

RESEARCH ARTICLE

The neural basis of motivational influences on cognitive control

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Abstract

Cognitive control mechanisms support the deliberate regulation of thought and behavior based on current goals. Recent work suggests that motivational incentives improve cognitive control and has begun to elucidate critical neural substrates. We conducted a quantitative meta-analysis of neuroimaging studies of motivated cognitive control using activation likelihood estimation (ALE) and Neurosynth to delineate the brain regions that are consistently activated across studies. The analysis included studies that investigated changes in brain activation during cognitive control tasks when reward incentives were present versus absent. The ALE analysis revealed consistent recruitment in regions associated with the frontoparietal control network including the inferior frontal sulcus and intraparietal sulcus, as well as regions associated with the salience network including the anterior insula and anterior mid-cingulate cortex. As a complementary analysis, we performed a large-scale exploratory meta-analysis using Neurosynth to identify regions that are recruited in studies using of the terms cognitive control and incentive. This analysis replicated the ALE results and also identified the rostrolateral prefrontal cortex, caudate nucleus, nucleus accumbens, medial thalamus, inferior frontal junction, premotor cortex, and hippocampus. Finally, we separately compared recruitment during cue and target periods, which tap into proactive engagement of rule-outcome associations, and the mobilization of appropriate visceromotor states to execute a response, respectively. We found that largely distinct sets of brain regions are recruited during cue and target periods. Altogether, these findings suggest that flexible interactions between frontoparietal, salience, and dopaminergic midbrain-striatal networks may allow control demands to be precisely tailored based on expected value.

KEYWORDS

cognitive control, control network, frontoparietal, reward

1 | INTRODUCTION

The ability to maintain attention during a lecture, or flexibly shift between writing a report and answering emails, or plan several steps ahead during a chess match all require cognitive control—the capacity to deliberately guide thought and behavior based on goals, especially in the presence of distraction or competing responses (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Desimone & Duncan, 1995; Duncan, 2013; Gollwitzer, 1999; Miller & Cohen, 2001; Miyake et al., 2000; Posner & Dehaene, 1994; Posner & DiGirolamo, 1998; Stuss & Knight, 2002). Cognitive control involves several related, yet dissociable abilities (Miyake et al., 2000), including working memory (D'Esposito & Postle, 2015; Funahashi, Chafee, & Goldman-Rakic, 1993; Fuster & Alexander, 1971;

Goldman-Rakic, 1987), representation of rules and context (Asaad, Rainer, & Miller, 2000; Bunge, 2004; Cohen & Servan-Schreiber, 1992; Dixon & Christoff, 2012; Koechlin, Ody, & Kouneiher, 2003; Miller & Cohen, 2001; Munakata et al., 2011), conflict and error detection (Botvinick et al., 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger, Danielmeier, & Jocham, 2014), inhibition of prepotent responses (Aron, Robbins, & Poldrack, 2004), abstract thought and reasoning (Christoff et al., 2001; Christoff, Keramatian, Gordon, Smith, & Madler, 2009), and set-shifting (Crone, Wendelken, Donohue, & Bunge, 2006; Dias, Robbins, & Roberts, 1996; Meiran, 1996; Meiran, 2000; Rushworth, Passingham, & Nobre, 2002).

While early work identified the prefrontal cortex (PFC) as a critical neural substrate (Desimone & Duncan, 1995; Duncan, 2001; Fuster,

1989; Miller & Cohen, 2001; Passingham & Wise, 2012; Stuss & Knight, 2002; Watanabe, 2017), it soon became clear that a much broader network of regions support cognitive control, including posterior parietal, lateral temporal, insular, and mid-cingulate cortices, as well as parts of the basal ganglia. Together, these regions are often referred to as the multiple demand (MD) system, although recent network neuroscience approaches suggest that they may form at least two distinct functional networks, known as the frontoparietal control network (FPCN), and the salience/cingulo-opercular network (Cole et al., 2013; Cole, Repovs, & Anticevic, 2014; Cole & Schneider, 2007; Crittenden, Mitchell, & Duncan, 2016; Dixon et al., 2018; Dosenbach et al., 2007; Duncan, 2010; Mitchell et al., 2016; Seeley et al., 2007; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). Cognitive control regions flexibly represent a variety of task-relevant information and exert a top-down influence on other regions, guiding activation in accordance with current task demands (Badre & D'Esposito, 2009; Braver, 2012; Buschman & Miller, 2007; Crowe et al., 2013; Desimone & Duncan, 1995; Dixon, Fox, & Christoff, 2014b; Duncan, 2010; Egner & Hirsch, 2005; Miller & Cohen, 2001; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999).

2 | THE EFFECTS OF MOTIVATION ON COGNITIVE CONTROL

As research progressed in delineating the components of cognitive control, a separate stream of inquiry focused on the neural mechanisms of assigning value to stimuli and value-guided decision making (Daw, Niv, & Dayan, 2005; Dixon & Christoff, 2014; Dixon, Thiruchselvam, Todd, & Christoff, 2017; Levy & Glimcher, 2012; O'Doherty et al., 2004; Rangel, Camerer, & Montague, 2008; Rangel & Hare, 2010; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011; Schoenbaum & Esber, 2010). The past decade has seen a synthesis of these fields with a surge of interest in understanding how value influences the decision of whether or not to engage cognitive control and the efficacy of implementing control (Botvinick & Braver, 2015; Braver et al., 2014; Cohen, Braver, & Brown, 2002; Cools, 2016; Dixon, 2015; Dixon & Christoff, 2012; Hazy, Frank, & O'Reilly, 2007; McGuire & Botvinick, 2010; O'Reilly, Herd, & Pauli, 2010). This line of inquiry is yielding new insights into mechanisms that allow the desire to achieve a specific outcome to interact with the cognitive processes that are necessary to realize that outcome and may ultimately provide critical information about pathological conditions that involve altered motivation-cognition interactions including depression, schizophrenia, ADHD, and anxiety (Barkley, 1997; Bishop, Duncan, Brett, & Lawrence, 2004; Chung & Barch, 2015; Davidson, 2000; Heller et al., 2009; Kaiser et al., 2015a; Kaiser, Andrews-Hanna, Wager, & Pizzagalli, 2015b; Nigg & Casey, 2005; Pessoa, 2008; Shackman et al., 2011; Shackman et al., 2016).

Recent studies have shown that individuals are strongly biased toward choosing habits and simple tasks over more complex or demanding tasks that require cognitive control (Botvinick & Braver, 2015; Dixon & Christoff, 2012; Kool, McGuire, Rosen, & Botvinick, 2010; McGuire & Botvinick, 2010). This has led to notion that

cognitive control carries an intrinsic *effort cost*. This effort cost can be offset by the opportunity to acquire a rewarding outcome. Studies have shown that participants are considerably more likely to engage cognitive control if doing so will result in a larger reward than if they chose a habitual action (Dixon & Christoff, 2012; Westbrook, Kester, & Braver, 2013). Thus, cognitive control engagement can be understood as a special case of cost/benefit decision-making whereby the expected value of the outcome that will result from engaging cognitive control is weighed against the effort cost of its implementation (Botvinick & Braver, 2015; Dixon & Christoff, 2012; Shenhav, Botvinick, & Cohen, 2013).

Following the decision to engage cognitive control, the opportunity to earn a reward can also influence the efficacy of implementing control processes. In one study, participants performed a modified Stroop task during which they decided whether an image was a building or a house and had to ignore letters overlaid on the images (Padmala & Pessoa, 2011). The letters could be neutral (XXXXX), congruent with the image (e.g., HOUSE printed over a house image), or incongruent (e.g., BLDNG printed over a house image). Pretrial cues indicated whether monetary rewards were available or not available, and participants could only earn rewards if performance was fast and accurate. The results demonstrated enhanced implementation of cognitive control, manifested as reduced interference effects on incongruent trials when rewards were available (Padmala & Pessoa, 2011). This incentive effect may reflect a sharpening of the representation of task-relevant information (Etzel, Cole, Zacks, Kay, & Braver, 2015; Histed, Pasupathy, & Miller, 2009), thus providing more effective modulation of sensorimotor processes that support performance. Incentive-based facilitation of behavioral performance has been reported across numerous studies using a range of cognitive control paradigms (Chiew & Braver, 2013, 2014; Chiew, Stanek, & Adcock, 2016; Dixon & Christoff, 2012; Etzel et al., 2015; Ivanov et al., 2012; Jimura, Locke, & Braver, 2010; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Locke & Braver, 2008; Padmala & Pessoa, 2011; Taylor et al., 2004).

3 | THE NEURAL BASIS OF MOTIVATIONAL EFFECTS ON COGNITIVE CONTROL

Functional neuroimaging studies have identified brain regions associated with the influence of motivation on the implementation of cognitive control (Bahlmann, Aarts, & D'Esposito, 2015; Beck, Locke, Savine, Jimura, & Braver, 2010; Engelmann, Damaraju, Padmala, & Pessoa, 2009; Gilbert & Fiez, 2004; Ivanov et al., 2012; Kouneiher, Charron, & Koechlin, 2009; Locke & Braver, 2008; Padmala & Pessoa, 2011; Pochon et al., 2002; Rowe, Eckstein, Braver, & Owen, 2008; Taylor et al., 2004). In one study, Jimura et al. (2010) used a Sternberg task with two types of task blocks. One block consisted of only nonreward trials, whereas the other block consisted of trials with varying outcomes: no reward, low reward (\$0.25), or high reward (\$0.75). On each trial, participants were presented with a five-word memory set and then had to indicate whether a subsequent probe word matched one of the items in the memory set. The results demonstrated a shift from transient to sustained activation in lateral prefrontal and parietal

cortices during reward versus no reward blocks, and individual differences in reward sensitivity correlated with the magnitude of sustained activation in reward contexts (Jimura et al., 2010).

These results can be interpreted in terms of the dual mechanisms of control (DMC) framework, which suggests that reward incentives shift the type and timing of cognitive control (Braver, 2012; Chiew & Braver, 2013; Jimura et al., 2010). This theory posits two temporally defined cognitive control mechanisms: (a) a *proactive* mechanism consisting of sustained activation of task-relevant information (e.g., task rules) across trials, which facilitates the encoding of new information on each trial and the preparation of a target response and (b) a *reactive* mechanism consisting of the stimulus-triggered transient re-activation of rule information on a trial-by-trial basis. Frontoparietal activation dynamics support the idea that reward incentives lead to greater reliance on proactive control, consistent with the DMC model.

Numerous studies have now observed elevated frontoparietal activation when cognitive control is performed in the service of obtaining rewarding outcomes (Boehler, Schevernels, Hopf, Stoppel, & Krebs, 2014; Engelmann et al., 2009; Gilbert & Fiez, 2004; Ivanov et al., 2012; Kouneiher et al., 2009; Locke & Braver, 2008; Padmala & Pessoa, 2011; Paschke et al., 2015; Pochon et al., 2002; Rowe et al., 2008; Soutschek, Stelzel, Paschke, Walter, & Schubert, 2015; Taylor et al., 2004). In addition, frontoparietal regions encode associations between specific rules and expected reward outcomes (Dixon & Christoff, 2012), exhibit more differentiated coding of task rules on incentivized trials (Etzel et al., 2015), and are sensitive to the interaction between control level and reward availability (Bahlmann et al., 2015; Ivanov et al., 2012; Padmala & Pessoa, 2011; Soutschek et al., 2015). These regions are also recruited during value-based decision-making, and when participants plan and monitor progress toward future desired outcomes (Crockett et al., 2013; Dixon, Fox, & Christoff, 2014a; Gerlach, Spreng, Madore, & Schacter, 2014; Jimura, Chushak, & Braver, 2013; McClure, Laibson, Loewenstein, & Cohen, 2004). Finally, single-cell recordings in nonhuman primates have revealed reward-contingent enhancement of lateral PFC neural firing related to working memory and task rules (Histed et al., 2009; Leon & Shadlen, 1999; Watanabe, 1996; Watanabe & Sakagami, 2007). Thus, frontoparietal regions may integrate task-relevant information and expected motivational outcomes (Dixon & Christoff, 2014; Pessoa, 2008; Watanabe, 2017; Watanabe & Sakagami, 2007).

4 | THE CURRENT META-ANALYSIS

Although numerous studies of motivated cognitive control have reported activation in frontoparietal regions, the consistency of activations across these studies has yet to be systematically examined. The present study sought to characterize the network of brain regions that are consistently recruited during motivated cognitive control. To this end, we used a quantitative approach, activation likelihood estimation (ALE), to identify regions that show consistent recruitment in human neuroimaging studies of cognitive control that included a manipulation of reward incentive availability. Meta-analyses are critical for identifying generalizable associations between cognitive processes and brain activation patterns, because it is not possible to

control for all extraneous variables and isolate a specific cognitive process in a single study (Yarkoni, Poldrack, Van Essen, & Wager, 2010). In addition, the small sample sizes of typical functional magnetic resonance imaging (fMRI) experiments mean that statistical analyses are susceptible to false positives (Yarkoni et al., 2010). A meta-analysis combines a set of studies that ostensibly tap a common cognitive process yet differ in specific task details and thereby provides strong inferences about brain-cognition mappings. We additionally used Neurosynth to identify regions that are consistently recruited in studies that use the term “cognitive control” and in studies that use the term “incentive.” Regions that are recruited by both domains may bridge cognitive and motivational functions. While the ALE analysis provided a conservative and rigorous analysis based on a set of carefully selected studies, the Neurosynth analysis provided a complementary perspective based on a liberal exploration of a much wider literature. In addition, this analysis allowed us to compare the overall collection of regions activated by cognitive control tasks to the subset of regions that are sensitive to both domains. This allows for some degree of specificity by distinguishing the regions that are important for incentive-based modulation of cognitive control from those that play a more general role in control-related functions. Finally, we performed two additional exploratory ALE analyses to examine activations separately during cue and target periods. During cue periods, participants are presented with information about task rules for responding to stimuli and expected payoffs. This period thus allows for preparatory construction rule-outcome associations in service of proactive control engagement. During target periods, participants respond to stimuli and must mobilize appropriate visceromotor states to facilitate faster and more accurate actions when a reward is on the line. This analysis allowed us to examine the extent to which cue and target periods rely on similar versus distinct brain systems.

5 | MATERIALS AND METHODS

5.1 | Search strategy

We conducted a literature search through PubMed and Google Scholar to identify peer-reviewed neuroimaging studies that have investigated motivated cognitive control. We began by searching the key terms “fMRI” AND (“reward” OR “motivation”) AND (“cognitive control” OR “executive function” OR “working memory”). We then read the abstract of each paper to confirm or reject it as a candidate study for inclusion in the meta-analysis. We only focused on activations, because there are very few deactivations reported in the literature. In addition we focused on the effect of reward, because only a few studies have looked at the effect of punishment. To be included in the analysis, studies had to fulfill the following criteria: (a) employ fMRI and report resulting activation coordinates; (b) include a cognitive control task (e.g., Stroop) with a manipulation of motivational incentive (i.e., reward versus no reward, or high versus low reward conditions); (c) include healthy adult human participants; and d) report results from a whole-brain analysis. Several studies of motivated cognitive control employed ROI-based analyses and were not included in the meta-analysis, given that ALE requires whole-brain analyses to

provide unbiased results. Sixteen studies were found that matched the inclusion criteria (Table 1). The presence of reward was associated with significantly improved behavioral performance (decreased reaction time and/or increased accuracy) in all but one of the 16 studies.

5.2 | Data extraction

From these 16 studies, we collected data on sample size, task, type of contrast (e.g., main effect of reward during task, or reward \times cognitive load interaction), task period (e.g., cue, delay, or target), and peak activation coordinates (Table 1). The meta-analysis included studies with

different types of contrasts, but each examined the neural substrates that link motivational incentives to cognitive control. In every study, participants were aware that they could earn reward incentives on certain trials contingent on their task performance. Incentive information was signaled with task cues. There were three categories of contrasts performed in these studies: (a) main effect of reward during a cognitive control task; (b) conjunction effects showing overlapping activation in relation to cognitive demands and sensitivity to reward value; and (c) interaction between cognitive control level and presence of incentive. While there are some differences in these three types of contrasts, all converge on related processes that support

TABLE 1 Studies included in the meta-analysis

Study	n	Task	Behavior	Trial period	Analysis	Number of peak foci
Pochon et al. (2002)	6	Working memory		Trial	Overlap of main effects of cognitive load and reward	10
Gilbert and Fiez (2004)	22	Working memory	Acc \uparrow	Delay	Main effect of reward	1
Taylor et al. (2004)	10	Working memory	RT \downarrow	Target	Main effect of reward	5
				Delay	Main effect of reward	6
				Target	Main effect of reward	3
					Cognitive load \times reward	1
				All (collapsed)	Main effect of reward	9
Locke and Braver (2008)	16	AX-CPT	Acc \uparrow , RT \downarrow	Block	Main effect of reward	20
Rowe et al. (2008)	20	AX-CPT	Acc \uparrow , RT \downarrow	Block	Parametric effect of reward \times trial type	14
Engelmann et al. (2009)	20	Attentional cueing	Acc \uparrow	Cue	Main effect of reward	20
				Target	Main effect of reward	10
					Cue validity \times reward	6
				Block	Main effect of reward	5
Kouneiher et al. (2009)	16	Rule-use	Acc \uparrow , RT \uparrow	Cue/target	Trial type \times reward value	3
				Block	Main effect of reward	3
Jimura et al. (2010)	31	Sternberg	RT \downarrow	Block	Main effect of reward	2
Padmala and Pessoa (2011)	50	Stroop	Acc \uparrow , RT \downarrow	Target	Main effect of reward	6
					Interference \times reward interaction	10
Dixon and Christoff (2012)	15	Rule use	RT \downarrow	Cue	Rule \times reward interaction	9
Krebs et al. (2012)	14	Attentional cueing	Acc \uparrow , RT \downarrow	Cue	Main effect of reward	13
					Overlap of main effects of difficulty and reward	10
					Difficulty \times reward interaction	7
Ivanov et al. (2012)	16	Flanker	RT \downarrow	Target	Conflict \times reward interaction	6
Boehler et al. (2014)	16	Stop signal	RT \downarrow	Target	Overlap of main effects of stopping and reward	3
Paschke et al. (2015)	115	Flanker	RT \downarrow	Target	Congruency \times reward interaction	1
				Block	Overlap of main effects of task and reward	1
				Target	Overlap of main effects of task and reward	4
Soutschek et al. (2015)	20	Stroop	RT \downarrow	Target	Main effect of reward	3
				Target	Congruency \times expectancy \times reward interaction	6
Etzel et al. (2015)	20	Rule-use	Acc \uparrow , RT \downarrow	Cue	Main effect of reward	7
Total = 16	407					204

Note. When specifying the trial period, "trial" indicates reward effect across entire trial period, while "block" indicates reward effect across multiple trials. The column behavior specifies the change in accuracy and/or reaction time (RT) on rewarded versus nonrewarded trials.

incentive-based modulation of cognitive control. It should be noted that we included results from the main effect of reward during task performance (e.g., during delay or target periods) but excluded results related to a main effect of reward during cue periods that only included the expected reward incentive, as this is likely to mainly capture reward processing alone, without an interaction with cognitive processes. Notably, if the cue period signaled motivational information *and* cognitive task demands (e.g., rules) that could be activated in a preparatory manner, then we included these foci.

Studies have repeatedly shown that responses are faster and/or more accurate on reward versus no reward trials during cognitive control tasks. While both types of trials involve control demands, the enhanced behavioral performance on reward trials indicate that the reward incentive is processed in a manner that facilitates control operations and the top-down modulation of action selection. Indeed, prior work suggests that on reward trials, there is a change in how task information is represented in the brain (Etzel et al., 2015; Histed et al., 2009; Watanabe, 1996). There is also documented evidence of a sustained change in activation within brain regions that are sensitive to control demands on reward versus no-reward trials (Jimura et al., 2010; Locke & Braver, 2008). Therefore, a main effect of reward in the context of engaging cognitive control-related functions is capturing something unique that goes beyond general reward processing in the absence of control demands. Supporting this idea, lateral fronto-parietal regions are rarely engaged in simple reward tasks that do not involve control demands, yet are robustly engaged during reward trials in the context of a cognitive control task. In addition, studies that use conjunction analyses target the neural basis of incentive-based modulation of cognitive control by identifying regions that are sensitive to task demands, and from these regions, identifying those that are also sensitive to reward value. The reported regions may contribute to the process whereby control demands become associated with expected reward outcomes.

For studies that had multiple periods (e.g., delay, probe), we included foci from each period; however, if a given brain region was activated in multiple periods, it was only included once in the meta-analysis. However, for the additional analyses that separately examined cue period and target period activations, we used all available foci. We based target- and cue-specific analyses on the results reported in each study. If a study reported that their task design allowed for separation of cue and target effects and reported results for one or both task phases then the foci were included in our meta-analysis. Given that not all studies had separate cue and target periods, this resulted in a smaller sample size for these analyses.

5.3 | ALE meta-analytic data analysis

We analyzed the activation coordinates using a random effects meta-analysis, ALE (Eickhoff et al., 2009; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Laird et al., 2005; Turkeltaub et al., 2012) implemented with GingerALE 2.3.6 software (UT Health Science Center Research Imaging Institute, San Antonio, TX). This is the updated version of GingerALE that has fixed the error related to cluster-level FWE correction (Eickhoff, Laird, Fox, Lancaster, & Fox, 2017). Coordinates reported in Talairach space were first converted to MNI space using Ginger ALE's

foci converter function: Talairach to MNI (SPM). ALE models the uncertainty in localization of activation foci across studies using Gaussian probability density distributions. The voxel-wise union of these distributions yields the ALE value, a voxel-wise estimate of the likelihood of activation, given the input data. The algorithm aims at identifying significantly overlapping clusters of activation between studies. ALE treats activation foci from single studies as 3D Gaussian probability distributions to compensate for spatial uncertainty. The width of these distributions was statistically determined based on empirical data for between subject and between template variability (Eickhoff et al., 2009). In addition, studies were weighted according to sample size, reflecting the idea that large sample sizes more likely reflect a true localization. This is implemented in terms of a widening Gaussian distribution with lower sample sizes and a smaller Gaussian distribution (and thus a stronger impact on ALE scores) with larger sample sizes (Eickhoff et al., 2009). Modeled activation maps for each study were generated by combining the probabilities of all activation foci for each voxel (Turkeltaub et al., 2012). These ALE scores were then compared to an ALE null distribution (Eickhoff et al., 2012) in which the same number of activation foci was randomly relocated and restricted by a gray matter probability map (Evans, Kamber, Collins, & MacDonald, 1994). Spatial associations between experiments were treated as random while the distribution of foci within an experiment was treated as fixed. Thereby random effects inference focuses on significant convergence of foci between studies rather than convergence within one study. The ALE scores from the actual meta-analysis were then tested against the ALE scores obtained under this null-distribution yielding a *p*-value based on the proportion of equal or higher random values. For the main ALE analysis, we used a cluster-forming threshold at the voxel level of $p < .001$ and a cluster-level threshold of $p < .05$ FWE corrected for multiple comparisons. We also ran separate analyses on foci from the cue period and foci from the target period. Given that fewer studies were included in each analysis, we used a more liberal $p < .001$, uncorrected threshold, with a minimum cluster size of 200 mm³. As such, the results should be interpreted with caution. Results were visualized with MRICron software (Rorden, Karnath, & Bonilha, 2007).

5.4 | Neurosynth meta-analyses

The main ALE analysis was based on a carefully selected group of studies and used a strict statistical threshold to control for false positives. Accordingly, it likely captures true regions underlying motivated cognitive control. On the other hand, it may overlook some regions that are below threshold, but nevertheless play a role in functions that contribute to motivated cognitive control. Thus, we also utilized an alternative, complementary approach: Neurosynth forward inference meta-analyses (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). Neurosynth makes it possible to examine consistent activation patterns across a massive database of studies, providing strong power to detect regions that are activated in the studies of interest. In this way, Neurosynth is less likely to miss relevant regions. However, Neurosynth performs an automated selection of studies based on certain key words (e.g., "cognitive control") and therefore has less specificity in terms of delineating a select group of studies. In this way,

Neurosynth analyses provide a complementary approach to ALE analyses. To perform such automated meta-analyses, Neurosynth divides the entire database of coordinates into two sets: those that occur in articles containing a particular term and those that do not. A large-scale meta-analysis is then performed comparing the coordinates reported for studies with and without the term of interest. Forward inference maps reflect z-scores corresponding to the likelihood that each voxel will activate if a study uses a particular term ($P[\text{Activation}|\text{Term}]$) and are corrected for multiple comparisons using a false discovery rate (FDR) of $q = .01$. Here, we conducted forward inference meta-analyses using the terms “cognitive control” and “incentive” and looked for brain areas demonstrating overlapping recruitment across both domains. We reasoned that if a brain region is activated in studies of cognitive control and is activated in studies of incentive processing, then it is a good candidate for bridging cognitive and motivational functions. We used forward inference rather than reverse inference analyses because we were not looking for regions that are selective to incentive processing or cognitive control, but rather, are just involved in these domains. In other words, we were not looking to identify functional specialization in any regions. Our aim was to identify the constellation of regions that together support motivated cognitive control. Given this aim, forward inference analyses were ideal.

6 | RESULTS

6.1 | ALE meta-analysis: All foci

We first performed an analysis on all foci to identify regions that consistently demonstrate increased activation during cognitive control when rewards are available versus not available. The ALE analysis

revealed four large clusters (Figure 1; Table 2). These right-lateralized regions included the inferior frontal sulcus (IFS) extending into the mid-dorsolateral PFC (mid-DLPFC), mid-intraparietal sulcus (mid-IPS) extending into the anterior inferior parietal lobule (aIPL), anterior insula, and the anterior mid-cingulate cortex (aMCC) extending into the adjacent pre-supplementary motor area (pre-SMA).

6.2 | Neurosynth meta-analyses

Although the strict inclusion criteria in the ALE analysis offer confidence that the identified regions do play a key role in motivated cognitive control, it is possible that this conservative analysis may overlook other relevant regions. Thus, as a complementary analysis, we used Neurosynth to identify regions that are consistently activated in studies that use the term “cognitive control” ($N = 428$ studies) and in studies that use the term “incentive” ($N = 109$ studies). We focused on brain areas demonstrating overlapping recruitment across these domains and may play a role in linking control demands to motivational outcomes. Notably, the regions demonstrating this pattern included all of the regions identified in the ALE meta-analysis (Figure 2). This analysis additionally identified homologous regions in the left hemisphere, as well as the right rostrolateral prefrontal cortex (RLPFC), bilateral inferior frontal junction (IFJ) and pre-motor cortex (PMC), bilateral caudate nucleus extending into the nucleus accumbens (NAcc), bilateral medial thalamus, and bilateral hippocampus (Figure 2). Interestingly, the regions that were sensitive to both cognitive control and incentive were a select subset of the regions engaged during cognitive control. This finding provides some preliminary evidence regarding specificity and functional differences across the cognitive control network. It suggests that only some regions within this broader network may facilitate the effect of reward-incentives on cognitive control performance.

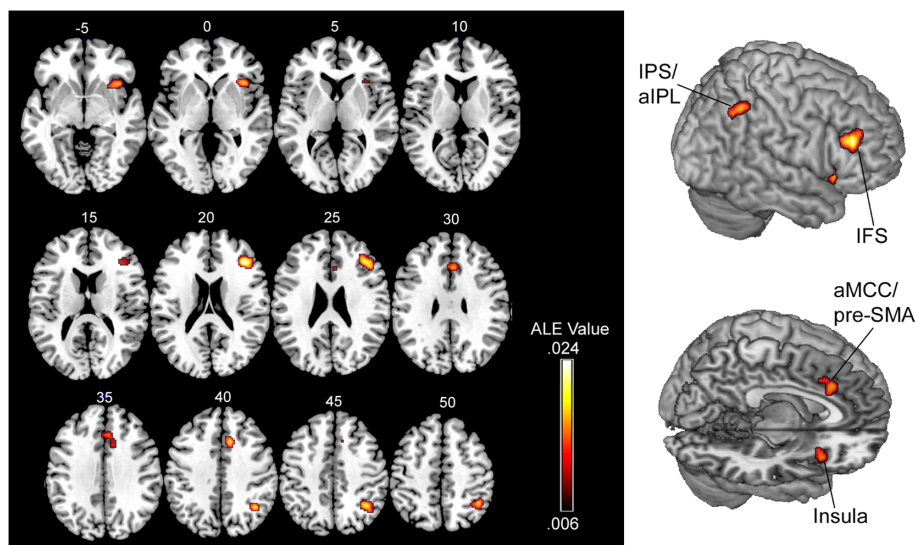


FIGURE 1 Whole-brain ALE meta-analytic results ($p < .05$ FWE corrected) showing brain regions that are consistently recruited across studies ($N = 16$) of motivated cognitive control. These results indicate that regions associated with the frontoparietal control network (IFS and IPS/aIPL) and regions associated with the salience network (insula and aMCC/pre-SMA) show greater activation during cognitive control tasks on trials in which a reward incentive can be earned based on performance, versus trials in which no incentive is presented. Numbers denote z-coordinates in MNI space. IFS, inferior frontal sulcus; IPS/aIPL, intraparietal sulcus/anterior inferior parietal lobule; aMCC/pre-SMA, anterior mid-cingulate cortex/pre-supplementary motor area [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Significant ALE clusters showing consistent recruitment in studies of motivated cognitive control

Region	Cluster size (mm ³)	Peak ALE value	Weighted peak foci in MNI space (x,y,z)
R IFS/mid-dorsolateral prefrontal cortex	2032	0.0252	40, 32, 22
R anterior insula	1,560	0.0168	38, 20, -2
R intraparietal sulcus/inferior parietal lobule	1,544	0.0213	39, -53, 45
R anterior mid-cingulate cortex/pre-supplementary motor area	1,288	0.0172	10, 20, 40

Note. L, left; R, right; DLPFC, dorsolateral prefrontal cortex.

6.3 | ALE meta-analyses: Cue and target period foci

In our final analysis, we examined similarities and differences in neural recruitment during cue and target periods. Given that these analyses were based on a limited number of studies and a more lenient statistical threshold, these results should be viewed as exploratory. The brain regions that were consistently recruited during the cue period and may contribute to the proactive engagement of value-modulated control signals included the right IFJ/PMC, left ventral IPS, bilateral caudate, right dorsal posterior cingulate cortex (PCC), right midbrain near the ventral tegmental area (VTA), and left medial thalamus (Figure 3). On the other hand, the brain regions that were consistently recruited during the target period and may contribute to the mobilization of visceromotor processes during action selection, included the right anterior insula, right aMCC, right IPS/aIPL, right medial thalamus, left ventral IPS, and left IFJ (Figure 3). The only region common to both trial events was the left ventral IPS, suggesting that value-based modulation of control processes during cue and target periods may rely on largely distinct neural systems. However, this is a tentative conclusion, tempered by the low power of these analyses.

7 | DISCUSSION

Cognitive control is often enhanced when rewards are contingent on performance. This enhancement manifests as faster and more accurate responses and is often accompanied by elevated brain activation in numerous cortical regions. Here, we sought to characterize the brain regions that reliably demonstrate this pattern and may support incentive-based behavioral improvements in cognitive control. Using quantitative ALE and Neurosynth meta-analyses, we identified a select constellation of multimodal association cortices and subcortical regions known to play key roles in cognitive and motivational processing. An exploratory analysis also revealed differences in recruitment during cue versus target periods, suggesting partially distinct systems may underlie the proactive engagement of control versus the mobilization of visceromotor states that support action execution.

Several regions were implicated in both the ALE and Neurosynth analyses including the IFS, intraparietal sulcus (IPS)/anterior inferior parietal lobule (aIPL), anterior mid-cingulate cortex (aMCC)/pre-supplementary motor area (pre-SMA), and anterior insula. The fact that similar results were obtained with different analysis criteria

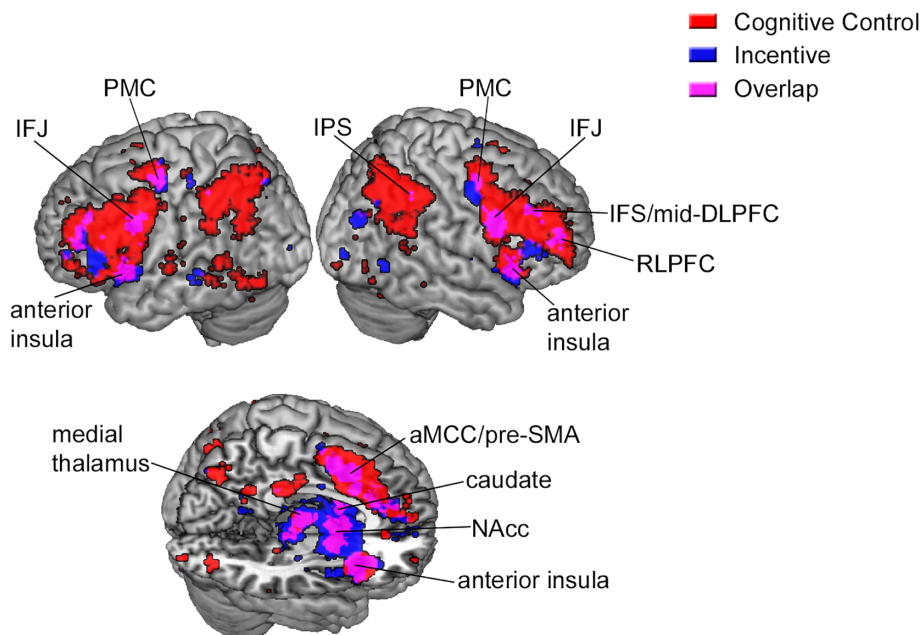


FIGURE 2 Rendered surface display of Neurosynth forward inference meta-analyses using the terms “cognitive control” and “incentive,” corrected for multiple comparisons using a false discovery rate of $q = .01$. While a broad network of regions is consistently activated in studies of cognitive control, only a subset of these regions are also recruited in studies of incentive processing, and may play a role in motivated cognitive control. This finding corroborates the ALE analysis, but also reveals a number of additional regions in the left hemisphere and subcortical structures. IFS, inferior frontal sulcus; IFJ, inferior frontal junction; PMC, premotor cortex; IPS, intraparietal sulcus; DLPFC, dorsolateral prefrontal cortex; aMCC/pre-SMA, anterior mid-cingulate cortex/pre-supplementary motor area; NAcc, nucleus accumbens [Color figure can be viewed at wileyonlinelibrary.com]

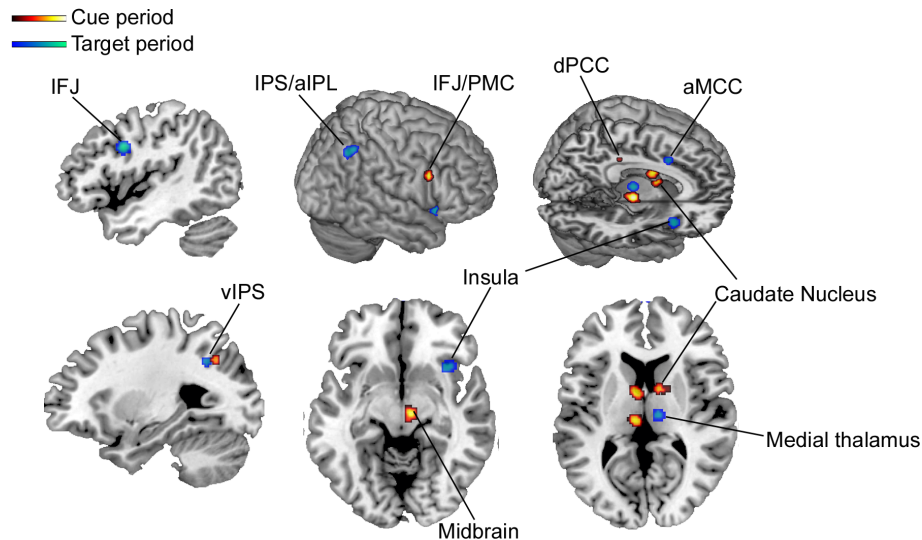


FIGURE 3 Significant ALE meta-analytic clusters associated with different trial periods during motivated cognitive control tasks ($p < .001$ uncorrected). The warm colors demonstrate regions that are consistently recruited during the cue period of motivated cognitive control tasks and may contribute to proactive control functions, whereas the cool colors demonstrate regions that are consistently recruited during the target (response) period of motivated cognitive control tasks and may contribute to reactive control functions. IPS/aIPL, intraparietal sulcus/anterior inferior parietal lobule; vIPS, ventral intraparietal sulcus; dPCC, dorsal posterior cingulate cortex; aMCC, anterior mid-cingulate cortex; IFJ, inferior frontal junction; PMC, pre-motor cortex [Color figure can be viewed at wileyonlinelibrary.com]

provides strong evidence that these regions are centrally involved in value-based modulation of cognitive control. Interestingly, the Neurosynth analysis revealed that only a subset of regions engaged during cognitive control are also engaged during reward processing. For example, the posterior middle temporal gyrus and parts of the lateral prefrontal and parietal cortices only demonstrated consistent recruitment during cognitive control. This suggests that there may be a select group of regions including the IFS, IPS/aIPL, aMCC/pre-SMA, and insula that integrate control demands and expected outcomes.

The aforementioned regions have well-established roles in supporting cognitive control and adaptive behavior via top-down modulation of sensory and motor processing (Cole et al., 2014; Dosenbach et al., 2006; Duncan, 2010; Miller & Cohen, 2001). The IFS and IPS/aIPL are part of the FPCN (Dixon et al., 2018; Power et al., 2011; Spreng et al., 2010; Vincent et al., 2008; Yeo et al., 2011) and contribute to working memory and the flexible representation of task rules (Badre & D'Esposito, 2009; Brass, Derrfuss, Forstmann, & von Cramon, 2005; Bunge, 2004; De Baene, Kuhn, & Brass, 2011; Derrfuss, Brass, Neumann, & von Cramon, 2005; Dixon & Christoff, 2012; Dumontheil, Thompson, & Duncan, 2011; Koechlin et al., 2003; Wallis, Anderson, & Miller, 2001). Neurons in these regions exhibit dynamic coding properties, signaling any currently relevant information (Duncan, 2010; Stokes et al., 2013), and rapidly updating their pattern of global functional connectivity according to task demands (Cole et al., 2013; Fornito, Harrison, Zalesky, & Simons, 2012; Gao & Lin, 2012; Spreng et al., 2010). One possibility is that elevated activation during motivated cognitive control reflects an amplification and sharpening of task information (e.g., rules) as a result of modulatory inputs from reward processing regions (Cohen et al., 2002; Etzel et al., 2015; Histed et al., 2009; Kouneiher et al., 2009). It could also reflect a shift in the temporal dynamics of cognitive control, toward a proactive mode of control (Braver, 2012; Jimura et al., 2010). When performance needs to be fast and accurate to procure a reward, FPCN

regions exhibit greater sustained activation and reduced transient/reactive activation, ostensibly reflecting the active maintenance of task rules across trials (Braver, 2012; Jimura et al., 2010).

Several lines of evidence suggest that FPCN regions may play an integrative role, directly representing control demands in relation to expected outcomes. First, Dixon and Christoff (2012) found that the FPCN flexibly represented trial-to-trial shifts in the association between specific task rules and expected reward outcomes (Dixon & Christoff, 2012). This finding is consistent with the fact that FPCN neurons encode not only rule information but also experienced and expected reward and punishment (Matsumoto, Suzuki, & Tanaka, 2003; Pan, Sawa, Tsuda, Tsukada, & Sakagami, 2008; Wallis & Miller, 2003; Watanabe, Hikosaka, Sakagami, & Shirakawa, 2002) (Abe & Lee, 2011; Asaad & Eskandar, 2011; Hikosaka et al., 2000; Histed et al., 2009; Hosokawa & Watanabe, 2012; Kennerley & Wallis, 2009; Kim, Hwang, & Lee, 2008; Klein, Deaner, & Platt, 2008; Kobayashi et al., 2006; Platt & Glimcher, 1999; Seo, Barraclough, & Lee, 2007; Watanabe, 1996; Watanabe et al., 2002). Second, McGuire and Botvinick (2010) found that the lateral PFC signaled the cost of exerting cognitive effort, suggesting that the FPCN plays a role in linking control demands to other parameters that are important for deciding when to implement control. In fact, numerous studies have demonstrated FPCN activation during value-based decision-making (Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009; Diekhof & Gruber, 2010; Gianotti et al., 2009; Huettel, Song, & McCarthy, 2005; Hutcherson, Plassmann, Gross, & Rangel, 2012; Jimura et al., 2013; Jimura & Poldrack, 2012; Lebreton et al., 2013; McClure et al., 2004; Plassmann, O'Doherty, & Rangel, 2007; Plassmann, O'Doherty, & Rangel, 2010; Tanaka et al., 2004; Tobler, Christopoulos, O'Doherty, Dolan, & Schultz, 2009; Vickery, Chun, & Lee, 2011; Weber & Huettel, 2008). Third, several studies have shown an interaction between control level and reward expectancy in the FPCN (Bahlmann et al., 2015; Ivanov et al., 2012; Padmala & Pessoa, 2011). Finally, disruption of the

FPCN—via transcranial magnetic stimulation or due to a lesion—disrupts value processing and leads to altered motivation (Camus et al., 2009; Essex, Clinton, Wonderley, & Zald, 2012; Paradiso, Chemerinski, Yazici, Tartaro, & Robinson, 1999; Zamboni, Huey, Krueger, Nichelli, & Grafman, 2008). Together, these findings suggest that the FPCN may play an integrative role, serving as a bridge between control demands and motivational outcomes (Dixon et al., 2017; Dixon & Christoff, 2014; Pessoa, 2008; Watanabe, 2017; Watanabe & Sakagami, 2007). In particular the FPCN may encode rule-outcome associations, specifying the likely reward or punishment to expect if a given set of task rules are employed or not employed.

Our meta-analytic results also revealed that the anterior insula and anterior mid-cingulate cortex play key roles in motivated cognitive control. These regions are part of the “salience network” (Menon & Uddin, 2010; Seeley et al., 2007). The insula has a well-established role in interoception—the representation of internal bodily signals including pain, temperature, respiratory and cardiac sensations (Craig, 2002; Critchley & Harrison, 2013; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Farb, Segal, & Anderson, 2012). This region is also activated during a variety of goal-directed tasks (Dixon et al., 2014a; Dosenbach et al., 2006; Duncan, 2010; Farb et al., 2012), suggesting that it may serve as a nexus between the FPCN and other interoceptive regions, allowing viscerosomatic signals to become integrated with task goals (Dixon et al., 2014a; Farb et al., 2012; Jezzini, Caruana, Stoianov, Gallese, & Rizzolatti, 2012). While the aMCC has long been associated with cognitive control, there is also a growing understanding of its role in motivational processes. One proposal is that the aMCC plays a role in determining the value of implementing control (Shenhav et al., 2013). The idea is that the aMCC contributes to a cost–benefit analysis based on an integration of various signals (e.g., effort, expected reward magnitude) which then influences the decision of whether it is worth engaging control during a given task, as well as just how much control to exert. Another perspective is that the aMCC plays a role in linking reinforcement to specific actions (i.e., represents action–outcome associations) (Camille, Tsuchida, & Fellows, 2011; Dixon et al., 2017; Rushworth, Behrens, Rudebeck, & Walton, 2007). Both proposals align with evidence that the aMCC is well connected to the motor system (Morecraft & Tanji, 2009), is sensitive to the effort costs of actions (Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Shidara & Richmond, 2002), and links actions to expected rewards and punishment (Alexander & Brown, 2011; Procyk et al., 2014; Rushworth et al., 2007; Shackman et al., 2011). The aMCC and insula may represent information about expected outcomes and task-related signals throughout different phases of a trial and contribute to anticipatory control processes including the preparation of rules (Denny, Ochsner, Weber, & Wager, 2014; Dosenbach et al., 2006; Knutson & Greer, 2008; Sridharan, Levitin, & Menon, 2008). Interestingly, we found that the anterior insula and aMCC were specifically recruited during the target rather than cue period of motivated cognitive control tasks, which suggests that they may be especially important for target-period control processes that allow for the efficient selection of task-relevant actions. One possibility is that these regions provide an interface that supports the translation of abstract task representations into more concrete body states

(autonomic activity and action plans) related to the initiation of goal-directed behavior (Dixon et al., 2017; Farb et al., 2012; Shackman et al., 2011). This idea aligns with prior work demonstrating the involvement of these regions in autonomic arousal (Medford & Critchley, 2010), response competition (Botvinick et al., 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; MacDonald 3rd, Cohen, Stenger, & Carter, 2000) and the activation of motor programs (Gaymard et al., 1998; Jezzini et al., 2012; Stuss et al., 2005; Turken & Swick, 1999).

The Neurosynth analysis also highlighted the caudate nucleus extending into the NAcc, while the cue period ALE analysis highlighted the caudate and the midbrain near the VTA. These regions are part of a dopaminergic midbrain–striatal circuit that signals prediction errors when there is a discrepancy between expected and actual rewards (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Montague, Dayan, & Sejnowski, 1996; O'Doherty et al., 2004; Schultz, Dayan, & Montague, 1997). Moreover, neurons in this circuit gradually shift the timing of maximal firing from actual outcomes to reward-predictive cues (Schultz et al., 1997). These regions play a fundamental role in goal-directed behavior via biasing action selection based on the anticipation of imminent rewards and the opportunity to exercise choice (Knutson, Adams, Fong, & Hommer, 2001; Leotti & Delgado, 2014). Accordingly, this circuit may play a role in broadcasting predicted cue values to other systems involved in constructing rule-outcome associations, and modulating visceromotor processing. Indeed, prior work has outlined detailed models of how the dopaminergic midbrain–striatal circuit serves a gating function that strengthens or destabilizes current working memory contents depending on task demands (Cohen et al., 2002; Cools, 2016; Hazy, Frank, & O'Reilly, 2006). Specifically, tonic dopamine in the PFC is thought to enhance the stability of working memory content via increased signal to noise ratio (that is, boosting the strength of local recurrent activity versus stimulus-evoked activity). On the other hand, phasic dopamine is thought to serve as a gating signal, allowing working memory to be updated based on reward-predicting events (Cohen et al., 2002; Cools, 2016; Hazy et al., 2006).

While the present work focused on identifying regions that are consistently activated during motivated cognitive control, it will be important for future work to characterize the functional interactions between these regions, and modulatory influences on other brain systems (e.g., sensory and motor systems). Functional connectivity and effective connectivity refer to the identification of undirected and directed functional coupling patterns, respectively (Friston, 2011), and provide a method for probing the nature of interactions between brain regions and making inferences about information flow across the network, and how that shapes task-related activation patterns (Cole, Ito, Bassett, & Schultz, 2016). In addition, it is possible to examine how regional interactions change as a function of task context using psychophysiological interactions among other methods (Smith, Gseir, Speer, & Delgado, 2016). This is particularly relevant for understanding the neural basis of cognitive control, which is thought to rely on distributed interactions among brain systems and the top-down modulation of task-specific processing via frontoparietal regions (Egner & Hirsch, 2005; Miller & Cohen, 2001). Indeed, recent work has shown that lateral frontal and parietal regions exhibit flexible,

task-dependent coupling patterns with other regions (Braun et al., 2015; Fornito et al., 2012; Smith et al., 2016; Spreng et al., 2010). To understand motivated cognitive control, it will be critical to understand the nature of interactions between the FPCN, salience network, and midbrain-striatal circuits.

A few limitations of the current findings should be noted. First, our meta-analyses were based on peak coordinates and therefore do not include the full extent of data present in raw statistical maps. Image-based meta-analyses that combine raw (unthresholded) statistical maps may provide additional information, particularly concerning small but reliable effects and relative deactivation patterns (Gorgolewski et al., 2015). A second limitation is that our analysis was based on studies that employed a number of different cognitive control tasks and functions. On the one hand, this suggests that the identified brain regions support motivated cognitive control in a general sense and are not tied to any particular task. On the other hand, this may obscure the delineation of neural systems that link expected outcomes to different types of executive control. As more studies examine this topic, future work may be able to discern whether incentive effects on different aspects of cognitive control (e.g., response inhibition versus working memory updating) have similar or distinct neural substrates. We were also unable to examine the effect of punishment on cognitive control given the small number of fMRI studies on this topic. Given that the observed frontoparietal regions have been shown to encode information about aversive outcomes in addition to rewarding outcomes (Asaad & Eskandar, 2011; Kobayashi et al., 2006), it is possible that substantial overlap with the current findings would be observed. However, there is some indication in prior work that differences may also appear (Paschke et al., 2015). Future studies may also be able to provide a more in-depth analysis of brain regions showing incentive effects during specific trial periods (e.g., cue versus delay and target processing). Our results were based on a small number of studies and should be seen as preliminary. Given that we found evidence of distinct brain regions involved in cue versus target periods, this may be a key area for future inquiry to investigate. Another important dimension of motivated cognitive control is incentive type (i.e., primary versus secondary). However, all studies included in this review operationalized motivation with monetary (i.e., secondary) incentives with the exception of Beck et al. (2010). This study compared the effects of primary (juice) and secondary (money) rewards on performance in a Sternberg task. The authors found no significant differences in behavioral improvement between the reward types but did find both regional and temporal differences in brain activation patterns. This underscores the importance of studying the different types of incentive effects separately. Another limitation is that the Neurosynth analysis may have identified regions that play a general role in processing reward information as opposed to incentive processing more specifically. However, the primary ALE analysis was based on studies in which reward was contingent on performance, suggesting that the regions identified in both analyses are likely to be specifically involved in mechanisms that underlie motivated cognitive control. With a growing number of studies in this area, it may be possible for future work to disentangle general and specific reward effects in a large sample of studies that can be meta-analyzed with Neurosynth. Finally, our analyses were based on regions that

were recruited in the relevant studies as a function of BOLD signal magnitude. It remains possible that we missed regions that would be identified using other analysis approaches (e.g., multivariate pattern analysis, or the effect of incentives on the sharpness of rule encoding as in the study by Etzel et al., 2015).

To summarize, the current findings reveal a select constellation of brain regions that are consistently recruited in studies of motivated cognitive control. Flexible interactions between frontoparietal, salience, and dopaminergic midbrain-striatal networks may underlie the dynamic process by which control signals are precisely tailored based on expected outcomes.

CONFLICT OF INTEREST STATEMENT

The authors declared no conflict of interest.

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