The Neural Basis of Motivational Influences on Cognitive Control: An ALE Meta-Analysis

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ABSTRACT

Cognitive control mechanisms support the deliberate regulation of thought and behavior based on internal goals. Many studies have now shown that motivational incentives improve cognitive control, reflected in faster and more accurate performance. While the neural basis of cognitive control has been thoroughly investigated, only recently has there been systematic investigation of the brain regions that may support motivation-related enhancements of cognitive control. Here, we present a quantitative meta-analysis of neuroimaging studies of motivated cognitive control using activation likelihood estimation (ALE) in order to delineate the brain regions that are consistently activated across studies. The analysis included functional neuroimaging studies that investigated changes in brain activation during cognitive control tasks when reward incentives were present versus absent. Consistent recruitment across studies was primarily observed in higher-order association cortices, including the inferior frontal sulcus (IFS), intraparietal sulcus (IPS), inferior frontal junction/premotor cortex (IFJ/PMC), and anterior insula. These activations were right-lateralized, with the exception of bilateral activations in the IFJ/PMC. A comparison with functional network boundaries revealed that the identified regions largely belong to the frontoparietal control network. Together, the distributed cortical regions identified here may contribute to enhanced top-down control by representing the relationship between task demands and expected motivational outcomes. Based on these findings, we propose a simple functional network model of motivated cognitive control.

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 (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 (Bunge, 2004; Cohen & Servan-Schreiber, 1992; 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 pre-potent responses (Aron, Robbins, & Poldrack, 2004), abstract thought and reasoning (Christoff et al., 2009; Christoff et al., 2001; Dias, Robbins, & Roberts, 1996), and set-shifting (Crone, Wendelken, Donohue, & Bunge, 2006; 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), 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 frontoparietal control network (FPCN) or Multiple Demand system (Cole, Repovs, & Anticevic, 2014; Cole et al., 2013; Cole & Schneider, 2007; Crittenden, Mitchell, & Duncan, 2016; Dixon et al., 2017; Dixon, Girn, & Christoff, in press; Dosenbach et al., 2007; Duncan, 2010; Mitchell et al., 2016; Spreng et al., 2010; Vincent et al., 2008). The FPCN flexibly represents a variety of task-relevant information, and exerts a top-down influence on other regions, guiding activation in accordance with current task demands (Buschman & Miller, 2007; Crowe et al., 2013; Desimone & Duncan, 1995; Dixon, Fox, & Christoff, 2014b; Egner & Hirsch, 2005; Miller & Cohen, 2001; Tomita et al., 1999).

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, in press; O'Doherty, 2004; Rangel, Camerer, & Montague, 2008; Rushworth et al., 2011). The past decade has seen a synthesis of these fields with a surge of interest in understanding how value influences the decision 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 R, 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, Andrews-Hanna, Spielberg, et al., 2015; Kaiser, Andrews-Hanna, Wager, & Pizzagalli, 2015; Nigg & Casey, 2005; Pessoa, 2008; Shackman et al., 2011; Shackman et al., 2016).

Recent studies have shown that individuals are strongly biased towards 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). Pre-trial 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, manifest 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 et al., 2015; Histed, Pasupathy, & Miller, 2009), thus providing more effective modulation of sensorimotor processes that support performance. Similar findings have been reported across numerous studies using a range of paradigms (Chiew & Braver, 2013, 2014; Chiew, Stanek, & Adcock, 2016; Dixon & Christoff, 2012; Etzel et al., 2015; Ivanov et al., 2012; Jimura, Locke, & Braver, 2010; Locke & Braver, 2008; Padmala & Pessoa, 2011; Taylor et al., 2004).

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 et al., 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 and colleagues (2010) employed a Sternberg task with two types of task blocks. One block consisted of only non-reward trials, while 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 5-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.

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: (i) 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 (ii) 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 et al., 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 et al., 2015; Taylor et al., 2004). Additionally, frontoparietal regions encode associations between specific rules and expected reward outcomes (Dixon & Christoff, 2012), exhibit stronger 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 towards 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 non-human 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 & Sakagami, 2007).

The current meta-analysis

While 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 sough 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. Additionally, we used well-established brain network boundaries (Yeo et al., 2011) to situate the meta-analytic results within the context of large-scale functional networks.

METHODS

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. Additionally, 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: (i) employ fMRI and report resulting activation coordinates; (ii) 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); (iii) include healthy adult human participants; and (iv) report results from a whole-brain analysis. Fifteen studies were found that matched the inclusion criteria (**Table 1**).

Data extraction

From these fifteen studies, we collected data on sample size, task, type of contrast (e.g., main effect of reward during task, or reward x 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. There were three categories of contrasts: (i) main effect of reward during a cognitive control task; (ii) conjunction effects showing overlapping activation in relation to cognitive demands and sensitivity to reward value; and (iii) 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 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 revealed the expected reward incentive, as this is likely to mainly capture reward processing alone, without an interaction with cognitive processes. If the cue period signaled motivational information *and* cognitive information (e.g., rules) that could be activated in a preparatory manner, then we included these foci. 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.

Meta-analytic data analysis

We performed analysis of the activation coordinates using a random-effects meta-analysis activation likelihood estimation (ALE) (Eickhoff et al., 2012; Eickhoff et al., 2009; Laird et al., 2005; Turkeltaub et al., 2012) implemented with GingerALE 2.3.6 software (San Antonio, TX: UT Health Science Center Research Imaging Institute). This is the updated version of GingerALE that has fixed the error related to cluster-level FWE correction (Eickhoff et al., 2017). Coordinates reported in Talairach space were converted to MNI space using GingerALE’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). Additionally, 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. To correct for multiple comparisons, we used a cluster-forming threshold at the voxel level of $p < 0.001$, and a cluster-level threshold of $p < 0.05$ FWE corrected. Results were visualized with MRIcron software (Rorden, Karnath, & Bonilha, 2007).

Functional network analysis

To identify the functional networks related to the regions identified in the meta-analysis, we plotted the significant meta-analytic clusters on a template brain, with well-established network demarcations from Yeo and colleagues (2011). This parcellation was based on resting-state functional connectivity data collected from 1000 adults, with regions clustered into networks based on the similarity of their functional connectivity profiles. Here we use the 7-network parcellation borders. These results were visualized with Caret software (Van Essen, 2005).

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 &Fiez (2004)	22	Working memory	Acc ↑	Delay	Main effect of reward	1
Taylor *et al.* (2004)	10	Working memory	RT ↓	Target	Main effect of reward	5
				Delay	Main effect of reward	6
				Probe	Main effect of reward	3
					Cognitive load x reward	1
				All (collapsed)	Main effect of reward	9

Locke & Braver (2008)	16	AX-CPT	Acc ↑, RT ↓	Block	Main effect of reward	20
Rowe *et al.* (2008)	20	AX-CPT	Acc ↑, RT ↓	Block	Parametric effect of reward x trial type	14
Engelmann *et al.* (2009)	20	Posner-cueing	Acc ↑	Cue	Main effect of reward	20
				Target	Main effect of reward	10
					Cue validity x reward	6
				Block	Main effect of reward	5
Kouneiher *et al.* (2009)	16	Rule-use	Acc ↑, RT ↑	Cue/target	Trial type x reward value	3
				Block	Main effect of reward	3
Jimura *et al.* (2010)	31	Sternberg	RT ↓	Block	Main effect of reward	2
Padmala & Pessoa (2011)	50	Stroop	Acc ↑, RT ↓	Target	Main effect of reward	6
					Interference x reward interaction	10
Dixon & Christoff (2012)	15	Rule Use	RT ↓	Cue	Rule x reward interaction	9
Ivanov *et al.* (2012)	16	Flanker	RT ↓	Target	Conflict x reward interaction	6
Boehler *et al.* (2014)	16	Stop Signal	RT ↓	Target	Overlap of main effects of stopping and reward	3
Paschke *et al.* (2015)	115	Flanker	RT ↓	Target	Congruency x 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 ↓	Target	Main effect of reward	3
				Target	Congruency x expectancy x reward interaction	6
Etzel *et al.* (2016)	20	Rule-Use	Acc ↑, RT ↓	Cue	Main effect of reward	7

Total = 15	**393**		**174**

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 non-rewarded trials.

RESULTS

The presence of reward significantly improved behavioral performance (decreased reaction time and/or increased accuracy) in all but one of the fifteen studies included in the meta-analysis. Accordingly, brain regions identified by the meta-analysis may support the enhancement of cognitive control by motivational incentives. We found five large activation clusters reflecting regions that exhibited consistent recruitment across studies (**Figures 1 and 2; Table 2**). These included regions linked to rule-use and shifting between stimulus-response contingencies such as the right inferior frontal sulcus (IFS) extending into the middle frontal gyrus (MFG), the right mid-intraparietal sulcus (mid-IPS) extending into the anterior inferior parietal lobule (aIPL), and bilateral inferior frontal junction/premotor cortex (IFJ/PMC). Additionally, the analysis revealed a significant cluster in the right anterior insula, which has been linked to mapping interoceptive states. Notably, four of the five identified regions were right-lateralized. Next, we examined the locations of the significant clusters in relation to the brain network boundaries delineated by a large-scale parcellation of resting state data (Yeo et al., 2011). The observed clusters largely fell within the boundaries of the frontoparietal control network (FPCN), with one exception, which was located within the boundaries of the dorsal attention network (DAN) (**Figure 3**).

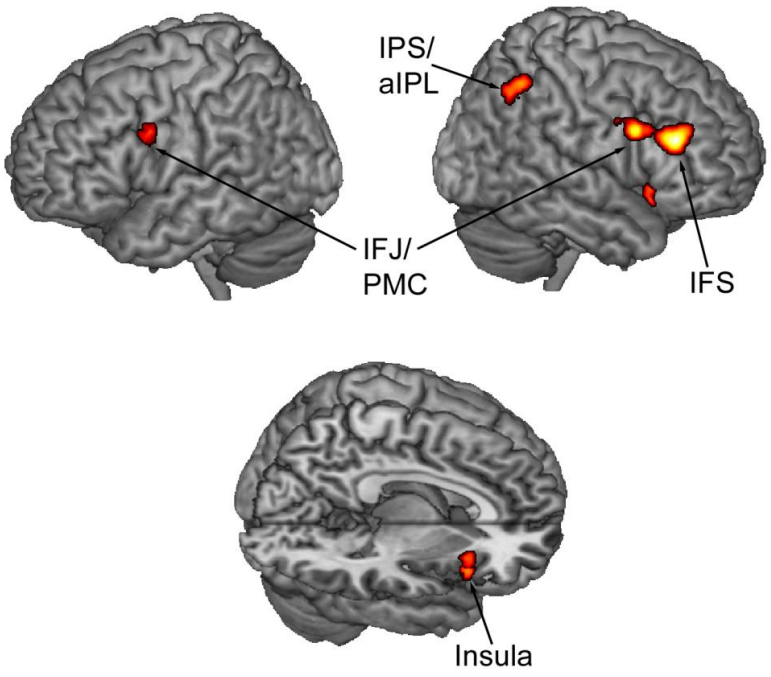

Figure 1. Meta-analytic clusters associated with motivated cognitive control. Abbreviations: IFS, inferior frontal sulcus; IPS/aIPL, intraparietal sulcus/anterior inferior parietal lobule; IFJ/PMC, inferior frontal junction/pre-motor cortex.

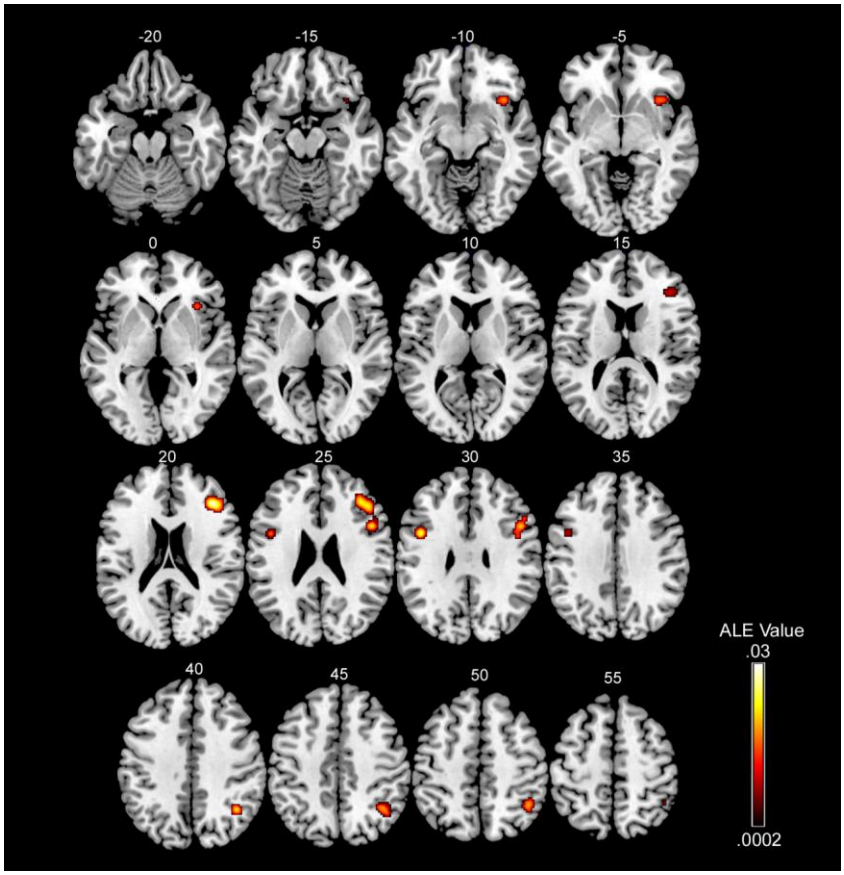

Figure 2. Whole-brain meta-analytic results. Numbers denote z-coordinates in MNI space.

Table 2. Brain regions consistently activated during motivated cognitive control

Region	Cluster size (mm^3)	Peak ALE value	Weighted peak foci in MNI space (x,y,z)
R inferior frontal sulcus	2080	0.0252	41, 32, 22
R inferior frontal junction/PMC	920	0.0215	47, 12, 28
L inferior frontal junction/PMC	656	0.0220	-44, 6, 30
R mid-intraparietal sulcus	1144	0.0188	40, -54, 45
R interior insula	840	0.0147	36, 20, -7

Note. Abbreviations: L, left; R, right; PMC, premotor cortex.

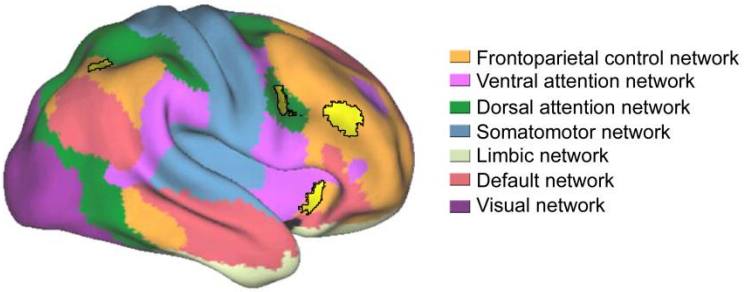

Figure 3. Location of meta-analytic clusters (yellow with black borders) in relation to the functional network boundaries from Yeo et al. (2011).

DISCUSSION

Cognitive control is often enhanced when reward incentives 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-related behavioral improvements in cognitive control. The results demonstrated significant meta-analytic clusters that were spatially localized to a largely right-lateralized constellation of multimodal association cortices, and not observed in primary sensorimotor regions, or classic reward-related regions. It is interesting that the analysis identified primarily frontoparietal regions even though most studies simply examined task performance in the presence or absence of reward incentives. It is unclear why classic reward-related regions such as the orbitofrontal cortex, amygdala, nucleus accumbens, or dopaminergic midbrain were not consistently recruited across studies. One possibility is that these regions exhibit a transient effect of reward during cue and outcome periods rather than sustained activation during task performance. These regions may also contribute to motivated cognitive control via changes in functional coupling patterns rather than changes in activation levels. Finally, it may be that these regions are primarily issuing rather than receiving influences in this context. Reward areas (e.g., dopaminergic midbrain and ventral striatal regions) may send signals that increase gain in frontoparietal regions. Accordingly, these regions may not show prominent activation because the fMRI signal likely reflects the synaptic inputs and local processing within an area, but not an areas synaptic output (Logothetis et al., 2001; Logothetis & Wandell, 2004).

Role of the frontoparietal control network

The meta-analytic clusters largely fell within the boundaries of the frontoparietal control network (FPCN), which has a well-established role in supporting cognitive control via top-down modulation of sensory and motor processing (Duncan, 2010; Miller & Cohen, 2001). This

network contributes 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 update their pattern of global functional connectivity according to task demands (Cole et al., 2013; Fornito, Harrison, Zalesky, & Simons, 2012; Spreng et al., 2010).

One possibility is that elevated FPCN 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 (Etzel et al., 2015; Histed et al., 2009; Kouneiher et al., 2009). This may result in enhanced top-down control, selectively boosting the processing of task-relevant information. It may also reflect a shift in the temporal dynamics of cognitive control, towards a proactive mode of control. When performance needs to be fast and accurate in order to procure a reward, the FPCN exhibits greater sustained activation and reduced transient/reactive activation, ostensibly reflecting the active maintenance of task rules across trials (Braver, 2012; Jimura et al., 2010). This sustained activation may also reflect the integration of expected reward information (Jimura et al., 2010). Several lines of evidence are consistent with the idea that the FPCN may represent motivational information in addition to cognitive information: (i) frontoparietal neurons signal information about expected and experienced reward and punishment , including the current reward context (Matsumoto, Suzuki, & Tanaka, 2003; Pan et al., 2008; Wallis & Miller, 2003; Watanabe, Hikosaka, Sakagami, & Shirakawa, 2002)(Abe & Lee, 2011; Asaad & Eskandar, 2011; Hikosaka & Watanabe, 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); (ii) the FPCN is recruited during human neuroimaging studies of value-based decision making, with widespread coding of motivational outcomes across frontoparietal cortex (Christopoulos et al., 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 et al., 2009; Vickery, Chun, & Lee, 2011; Weber & Huettel, 2008); (iii) transcranial magnetic stimulation applied to FPCN regions disrupts value processing (Camus et al., 2009; Essex, Clinton, Wonderley, & Zald, 2012); and (iv) FPCN lesions are associated with altered motivation (Paradiso et al., 1999; Zamboni et al., 2008).

Together, these findings suggest that the FPCN may play an integrative role, and serve as a bridge between motivational and cognitive processes (Dixon & Christoff, 2014; Pessoa, 2008; Watanabe & Sakagami, 2007). Dixon and Christoff (2012) provided direct evidence for this view, demonstrating that the FPCN encodes associations between specific task rules and expected reward outcomes. McGuire and Botvinick (2010) further found that the lateral PFC signals the cost of exerting cognitive effort. Finally, 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). One possibility is that information about rules and information about reward/punishment is first registered in separate specialized posterior brain regions, and then is passed to the FPCN which creates temporary mappings between this information within

working memory on each trial (Dixon, 2015). The adaptive coding properties of FPCN neurons (Duncan, 2001; Stokes et al., 2013) are consistent with this possibility. Interestingly, Dixon and Christoff (2012) found that right but not left frontoparietal regions represented specific rule-outcome associations. Based on these findings, the right-lateralized network revealed by the current meta-analysis could be interpreted in terms of encoding associations between task rules and expected reward outcomes.

Role of the Insula

Our meta-analytic results also identified the anterior insula. While this region is part of the FPCN at a course level of resolution, it demonstrates heterogeneous functional connectivity patterns at finer levels of resolution. In particular, the anterior insula has been linked to a "salience" network (Seeley et al., 2007), a ventral attention network (Fox et al., 2006), and a cingulo-opercular network (Dosenbach et al., 2007). It is thought to play a broad role in responding to salient stimuli (Menon & Uddin, 2010), likely due to its role in interoception—the representation of internal bodily signals including pain, temperature, respiratory and cardiac sensations (Craig, 2002; Critchley & Harrison, 2013; Critchley et al., 2004; Farb, Segal, & Anderson, 2012). The anterior insula may specifically contribute to awareness of interoceptive signals (Craig, 2002; Critchley et al., 2004). Given that 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), it may serve as a nexus between frontoparietal regions and other interoceptive regions, allowing viscero-somatic signals to become integrated with information about one's current context and task goals (Dixon et al., 2014a; Farb et al., 2012; Jezzini et al., 2012). During motivated cognitive control, the insula and other salience processing regions may register bodily sensations elicited by the prospect of obtaining a reward, and link these body states to task demands, thus enhancing response accuracy and speed.

Network model of motivated cognitive control

Based on a synthesis of our meta-analytic findings and other proposals about regions that may play a key role in motivated cognitive control, we propose a simplified network model (**Figure 4**). A substantial literature supports the idea that the orbitofrontal cortex (OFC), amygdala, and mediodorsal (MD) thalamus work together as a network for valuing sensory objects (Anderson & Phelps, 2001; Bouret & Richmond, 2010; Chikazoe, Lee, Kriegeskorte, & Anderson, 2014; Gottfried, O'Doherty, & Dolan, 2003; Morrison & Salzman, 2009; Padoa-Schioppa, 2011; Padoa-Schioppa & Assad, 2006; Rolls, 2004; Rudebeck & Murray, 2014; Rushworth et al., 2011; Sander, Grafman, & Zalla, 2003; Schoenbaum & Esber, 2010; Todd et al., 2012; Wallis, 2007; Walton et al., 2010). Accordingly, these regions may rapidly signal the presence and value of outcomes signaled by visual cues. This information may then be passed to the FPCN where it can be combined with task rules and information about effort costs and used to construct rule-outcome associations that specify the value of engaging cognitive control (Dixon & Christoff, 2012; McGuire & Botvinick, 2010). Consistent with this idea, neural selectivity for rewards arises faster in the OFC than lateral PFC, but in the latter region there is evidence that reward information is combined with information about task demands (Histed et al., 2009; Wallis & Miller, 2003; Watanabe & Sakagami, 2007). Reward-related inputs to the FPCN may amplify and sharpen the representation of task-relevant information, thus contributing to more effective top-down control (Etzel et al., 2015; Histed et al., 2009; Kouneiher et al., 2009).

Regions that contribute to interoceptive awareness and salience processing including the insula, anterior mid-cingulate cortex, and anterior temporoparietal junction may translate rule-outcome associations encoded by the FPCN into appropriate viscero-somatic body states that drive optimal behavior in service of acquiring a desired outcome (Dixon et al., 2014a; Rushworth et al., 2011; Shima & Tanji, 1998). These regions may contribute to anticipatory autonomic responses and action tendencies (Knutson & Greer, 2008; Medford & Critchley, 2010) that may facilitate the maintenance of effort prior to, and during, action execution (Croxson et al., 2009; Parvizi et al., 2013; Shidara & Richmond, 2002). Coordination between the FPCN and interoceptive/salience processing regions may support the enhanced regulation of perceptual and motor processes during motivated cognitive control. Finally, once an action has been selected and an outcome is revealed, a dopaminergic midbrain-striatal circuit may report prediction errors when there is a discrepancy between expected and actual rewards (Hare et al., 2008; Montague, Dayan, & Sejnowski, 1996; O'Doherty et al., 2004; Schultz, 1997). This prediction error may be broadcast to each of the other systems to update predicted cue values, modulate the strength of rule-outcome associations, and alter viscero-somatic processing. 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). Thus, distributed network interactions may underlie the dynamic process by which motivational incentives influence cognitive control.

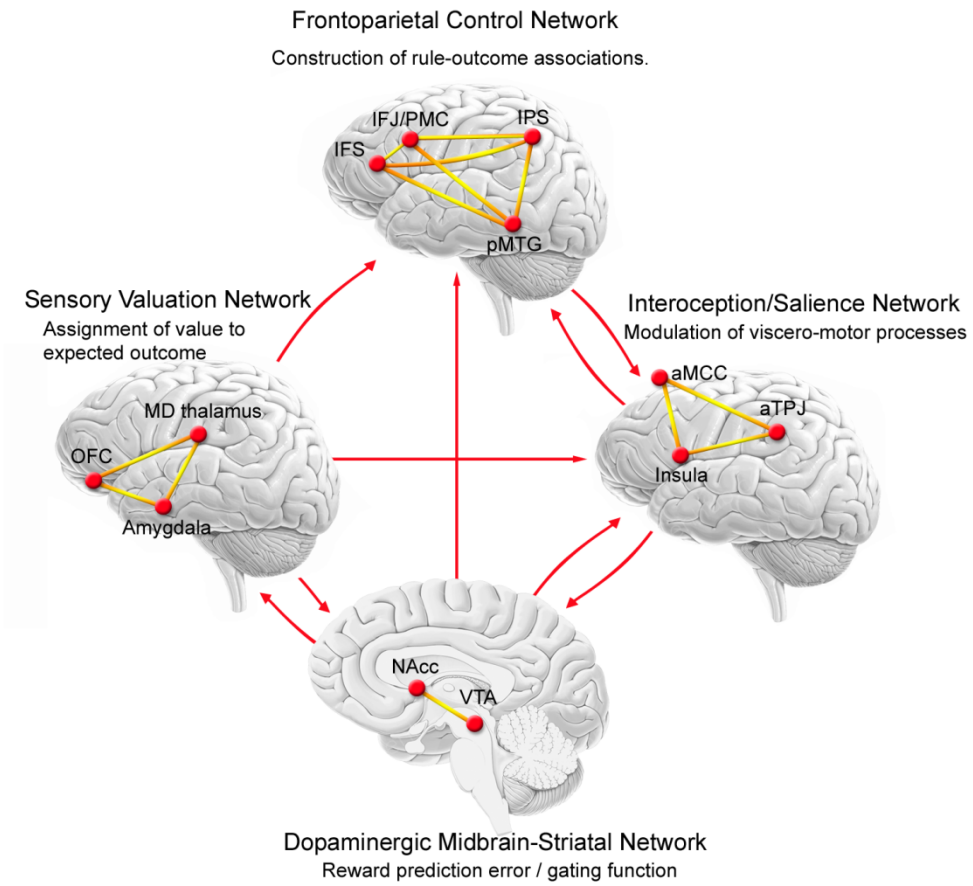

Figure 4. Network model of motivated cognitive control.

Limitations and Future directions

In the present analysis, we examined the neural basis of reward incentive effects on a cognitive control in general. 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. Furthermore, there have been few studies examining the effect of punishment on cognitive control. 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, some differences may also appear (Paschke et al. 2015). Future studies may also be able to isolate brain regions that show incentive effects during specific trial periods (e.g., cue versus delay and target processing). There may also be differences in the brain systems that support sustained versus transient incentive effects on cognitive control. There is some evidence to suggest that anterior frontoparietal regions are preferentially involved in processing long-term motivational goals, whereas posterior frontoparietal regions are preferentially involved in transient, trial-by-trial goals (Dixon, 2015; Dixon & Christoff, 2014; Dixon, Girn, et al., in press). 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 except for 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.

Conclusions

Cognitive control plays a critical role in supporting adaptive human behavior. Here we provide meta-analytic evidence that a set of right-lateralized frontoparietal regions are consistently recruited when cognitive control is engaged in service of attaining a reward outcome. This network may contribute to the construction of an internal model of the world, including the relationships between context, task-rules, and anticipated outcomes, thus specifying the value of control (Buckholtz, 2015; Dixon & Christoff, 2012; Smittenaar et al., 2013). The present results reflect a synthesis of the exciting work conducted on this topic. The next step will be to examine in more detail the differences and commonalties in how brain regions are recruited as a function of variables such as the properties of the incentive and the component of cognitive control.

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