of drift rate and higher levels of threshold will both be experienced as effortful (cf. Shenhav et al., 2013). While there is consistent evidence that enhancements to drift rate incur a cost, it remains less clear whether adjustments to response threshold incur a cost over and above the reductions to reward rate they can cause (cf. Leng et al., 2020). Further research is needed to examine this question and to explore both the magnitude and functional form of these cost functions across a wider array of control signals, especially with respect to deviations from participants' default configurations.

Our cognitive control is extremely complex, flexible, primarily operates over latent processes like decision making, all features that make studying cognitive control a challenge. Thankfully, we can gain better traction on this inference by drawing from the rich empirical and theoretical traditions in better-constrained fields like motor control (Broadbent, 1977). The normative principles of optimal control theory, which have proven so fruitful in motor control, can similarly help inform our theories and investigations into cognitive control. While our cognition will certainly diverge from these normative theories, these approaches can provide a core foundation for understanding how we control our thoughts and actions.

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References

- Abrahamse E, Braem S, Notebaert W, Verguts T. 2016. Grounding cognitive control in associative learning. *Psychol Bull* **142**:693–728.
- Adam KCS, Serences JT. 2021. History modulates early sensory processing of salient distractors. *J Neurosci*. doi:10.1523/JNEUROSCI.3099-20.2021
- Adkins TJ, Lee T. 2021. Reward reduces habitual errors by enhancing the preparation of goal-directed actions. doi:10.31234/osf.io/hv9mz
- Alonso LM, Marder E. 2019. Visualization of currents in neural models with similar behavior and different conductance densities. *Elife* 8. doi:10.7554/eLife.42722
- Aron AR. 2007. The Neural Basis of Inhibition in Cognitive Control. *The Neuroscientist*. doi:10.1177/1073858407299288
- Athalye VR, Carmena JM, Costa RM. 2019. Neural reinforcement: re-entering and refining neural dynamics leading to desirable outcomes. *Curr Opin Neurobiol* **60**:145–154.
- Athalye VR, Khanna P, Gowda S, Orsborn AL, Costa RM, Carmena JM. 2021. The brain uses invariant dynamics to generalize outputs across movements. *bioRxiv*. doi:10.1101/2021.08.27.457931
- Balci F, Simen P, Niyogi R, Saxe A, Hughes JA, Holmes P, Cohen JD. 2011. Acquisition of decision making criteria: reward rate ultimately beats accuracy. *Atten Percept Psychophys* **73**:640–657.
- Bandura A. 1977. Self-efficacy: toward a unifying theory of behavioral change. *Psychol Rev* **84**:191–215.
- Bays PM, Husain M. 2008. Dynamic shifts of limited working memory resources in human vision. *Science* **321**:851–854.
- Berlyne DE. 1957. Uncertainty and conflict: a point of contact between information-theory and behavior-theory concepts. *Psychol Rev* **64**:329.
- Bernstein NA. 1935. The co-ordination and regulation of movements.
- Bertero M, Poggio TA, Torre V. 1988. Ill-posed problems in early vision. *Proc IEEE* **76**:869–889.
- Betzel RF, Gu S, Medaglia JD, Pasqualetti F, Bassett DS. 2016. Optimally controlling the human connectome: the role of network topology. *Sci Rep* **6**:30770.
- Białaszek W, Marcowski P, Ostaszewski P. 2017. Physical and cognitive effort discounting across different reward magnitudes: Tests of discounting models. *PLoS One* **12**:e0182353.
- Bogacz R. 2007. Optimal decision-making theories: linking neurobiology with behaviour. *Trends Cogn Sci* **11**:118–125.
- Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD. 2006. The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol Rev* **113**:700–765.
- Boksem MAS, Meijman TF, Lorist MM. 2006. Mental fatigue, motivation and action monitoring. *Biol Psychol* **72**:123–132.
- Botvinick M, Toussaint M. 2012. Planning as inference. *Trends Cogn Sci* **16**:485–488.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD. 2001. Conflict monitoring and cognitive control. *Psychol Rev* **108**:624–652.
- Botvinick MM, Cohen JD. 2014. The computational and neural basis of cognitive control: charted territory and new frontiers. *Cogn Sci* **38**:1249–1285.

- Boureau Y-L, Sokol-Hessner P, Daw ND. 2015. Deciding How To Decide: Self-Control and Meta-Decision Making. *Trends Cogn Sci* **19**:700–710.
- Braem S, Verguts T, Roggeman C, Notebaert W. 2012. Reward modulates adaptations to conflict. *Cognition* **125**:324–332.
- Braun U, Harneit A, Pergola G, Menara T, Schäfer A, Betzel RF, Zang Z, Schweiger JI, Zhang X, Schwarz K, Chen J, Blasi G, Bertolino A, Durstewitz D, Pasqualetti F, Schwarz E, Meyer-Lindenberg A, Bassett DS, Tost H. 2021. Brain network dynamics during working memory are modulated by dopamine and diminished in schizophrenia. *Nat Commun* 12:3478.
- Braver TS, Barch DM. 2002. A theory of cognitive control, aging cognition, and neuromodulation. *Neurosci Biobehav Rev* **26**:809–817.
- Braver TS, Cohen JD, Nystrom LE, Jonides J, Smith EE, Noll DC. 1997. A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* **5**:49–62.
- Brittain J-S, Watkins KE, Joundi RA, Ray NJ, Holland P, Green AL, Aziz TZ, Jenkinson N. 2012. A role for the subthalamic nucleus in response inhibition during conflict. *J Neurosci* **32**:13396–13401.
- Broadbent DE. 1977. Levels, Hierarchies, and the Locus of Control. *Quarterly Journal of Experimental Psychology*. doi:10.1080/14640747708400596
- Bugg JM, Chanani S. 2011. List-wide control is not entirely elusive: evidence from picture-word Stroop. *Psychon Bull Rev* **18**:930–936.
- Bugg JM, Crump MJC. 2012. In Support of a Distinction between Voluntary and Stimulus-Driven Control: A Review of the Literature on Proportion Congruent Effects. *Front Psychol* **3**:367.
- Bugg JM, Hutchison KA. 2013. Converging evidence for control of color-word Stroop interference at the item level. *J Exp Psychol Hum Percept Perform* **39**:433–449.
- Bustamante L, Lieder F, Musslick S, Shenhav A, Cohen J. 2021. Learning to Overexert Cognitive Control in a Stroop Task. *Cogn Affect Behav Neurosci*. doi:10.3758/s13415-020-00845-x
- Calvetti D, Somersalo E. 2018. Inverse problems: From regularization to Bayesian inference. *Wiley Interdiscip Rev Comput Stat* **10**:e1427.
- Casey BJ, Epstein JN, Buhle J, Liston C, Davidson MC, Tonev ST, Spicer J, Niogi S, Millner AJ, Reiss A, Garrett A, Hinshaw SP, Greenhill LL, Shafritz KM, Vitolo A, Kotler LA, Jarrett MA, Glover G. 2007. Frontostriatal connectivity and its role in cognitive control in parent-child dyads with ADHD. *Am J Psychiatry* **164**:1729–1736.
- Cavanagh JF, Frank MJ. 2014. Frontal theta as a mechanism for cognitive control. *Trends Cogn Sci* **18**:414–421.
- Cavanagh JF, Wiecki TV, Cohen MX, Figueroa CM, Samanta J, Sherman SJ, Frank MJ. 2011. Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold. *Nat Neurosci* **14**:1462–1467.
- Chiew KS, Braver TS. 2016. Reward favors the prepared: Incentive and task-informative cues interact to enhance attentional control. *J Exp Psychol Hum Percept Perform* **42**:52–66.
- Chong TT-J, Apps M, Giehl K, Sillence A, Grima LL, Husain M. 2017. Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLoS Biol* **15**:e1002598.
- Chow CK, Jacobson DH. 1971. Studies of human locomotion via optimal programming. *Math Biosci* **10**:239–306.
- Codol O, Forgaard CJ, Galea JM, Gribble PL. 2021. Sensorimotor feedback loops are selectively

- sensitive to reward. bioRxiv. doi:10.1101/2021.09.16.460659
- Codol O, Holland PJ, Manohar SG, Galea JM. 2020. Reward-based improvements in motor control are driven by multiple error-reducing mechanisms. *J Neurosci*. doi:10.1523/JNEUROSCI.2646-19.2020
- Cohen JD, Servan-Schreiber D, McClelland JL. 1992. A parallel distributed processing approach to automaticity. *Am J Psychol* **105**:239–269.
- Danielmeier C, Allen EA, Jocham G, Onur OA, Eichele T, Ullsperger M. 2015. Acetylcholine mediates behavioral and neural post-error control. *Curr Biol* 25:1461–1468.
- Danielmeier C, Eichele T, Forstmann BU, Tittgemeyer M, Ullsperger M. 2011. Posterior medial frontal cortex activity predicts post-error adaptations in task-related visual and motor areas. *J Neurosci* **31**:1780–1789.
- Danielmeier C, Ullsperger M. 2011. Post-error adjustments. Front Psychol 2:233.
- Debener S, Ullsperger M, Siegel M, Fiehler K, von Cramon DY, Engel AK. 2005. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *J Neurosci* **25**:11730–11737.
- Diedrichsen J. 2007. Optimal task-dependent changes of bimanual feedback control and adaptation. *Curr Biol* **17**:1675–1679.
- Diedrichsen J, Shadmehr R, Ivry RB. 2010. The coordination of movement: optimal feedback control and beyond. *Trends Cogn Sci* **14**:31–39.
- Dix A, Li S-C. 2020. Incentive motivation improves numerosity discrimination: Insights from pupillometry combined with drift-diffusion modelling. *Sci Rep* **10**:2608.
- Dutilh G, Vandekerckhove J, Forstmann BU, Keuleers E, Brysbaert M, Wagenmakers E-J. 2012. Testing theories of post-error slowing. *Atten Percept Psychophys* **74**:454–465.
- Egner T. 2007. Congruency sequence effects and cognitive control. *Cogn Affect Behav Neurosci* 7:380–390.
- Egner T, Delano M, Hirsch J. 2007. Separate conflict-specific cognitive control mechanisms in the human brain. *Neuroimage* **35**:940–948.
- Egner T, Hirsch J. 2005. Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nat Neurosci* **8**:1784–1790.
- Engl HW, Hanke M, Neubauer A. 1996. Regularization of Inverse Problems. Springer Science & Business Media.
- Esterman M, Grosso M, Liu G, Mitko A, Morris R, DeGutis J. 2016. Anticipation of Monetary Reward Can Attenuate the Vigilance Decrement. *PLoS One* **11**:e0159741.
- Esterman M, Poole V, Liu G, DeGutis J. 2017. Modulating Reward Induces Differential Neurocognitive Approaches to Sustained Attention. *Cereb Cortex* 27:4022–4032.
- Esterman M, Reagan A, Liu G, Turner C, DeGutis J. 2014. Reward reveals dissociable aspects of sustained attention. *J Exp Psychol Gen* **143**:2287–2295.
- Etzel JA, Cole MW, Zacks JM, Kay KN, Braver TS. 2016. Reward Motivation Enhances Task Coding in Frontoparietal Cortex. *Cereb Cortex* **26**:1647–1659.
- Evans NJ, Servant M. 2020. A model-based approach to disentangling facilitation and interference effects in conflict tasks. doi:10.31234/osf.io/tu8ym
- Evans SN, Stark PB. 2002. Inverse problems as statistics. *Inverse Probl* 18:R55.
- Fischer AG, Nigbur R, Klein TA, Danielmeier C, Ullsperger M. 2018. Cortical beta power reflects decision dynamics and uncovers multiple facets of post-error adaptation. *Nat Commun* **9**:5038.
- Flash T, Hogan N. 1985. The coordination of arm movements: an experimentally confirmed

- mathematical model. J Neurosci 5:1688–1703.
- Fontanesi L, Gluth S, Spektor MS, Rieskamp J. 2019. A reinforcement learning diffusion decision model for value-based decisions. *Psychon Bull Rev* **26**:1099–1121.
- Fortenbaugh FC, DeGutis J, Esterman M. 2017. Recent theoretical, neural, and clinical advances in sustained attention research. *Ann N Y Acad Sci* **1396**:70–91.
- Fortenbaugh FC, DeGutis J, Germine L, Wilmer JB, Grosso M, Russo K, Esterman M. 2015. Sustained Attention Across the Life Span in a Sample of 10,000: Dissociating Ability and Strategy. *Psychol Sci* **26**:1497–1510.
- Frank MJ, Gagne C, Nyhus E, Masters S, Wiecki TV, Cavanagh JF, Badre D. 2015. fMRI and EEG predictors of dynamic decision parameters during human reinforcement learning. *J Neurosci* **35**:485–494.
- Friedman NP, Miyake A. 2017. Unity and diversity of executive functions: Individual differences as a window on cognitive structure. *Cortex* **86**:186–204.
- Friedman NP, Robbins TW. 2021. The role of prefrontal cortex in cognitive control and executive function. *Neuropsychopharmacology* 1–18.
- Friston K, Samothrakis S, Montague R. 2012. Active inference and agency: optimal control without cost functions. *Biol Cybern* **106**:523–541.
- Fröber K, Dreisbach G. 2014. The differential influences of positive affect, random reward, and performance-contingent reward on cognitive control. *Cogn Affect Behav Neurosci* **14**:530–547.
- Frömer R, Lin H, Dean Wolf CK, Inzlicht M, Shenhav A. 2021. Expectations of reward and efficacy guide cognitive control allocation. *Nat Commun* 12:1–11.
- Funes MJ, Lupiáñez J, Humphreys G. 2010. Sustained vs. transient cognitive control: evidence of a behavioral dissociation. *Cognition* **114**:338–347.
- Gehring WJ, Fencsik DE. 2001. Functions of the medial frontal cortex in the processing of conflict and errors. *J Neurosci* **21**:9430–9437.
- Goaillard J-M, Marder E. 2021. Ion Channel Degeneracy, Variability, and Covariation in Neuron and Circuit Resilience. *Annu Rev Neurosci* **44**:335–357.
- Golowasch J, Goldman MS, Abbott LF, Marder E. 2002. Failure of averaging in the construction of a conductance-based neuron model. *J Neurophysiol* **87**:1129–1131.
- Gonthier C, Braver TS, Bugg JM. 2016. Dissociating proactive and reactive control in the Stroop task. *Mem Cognit* **44**:778–788.
- Grahek I, Schettino A, Koster EHW, Andersen SK. 2021. Dynamic Interplay between Reward and Voluntary Attention Determines Stimulus Processing in Visual Cortex. *J Cogn Neurosci* 1–15.
- Grahek I, Shenhav A, Musslick S, Krebs RM, Koster EHW. 2019. Motivation and cognitive control in depression. *Neurosci Biobehav Rev* **102**:371–381.
- Gratton G, Coles MGH, Donchin E. 1992. Optimizing the use of information: strategic control of activation of responses. *J Exp Psychol Gen* **121**:480.
- Gu S, Fotiadis P, Parkes L, Xia CH, Gur RC, Gur RE, Roalf DR, Satterthwaite TD, Bassett DS. 2021. Network controllability mediates the relationship between rigid structure and flexible dynamics. *bioRxiv*. doi:10.1101/2021.04.23.441156
- Gu S, Pasqualetti F, Cieslak M, Telesford QK, Yu AB, Kahn AE, Medaglia JD, Vettel JM, Miller MB, Grafton ST, Bassett DS. 2015. Controllability of structural brain networks. *Nat Commun* **6**:8414.
- Guitart-Masip M, Beierholm UR, Dolan R, Duzel E, Dayan P. 2011. Vigor in the face of

- fluctuating rates of reward: an experimental examination. *J Cogn Neurosci* **23**:3933–3938.
- Haar S, Donchin O. 2020. A Revised Computational Neuroanatomy for Motor Control. *J Cogn Neurosci* 1–14.
- Hadamard J. 1902. Sur les problèmes aux dérivées partielles et leur signification physique. *Princeton university bulletin* 49–52.
- Hall-McMaster S, Muhle-Karbe PS, Myers NE, Stokes MG. 2019. Reward Boosts Neural Coding of Task Rules to Optimize Cognitive Flexibility. *J Neurosci* **39**:8549–8561.
- Harris CM, Wolpert DM. 2006. The main sequence of saccades optimizes speed-accuracy trade-off. *Biol Cybern* **95**:21–29.
- Harris CM, Wolpert DM. 1998. Signal-dependent noise determines motor planning. *Nature* **394**:780–784.
- Herz DM, Zavala BA, Bogacz R, Brown P. 2016. Neural correlates of decision thresholds in the human subthalamic nucleus. *Curr Biol* **26**:916–920.
- Hess TM, Lothary AF, O'Brien EL, Growney CM, DeLaRosa J. 2021. Predictors of engagement in young and older adults: The role of specific activity experience. *Psychol Aging* **36**:131–142.
- Jang H, Lewis R, Lustig C. 2021. Opposite reactions to loss incentive by young and older adults: Insights from diffusion modeling. *PsyArXiv*. doi:10.31234/osf.io/4a3rc
- Jentzsch I, Dudschig C. 2009. Why do we slow down after an error? Mechanisms underlying the effects of posterror slowing. *Q J Exp Psychol (Hove)* **62**:209–218.
- Jiang J, Beck J, Heller K, Egner T. 2015. An insula-frontostriatal network mediates flexible cognitive control by adaptively predicting changing control demands. *Nat Commun* **6**:8165.
- Jiang J, Egner T. 2013. Using Neural Pattern Classifiers to Quantify the Modularity of Conflict—Control Mechanisms in the Human Brain. *Cereb Cortex* **24**:1793–1805.
- Jordan MI. 1989. Indeterminate motor skill learning problems. Attention and performance.
- Kawato M, Maeda Y, Uno Y, Suzuki R. 1990. Trajectory formation of arm movement by cascade neural network model based on minimum torque-change criterion. *Biol Cybern* **62**:275–288.
- Kerns JG. 2006. Anterior cingulate and prefrontal cortex activity in an FMRI study of trial-to-trial adjustments on the Simon task. *Neuroimage* **33**:399–405.
- Kerns JG, Cohen JD, MacDonald AW 3rd, Cho RY, Stenger VA, Carter CS. 2004. Anterior cingulate conflict monitoring and adjustments in control. *Science* **303**:1023–1026.
- King JA, Korb FM, von Cramon DY, Ullsperger M. 2010. Post-error behavioral adjustments are facilitated by activation and suppression of task-relevant and task-irrelevant information processing. *J Neurosci* **30**:12759–12769.
- Knill DC, Bondada A, Chhabra M. 2011. Flexible, task-dependent use of sensory feedback to control hand movements. *J Neurosci* **31**:1219–1237.
- Koch I, Poljac E, Müller H, Kiesel A. 2018. Cognitive structure, flexibility, and plasticity in human multitasking-An integrative review of dual-task and task-switching research. *Psychol Bull* **144**:557–583.
- Kool W, Botvinick M. 2018. Mental labour. Nat Hum Behav 2:899–908.
- Krakauer JW, Ghazanfar AA, Gomez-Marin A, MacIver MA, Poeppel D. 2017. Neuroscience Needs Behavior: Correcting a Reductionist Bias. *Neuron* **93**:480–490.
- Krebs RM, Boehler CN, Woldorff MG. 2010. The influence of reward associations on conflict

- processing in the Stroop task. *Cognition* **117**:341–347.
- Laming D. 1979a. Choice reaction performance following an error. Acta Psychol 43:199–224.
- Laming D. 1979b. Choice reaction performance following an error. *Acta Psychol (Amst)* **43**:199–224
- Laming DRJ. 1968. Information Theory of Choice-reaction Times. Academic P.
- Leng X, Yee D, Ritz H, Shenhav A. 2020. Dissociable influences of reward and punishment on adaptive cognitive control. *bioRxiv*. doi:10.1101/2020.09.11.294157
- Lesh TA, Niendam TA, Minzenberg MJ, Carter CS. 2011. Cognitive control deficits in schizophrenia: mechanisms and meaning. *Neuropsychopharmacology* **36**:316–338.
- Ličen M, Hartmann F, Repovš G, Slapničar S. 2016. The Impact of Social Pressure and Monetary Incentive on Cognitive Control. *Front Psychol* 7:93.
- Lieder F, Shenhav A, Musslick S, Griffiths TL. 2018. Rational metareasoning and the plasticity of cognitive control. *PLoS Comput Biol* **14**:e1006043.
- Liu D, Todorov E. 2007. Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci* **27**:9354–9368.
- Logan GD, Zbrodoff NJ. 1979. When it helps to be misled: Facilitative effects of increasing the frequency of conflicting stimuli in a Stroop-like task. *Mem Cognit* 7:166–174.
- Luna B. 2009. Developmental changes in cognitive control through adolescence. *Adv Child Dev Behav* **37**:233–278.
- Ma WJ, Husain M, Bays PM. 2014. Changing concepts of working memory. *Nat Neurosci* **17**:347–356.
- Maier ME, Yeung N, Steinhauser M. 2011. Error-related brain activity and adjustments of selective attention following errors. *Neuroimage* **56**:2339–2347.
- Manohar SG, Chong TT-J, Apps MAJ, Batla A, Stamelou M, Jarman PR, Bhatia KP, Husain M. 2015. Reward Pays the Cost of Noise Reduction in Motor and Cognitive Control. *Curr Biol* 25:1707–1716.
- Manohar SG, Finzi RD, Drew D, Husain M. 2017. Distinct Motivational Effects of Contingent and Noncontingent Rewards. *Psychol Sci* **28**:1016–1026.
- Manohar SG, Muhammed K, Fallon SJ, Husain M. 2019. Motivation dynamically increases noise resistance by internal feedback during movement. *Neuropsychologia* **123**:19–29.
- Mante V, Sussillo D, Shenoy KV, Newsome WT. 2013. Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* **503**:78–84.
- Marco-Pallarés J, Camara E, Münte TF, Rodríguez-Fornells A. 2008. Neural mechanisms underlying adaptive actions after slips. *J Cogn Neurosci* **20**:1595–1610.
- Marcora S. 2009. Perception of effort during exercise is independent of afferent feedback from skeletal muscles, heart, and lungs. *J Appl Physiol* **106**:2060–2062.
- Marder E, Goaillard J-M. 2006. Variability, compensation and homeostasis in neuron and network function. *Nat Rev Neurosci* 7:563–574.
- Massar SAA, Pu Z, Chen C, Chee MWL. 2020. Losses Motivate Cognitive Effort More Than Gains in Effort-Based Decision Making and Performance. *Front Hum Neurosci* 14:287.
- McGuigan S, Zhou SH, Brosnan MB, Thyagarajan D. 2019. Dopamine restores cognitive motivation in Parkinson's disease. *Brain*.
- McNamee D, Wolpert DM. 2019. Internal Models in Biological Control. *Annu Rev Control Robot Auton Syst* **2**:339–364.
- Menon V, D'Esposito M. 2021. The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology* 1–14.

- Miletić S, Turner BM, Forstmann BU, van Maanen L. 2017. Parameter recovery for the Leaky Competing Accumulator model. *J Math Psychol* **76**:25–50.
- Monsell S. 2003. Task switching. Trends Cogn Sci 7:134–140.
- Morel P, Ulbrich P, Gail A. 2017. What makes a reach movement effortful? Physical effort discounting supports common minimization principles in decision making and motor control. *PLoS Biol* **15**:e2001323.
- Musslick S, Bizyaeva A, Agaron S, Leonard N, Cohen JD. 2019a. Stability-flexibility dilemma in cognitive control: a dynamical system perspectiveProceedings of the 41st Annual Meeting of the Cognitive Science Society.
- Musslick S, Cohen JD. 2021. Rationalizing constraints on the capacity for cognitive control. *Trends Cogn Sci* **0**. doi:10.1016/j.tics.2021.06.001
- Musslick S, Cohen JD, Shenhav A. 2019b. Decomposing Individual Differences in Cognitive Control: A Model-Based ApproachProceedings of the 41st Annual Meeting of the Cognitive Science Society.
- Musslick S, Saxe A, Hoskin AN, Reichman D, Cohen JD. 2020. On the Rational Boundedness of Cognitive Control: Shared Versus Separated Representations. doi:10.31234/osf.io/jkhdf
- Musslick S, Shenhav A, Botvinick M, Cohen J. 2015. A Computational Model of Control Allocation based on the Expected Value of Control2nd Multidisciplinary Conference on Reinforcement Learning and Decision Making. Presented at the Multidisciplinary Conference on Reinforcement Learning and Decision Making.
- Nakajima M, Schmitt LI, Halassa MM. 2019. Prefrontal Cortex Regulates Sensory Filtering through a Basal Ganglia-to-Thalamus Pathway. *Neuron*. doi:10.1016/j.neuron.2019.05.026
- Nashed JY, Crevecoeur F, Scott SH. 2012. Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J Neurophysiol* **108**:999–1009.
- Nelson WL. 1983. Physical principles for economies of skilled movements. *Biol Cybern* **46**:135–147.
- Niv Y, Daw ND, Joel D, Dayan P. 2007. Tonic dopamine: opportunity costs and the control of response vigor. *Psychopharmacology* **191**:507–520.
- O'Sullivan I, Burdet E, Diedrichsen J. 2009. Dissociating variability and effort as determinants of coordination. *PLoS Comput Biol* **5**:e1000345.
- Otto AR, Daw ND. 2019. The opportunity cost of time modulates cognitive effort. *Neuropsychologia* **123**:92–105.
- Padmala S, Pessoa L. 2011. Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *J Cogn Neurosci* **23**:3419–3432.
- Parro C, Dixon ML, Christoff K. 2018. The neural basis of motivational influences on cognitive control. *Hum Brain Mapp* **39**:5097–5111.
- Pekny SE, Izawa J, Shadmehr R. 2015. Reward-dependent modulation of movement variability. *J Neurosci* 35:4015–4024.
- Petitet P, Attaallah B, Manohar SG, Husain M. 2021. The computational cost of active information sampling before decision-making under uncertainty. *Nature Human Behaviour* 1–12.
- Piray P, Daw ND. 2021. Linear reinforcement learning in planning, grid fields, and cognitive control. *Nat Commun* **12**:4942.
- Poggio T, Koch C, Brenner S. 1985a. III-Posed problems early vision: from computational theory to analogue networks. *Proceedings of the Royal Society of London Series B*

- Biological Sciences **226**:303–323.
- Poggio T, Torre V, Koch C. 1985b. Computational vision and regularization theory. *Nature* **317**:314–319.
- Posner M, Snyder C. 1975. Attention and cognitive control.
- Prinz AA, Bucher D, Marder E. 2004. Similar network activity from disparate circuit parameters. *Nat Neurosci* 7:1345–1352.
- Prsa M, Galiñanes GL, Huber D. 2017. Rapid Integration of Artificial Sensory Feedback during Operant Conditioning of Motor Cortex Neurons. *Neuron* **93**:929-939.e6.
- Putnam H. 1967. Psychological predicates. Art, mind, and religion 1:37–48.
- Rabbitt PM. 1966. Errors and error correction in choice-response tasks. *J Exp Psychol* **71**:264–272.
- Ratcliff R. 1978. A theory of memory retrieval. *Psychol Rev* **85**:59–108.
- Ratcliff R, Frank MJ. 2012. Reinforcement-based decision making in corticostriatal circuits: mutual constraints by neurocomputational and diffusion models. *Neural Comput* **24**:1186–1229.
- Ratcliff R, McKoon G. 2008. The diffusion decision model: theory and data for two-choice decision tasks. *Neural Comput* **20**:873–922.
- Ratcliff R, Rouder JN. 1998. Modeling Response Times for Two-Choice Decisions. *Psychol Sci* **9**:347–356.
- Ridderinkhof KR. 2002. Micro- and macro-adjustments of task set: activation and suppression in conflict tasks. *Psychol Res* **66**:312–323.
- Ritz H, DeGutis J, Frank MJ, Esterman M, Shenhav A. 2020. An evidence accumulation model of motivational and developmental influences over sustained attention42nd Annual Meeting of the Cognitive Science Society.
- Ritz H, Shenhav A. 2021. Humans reconfigure target and distractor processing to address distinct task demands. *bioRxiv*. doi:10.1101/2021.09.08.459546
- Rogers RD, Monsell S. 1995. Costs of a predictible switch between simple cognitive tasks. *J Exp Psychol Gen* **124**:207.
- Schroeder U, Kuehler A, Haslinger B, Erhard P, Fogel W, Tronnier VM, Lange KW, Boecker H, Ceballos Baumann AO. 2002. Subthalamic nucleus stimulation affects striato anterior cingulate cortex circuit in a response conflict task: a PET study. *Brain* **125**:1995 2004.
- Servant M, Montagnini A, Burle B. 2014. Conflict tasks and the diffusion framework: Insight in model constraints based on psychological laws. *Cogn Psychol* **72**:162–195.
- Shadmehr R, Ahmed AA. 2020. Vigor: Neuroeconomics of movement control. MIT Press.
- Shadmehr R, Krakauer JW. 2008. A computational neuroanatomy for motor control. *Exp Brain Res* **185**:359–381.
- Shadmehr R, Orban de Xivry JJ, Xu-Wilson M, Shih T-Y. 2010. Temporal discounting of reward and the cost of time in motor control. *J Neurosci* **30**:10507–10516.
- Shenhav A, Botvinick MM, Cohen JD. 2013. The expected value of control: an integrative theory of anterior cingulate cortex function. *Neuron* **79**:217–240.
- Shenhav A, Musslick S, Lieder F, Kool W, Griffiths TL, Cohen JD, Botvinick MM. 2017. Toward a rational and mechanistic account of mental effort. *Annu Rev Neurosci* **40**:99–124.
- Shenhav A, Prater Fahey M, Grahek I. 2021. Decomposing the Motivation to Exert Mental Effort. *Curr Dir Psychol Sci* **30**:307–314.
- Shiffrin RM, Schneider W. 1977. Controlled and automatic human information processing: II.

- Perceptual learning, automatic attending and a general theory. Psychol Rev 84:127.
- Simen P, Contreras D, Buck C, Hu P, Holmes P, Cohen JD. 2009. Reward rate optimization in two-alternative decision making: empirical tests of theoretical predictions. *J Exp Psychol Hum Percept Perform* **35**:1865–1897.
- Sims CR. 2015. The cost of misremembering: Inferring the loss function in visual working memory. *J Vis* **15**. doi:10.1167/15.3.2
- Sims CR, Jacobs RA, Knill DC. 2012. An ideal observer analysis of visual working memory. *Psychol Rev* **119**:807–830.
- Solway A, Botvinick MM. 2012. Goal-directed decision making as probabilistic inference: a computational framework and potential neural correlates. *Psychol Rev* **119**:120–154.
- Soutschek A, Stelzel C, Paschke L, Walter H, Schubert T. 2015. Dissociable effects of motivation and expectancy on conflict processing: an fMRI study. *J Cogn Neurosci* **27**:409–423.
- Soutschek A, Strobach T, Schubert T. 2014. Motivational and cognitive determinants of control during conflict processing. *Cogn Emot* **28**:1076–1089.
- Sprague TC, Ester EF, Serences JT. 2016. Restoring Latent Visual Working Memory Representations in Human Cortex. *Neuron* **91**:694–707.
- Starns JJ, Ratcliff R. 2010. The effects of aging on the speed-accuracy compromise: Boundary optimality in the diffusion model. *Psychol Aging* **25**:377–390.
- Steinhauser M, Andersen SK. 2019. Rapid adaptive adjustments of selective attention following errors revealed by the time course of steady-state visual evoked potentials. *Neuroimage* **186**:83–92.
- Stevenson IH, Fernandes HL, Vilares I, Wei K, Kording KP. 2009. Bayesian integration and non-linear feedback control in a full-body motor task. *PLoS Comput Biol* **5**:e1000629.
- Steyvers M, Hawkins GE, Karayanidis F, Brown SD. 2019. A large-scale analysis of task switching practice effects across the lifespan. *Proc Natl Acad Sci U S A*. doi:10.1073/pnas.1906788116
- Stiso J, Khambhati AN, Menara T, Kahn AE, Stein JM, Das SR, Gorniak R, Tracy J, Litt B, Davis KA, Pasqualetti F, Lucas TH, Bassett DS. 2019. White Matter Network Architecture Guides Direct Electrical Stimulation through Optimal State Transitions. *Cell Rep* **28**:2554-2566.e7.
- Stokes MG, Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J. 2013. Dynamic coding for cognitive control in prefrontal cortex. *Neuron* **78**:364–375.
- Sukumar S, Shadmehr R, Ahmed AA. 2021. Effects of reward history on decision-making and movement vigor. *bioRxiv*. doi:10.1101/2021.07.22.453376
- Takei T, Lomber SG, Cook DJ, Scott SH. 2021. Transient deactivation of dorsal premotor cortex or parietal area 5 impairs feedback control of the limb in macaques. *Curr Biol* **0**. doi:10.1016/j.cub.2021.01.049
- Tang E, Bassett DS. 2018. Colloquium: Control of dynamics in brain networks. Rev Mod Phys.
- Tenenbaum JB, Griffiths TL, Kemp C. 2006. Theory-based Bayesian models of inductive learning and reasoning. *Trends Cogn Sci* **10**:309–318.
- Tenenbaum JB, Kemp C, Griffiths TL, Goodman ND. 2011. How to grow a mind: statistics, structure, and abstraction. *Science* **331**:1279–1285.
- Thurm F, Zink N, Li S-C. 2018. Comparing effects of reward anticipation on working memory in younger and older adults. *Front Psychol* **9**:2318.
- Tikhonov AN. 1963. On the solution of ill-posed problems and the method of

- regularizationDoklady Akademii Nauk. Russian Academy of Sciences. pp. 501-504.
- Todorov E. 2005. Stochastic optimal control and estimation methods adapted to the noise characteristics of the sensorimotor system. *Neural Comput* **17**:1084–1108.
- Todorov E, Jordan MI. 2002. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* **5**:1226–1235.
- Trommershäuser J, Maloney LT, Landy MS. 2003a. Statistical decision theory and trade-offs in the control of motor response. *Spat Vis* **16**:255–275.
- Trommershäuser J, Maloney LT, Landy MS. 2003b. Statistical decision theory and the selection of rapid, goal-directed movements. *J Opt Soc Am A Opt Image Sci Vis* **20**:1419–1433.
- Ullsperger M, Bylsma LM, Botvinick MM. 2005. The conflict adaptation effect: It's not just priming. *Cogn Affect Behav Neurosci* **5**:467–472.
- Uno Y, Kawato M, Suzuki R. 1989. Formation and control of optimal trajectory in human multijoint arm movement. *Biological Cybernetics*. doi:10.1007/bf00204593
- Usher M, McClelland JL. 2001. The time course of perceptual choice: the leaky, competing accumulator model. *Psychol Rev* **108**:550–592.
- van den Berg R, Shin H, Chou W-C, George R, Ma WJ. 2012. Variability in encoding precision accounts for visual short-term memory limitations. *Proc Natl Acad Sci U S A* **109**:8780–8785.
- Van Rooij I. 2008. The tractable cognition thesis. *Cogn Sci* **32**:939–984.
- Verguts T, Notebaert W, Kunde W, Wühr P. 2011. Post-conflict slowing: cognitive adaptation after conflict processing. *Psychon Bull Rev* **18**:76–82.
- Verguts T, Vassena E, Silvetti M. 2015. Adaptive effort investment in cognitive and physical tasks: a neurocomputational model. *Front Behav Neurosci* **9**:57.
- Vogel TA, Savelson ZM, Otto AR, Roy M. 2020. Forced choices reveal a trade-off between cognitive effort and physical pain. *Elife* 9. doi:10.7554/eLife.59410
- von Bastian CC, Blais C, Brewer GA, Gyurkovics M, Hedge C, Kałamała P, Meier ME, Oberauer K, Rey-Mermet A, Rouder JN, al. E. 2020. Advancing the understanding of individual differences in attentional control: Theoretical, methodological, and analytical considerations. doi:10.31234/osf.io/x3b9k
- Weichart ER, Turner BM, Sederberg PB. 2020. A model of dynamic, within-trial conflict resolution for decision making. *Psychol Rev.* doi:10.1037/rev0000191
- Wessel JR, Waller DA, Greenlee JD. 2019. Non-selective inhibition of inappropriate motor-tendencies during response-conflict by a fronto-subthalamic mechanism. *Elife* **8**. doi:10.7554/eLife.42959
- Westbrook A, Braver TS. 2015. Cognitive effort: A neuroeconomic approach. *Cogn Affect Behav Neurosci* **15**:395–415.
- Westbrook A, Kester D, Braver TS. 2013. What is the subjective cost of cognitive effort? Load, trait, and aging effects revealed by economic preference. *PLoS One* **8**:e68210.
- White CN, Ratcliff R, Starns JJ. 2011. Diffusion models of the flanker task: discrete versus gradual attentional selection. *Cogn Psychol* **63**:210–238.
- Whiting HTA. 1983. Human Motor Actions: Bernstein Reassessed. Elsevier.
- Wiecki TV, Frank MJ. 2013. A computational model of inhibitory control in frontal cortex and basal ganglia. *Psychol Rev* **120**:329–355.
- Wilken P, Ma WJ. 2004. A detection theory account of change detection. J Vis 4:1120–1135.
- Willcox KE, Ghattas O, Heimbach P. 2021. The imperative of physics-based modeling and inverse theory in computational science. *Nature Computational Science* 1:166–168.

- Wolpert DM, Landy MS. 2012. Motor control is decision-making. *Curr Opin Neurobiol* **22**:996–1003.
- Yan G, Vértes PE, Towlson EK, Chew YL, Walker DS, Schafer WR, Barabási A-L. 2017. Network control principles predict neuron function in the Caenorhabditis elegans connectome. *Nature* **550**:519–523.
- Yee DM, Braver TS. 2018. Interactions of Motivation and Cognitive Control. *Curr Opin Behav Sci* **19**:83–90.
- Yee DM, Krug MK, Allen AZ, Braver TS. 2016. Humans Integrate Monetary and Liquid Incentives to Motivate Cognitive Task Performance. *Front Psychol* **6**:2037.
- Yeo S-H, Franklin DW, Wolpert DM. 2016. When Optimal Feedback Control Is Not Enough: Feedforward Strategies Are Required for Optimal Control with Active Sensing. *PLoS Comput Biol* 12:e1005190.
- Yoon T, Jaleel A, Ahmed AA, Shadmehr R. 2020. Saccade vigor and the subjective economic value of visual stimuli. *J Neurophysiol*. doi:10.1152/jn.00700.2019
- Yu AJ, Dayan P, Cohen JD. 2009. Dynamics of attentional selection under conflict: toward a rational Bayesian account. *J Exp Psychol Hum Percept Perform* **35**:700–717.
- Zénon A, Solopchuk O, Pezzulo G. 2019. An information-theoretic perspective on the costs of cognition. *Neuropsychologia* **123**:5–18.