

RESEARCH ARTICLE OPEN ACCESS

Deciphering the Neural Effects of Emotional, Motivational, and Cognitive Challenges on Inhibitory Control Processes

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ABSTRACT

Converging lines of research indicate that inhibitory control is likely to be compromised in contexts that place competing demands on emotional, motivational, and cognitive systems, potentially leading to damaging impulsive behavior. The objective of this study was to identify the neural impact of three challenging contexts that typically compromise self-regulation and weaken impulse control. Participants included 66 healthy adults ($M/SD_{\text{age}} = 29.82/10.21$ years old, 63.6% female) who were free of psychiatric disorders and psychotropic medication use. Participants completed a set of novel Go/NoGo (GNG) paradigms in the scanner, which manipulated contextual factors to induce (i) aversive emotions, (ii) appetitive drive, or (iii) concurrent working memory load. Voxelwise analysis of neural activation during each of these tasks was compared to that of a neutral GNG task. Findings revealed differential inhibition-related activation in the aversive emotions and appetitive drive GNG tasks relative to the neutral task in frontal, parietal and temporal cortices, suggesting emotional and motivational contexts may suppress activation of these cortical regions during inhibitory control. In contrast, the GNG task with a concurrent working memory load showed widespread increased activation across the cortex compared to the neutral task, indicative of enhanced recruitment of executive control regions. Results suggest the neural circuitry recruited for inhibitory control varies depending on the concomitant emotional, motivational, and cognitive demands of a given context. This battery of GNG tasks can be used by researchers interested in studying unique patterns of neural activation associated with inhibitory control across three clinically relevant contexts that challenge self-regulation and confer risk for impulsive behavior.

1 | Introduction

The capacity for self-control is one of the strongest predictors of psychological and physical well-being, and researchers estimate that 80%–90% of self-control in everyday life relies on inhibitory processes (Baumeister, Heatherton, and Tice 1994). Decades of research on inhibitory control have culminated in a wealth of

knowledge about the brain regions involved in supporting this core regulatory process. However, our understanding of this circuitry is impeded by a lack of research on how situations that threaten successful inhibition, such as negative mood states and temptations or rewards, impact the brain regions involved in inhibitory control (Baumeister 2014; Heatherton and Wagner 2011). The objective of this study was to examine the utility of three

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Summary

- Examining the impact of context on the neural mechanisms supporting inhibitory control is critical for furthering the field's understanding of self-regulation.
- This study assessed the utility of three new fMRI Go/NoGo tasks for examining how emotional, motivational, and cognitive contexts influence the neural circuits involved in inhibitory control.
- Results revealed differential recruitment of inhibitory control-related brain regions depending on contextual demands, underscoring the utility of examining inhibitory control across challenging contexts using these novel Go/NoGo fMRI tasks.

novel fMRI Go/NoGo (GNG) tasks, each of which implements one such challenging context, for indexing the impact of context on the neural mechanisms supporting inhibitory control.

2 | Inhibition as a Core Regulatory Process

Inhibition involves the control of an automatic or dominant behavioral response (Friedman and Miyake 2004), ranging from a simple button press to more complex behaviors, such as resisting the urge to self-harm or refraining from aggression in response to provocation. Behavioral tasks recruiting inhibitory control, such as the widely used GNG task (Criaud and Boulinguez 2013), are designed to induce a prepotent bias to execute a motor response (e.g., click a button when “Go” stimuli are encountered) and then test how well an individual can inhibit this response (e.g., when less-frequent “NoGo” stimuli are presented).

A meta-analysis of fMRI data collected on classic inhibition tasks reports consistent activation in bilateral inferior frontal gyrus (IFG), right dorsolateral prefrontal cortex (dlPFC), and anterior cingulate cortex (ACC) when inhibitory control processes are engaged (Criaud and Boulinguez 2013). More recent meta-analyses expand on these findings by identifying networks of neural activation related to inhibition. For example, a study of 68 experiments identified reliable engagement of left supplementary motor area, left inferior parietal lobule, left precentral gyrus, right insula, right middle frontal gyrus (MFG), and bilateral IFG during interference resolution (Zhang, Geng, and Lee 2017). Given that inhibition is inexorably intertwined with the situations in which it occurs, a more comprehensive understanding of the mechanisms supporting context-dependent inhibitory control would further our knowledge of how this core regulatory process promotes successful behavioral control in the face of competing demands. Furthermore, deciphering how the neural activation supporting inhibitory control is modulated by different challenging contexts could have translational significance for understanding why different inhibitory processes degrade as a function of competing situational demands.

3 | Contextual Challenges to Inhibition

Multiple literatures underscore the importance of context for predicting when inhibition will break down. Among the most

robust triggers of self-regulation failure are contexts that evoke a negative or aversive mood state, such as general stress, anger, sadness, and fear. Indeed, research indicates that negative mood can lead people to act aggressively toward others and themselves (Bushman et al. 2005; Sadeh et al. 2011), consume alcohol and drugs (Cooney et al. 1997), engage in unprotected sex (Bousman et al. 2009), and gamble excessively (Raviv 1993). Notably, research finds that the impact of negative mood states on self-regulation is evident following acute and chronic stress, aggressive provocation, social rejection, negative feedback, and activation of threat/fear systems, among others (Baumeister et al. 2005; Hartikainen, Siiskonen, and Ogawa 2012; Sinha 2008).

Another commonly encountered context that challenges self-control is exposure to stimuli that activate appetitive or reward circuits, which increase the likelihood that cued stimuli will be attended to, craved, and/or pursued (Baler and Volkow 2006; Hariri et al. 2006; Volkow et al. 2008). Successful long-term self-regulation requires an individual to transcend immediate temptations and delay gratification, countering the reward circuitry that is activated by hedonic stimuli, which can include a wide range of pleasurable experiences and cues that elicit positive feelings (e.g., high-caloric foods, monetary rewards, sexually explicit material, drugs of abuse; Knutson, Adams, and Hommer 2001; O'Doherty et al. 2002; Stark et al. 2019; Volkow, Wang, and Baler 2011). The compromising effects of competing reward cues on self-regulation has been demonstrated robustly across populations, including smokers, dieters, substance users, and healthy controls (Bonitz and Gordon 2008; Cooney et al. 1997; Cornell, Rodin, and Weingarten 1989; Hill and Peters 1998; Volkow et al. 2012).

Third, cognitive depletion theory (Baumeister, Heatherton, and Tice 1994) posits self-regulatory processes—including inhibition—depend on a limited resource that diminishes or fatigues with use over time (akin to a muscle). Numerous studies have shown that expending resources on self-regulation leads to poorer performance on subsequent tasks requiring self-control (Baumeister 2014; Hagger et al. 2010). A temporary reduction in executive function capacity (e.g., from a concurrent load like taxing working memory) also reduces regulatory capacity and contributes to inhibition failure (Hofmann, Schmeichel, and Baddeley 2012).

Prior work has identified sets of brain regions that are consistently activated in response to these contexts, when inhibitory control is not being manipulated. For example, aversive stimuli consistently activate amygdala and other regions that support emotional reactivity (Costafreda et al. 2008; Phan et al. 2002), and appetitive stimuli are known to activate circuitry predictive of reward, especially nucleus accumbens (NAcc; Everitt and Robbins 2005; Ikemoto 2007). Self-regulation involves a balance between “bottom-up” processing in these subcortical regions that signal the affective and motivational salience of stimuli and “top-down” regulatory processing in the prefrontal cortex (PFC; Heatherton and Wagner 2011). Impaired impulse control can occur when the balance is offset by a failure of PFC to adequately engage (e.g., due to cognitive resource depletion) and/or a particularly strong bottom-up impulse (e.g., hyperactivation in NAcc or amygdala). Incorporating context

as a level of analysis in neural models of inhibition could prove crucial for teasing apart heterogeneity in the disruptions that contribute to poor self-regulation, which has translational significance for a range of mental disorders and risky behaviors (e.g., Baumeister 2014; Brown et al. 2012, 2015; Heatherton and Wagner 2011).

Although most of the fMRI research has focused on “bottom-up” emotional processing or “top-down” cognitive control independently, a growing body of work has shown evidence of changes in inhibitory control-related activation as a function of competing contextual demands.

For example, Brown et al. (2012) utilized an fMRI GNG task that superimposed *aversive* pictures (e.g., attacking animals, aimed weapons) on inhibition cues (circle for Go trials vs. square for NoGo trials) to examine how aversive emotional distractors influence neural activation during inhibitory control (NoGo vs. Go). In a sample of 20 healthy young adults, they found an interaction effect such that neural activation during inhibitory control differed as a function of emotional context (aversive vs. neutral) in several cortical brain regions involved in attentional control (e.g., middle temporal and angular gyri, right frontal eye field). Another investigation examined neural activation during a task that superimposed a working memory load (N-back task) on a typical GNG paradigm in a sample of 28 healthy adults (Mostofsky et al. 2003). Although they did not explicitly test whether cognitive context (high vs. low working memory load) moderated inhibitory control (NoGo vs. Go), the authors reported that a concurrent working memory load was linked to greater recruitment of right dlPFC during NoGo trials. Thus, prior work suggests neural activation patterns during GNG tasks differ as a function of competing contextual demands. However, most of these fMRI studies manipulated only a single context in isolation, limiting the insight that can be gained about how the brain adapts to maintain inhibitory control and self-regulation across different types of challenges.

These findings are generally consistent with recent large-scale studies examining context-specific inhibitory processing systems. A meta-analysis of 66 fMRI studies on inhibition, for example, identified a dorsal frontal inhibitory system that was reliably activated during tasks requiring the inhibition of cognitive interference (e.g., Stroop, Flanker), whereas a ventral inhibitory system was reliably activated by inhibition tasks with emotionally distracting stimuli (Hung et al. 2018). The former system engaged dorsal anterior cingulate and bilateral medial frontal regions, dlPFC (BA9, BA6), and parietal lobe areas, and the latter system activated the left anterior insula, IFG (BA47) and amygdala. This pattern of results suggests that distinct inhibitory control systems are activated depending on the specific interference demands placed by the context.

4 | Present Study

The present study builds on previous research examining the neural correlates of emotional and cognitive interference by examining how neural processes respond to multiple challenging inhibitory contexts in a more comprehensive manner than has

been previously explored in a single study. Specifically, we investigated how neural activation differed across GNG tasks that varied as a function of competing emotional (aversive emotional distractors), motivational (appetitive distractors), and cognitive demands (working memory load) in a healthy sample of adults and compared neural activation in these three contexts to a neutral GNG task.

We hypothesized that: (i) neural activation during the GNG task with aversive emotional distractors and the task with appetitive distractors would show interactive effects of context (e.g., aversive mood vs. neutral) with inhibitory control (NoGo vs. Go) in cortical brain regions involved in attentional control, including bilateral posterior middle temporal gyri (MTG), angular gyri, and the right frontal eye field (Brown et al. 2012), along with the regions involved with emotional and motivational processing (e.g., medial PFC; Sabatinelli et al. 2007); and (ii) neural activation during the GNG task with a working memory load component would show interactive effects of cognitive context (cognitive depletion vs. neutral) with inhibitory control (NoGo vs. Go) in right dlPFC (Hung et al. 2018; Mostofsky et al. 2003). In terms of mood, we expected no changes in self-reported mood during the neutral or cognitive load task, increases in negative mood during the task with aversive emotional distractors, and increases in positive mood during the task with appetitive distractors.

5 | Methods

5.1 | Participants

The final sample included in our analyses consisted of 66 healthy adults who were recruited from the community through advertisements for a study on risky behavior. Individuals were eligible to participate if they were between the ages of 18 and 55 and spoke fluent English. Exclusion criteria included current psychosis, serious medical or neurological condition, history of head injury with loss of consciousness > 30 min or lasting effects, and presence of MRI contraindications (e.g., pregnancy, metallic implants).

The initial sample included 277 participants with complete MRI data across all four tasks. Given our interest in validating the fMRI tasks among healthy adults, we assessed individuals for mental disorders using the Structured Clinical Interview for DSM-5 (SCID-5; First et al. 2015) and excluded those from the present analyses who met criteria for a psychiatric disorder ($n=197$) or used psychotropic medication in the prior month ($n=3$). In addition to these exclusionary criteria, eight participants were excluded due to low performance on GNG tasks (outliers over three standard deviations from the median), and three subjects who did not meet MRI data quality standards were excluded (i.e., excessive motion).

Participants ranged in age from 18 to 52 years old ($M/SD_{age} = 29.82/10.21$) and were predominantly female (63.6%). Most participants were White (60.6%), followed by Black (21.2%), Asian (15.2%), Native Hawaiian or Pacific Islander (1.5%), or Bi-racial (1.5%). Only three adults (4.5% of the sample) identified as Latinx. Half of the sample (50.0%) was working full-time, 19.7% were

working part-time, 22.7% were full-time students, and 7.6% were unemployed at the time of the study. Past-year income ranged from \$10,000 to \$300,000, with a median income of \$73,500.

The University of Delaware's Institutional Review Board approved all protocols and procedures (Protocol No. 1073423-17). The study was carried out in accordance with the provisions of the World Medical Association Declaration of Helsinki.

5.2 | Measures

5.2.1 | Inhibition Tasks

Inhibitory control processes were measured using four variations of fMRI-adapted GNG tasks (Criaud and Boulinguez 2013; see Figure 1). Across all four tasks, we induced a prepotent bias to execute a motor response, specifically to click a button when “Go” stimuli were encountered on the majority of trials (75% of trials) and examined the ability to override or inhibit this automatic response when less-frequent “NoGo” stimuli were presented (25% of trials). For all tasks, a target stimulus was presented for 2000ms, followed by a jittered intertrial interval ranging from 2000 to 6000ms. Trial order and jitter were optimized via a pseudo-genetic algorithm to maximize separability of effects, and each task lasted 10 min.

In all contexts, GNG target stimuli were superimposed on pictures selected from the International Affective Picture System (IAPS; Lang, Bradley, and Cuthbert 2008) based on normed ratings of valence and arousal. IAPS stimuli that were rated the most negatively and highly arousing were selected for the Aversive Emotion Task (mean valence rating=2.0; mean arousal rating=6.2), and erotic images that were rated the most positively and highly arousing were selected for the Appetitive Drive Task (mean valence rating=6.2; mean arousal

rating=5.4). Pictures rated as neutral and low arousal were selected for the Neutral Task, and the same pictures were used for the Cognitive Depletion task (mean valence rating=4.8; mean arousal rating=3.4). Within each task, the NoGo and Go stimuli were selected to have equivalent average normative ratings of valence and arousal. The task design is similar to that used in other neuroimaging studies of inhibitory control (e.g., Brown et al. 2012).

Four items from the *Positive and Negative Affect Schedule* (PANAS; Watson, Clark, and Tellegen 1988) were administered in the MRI scanner before and after each functional task. These items were administered as a manipulation check to assess how negative (e.g., sad, upset) and positive (e.g., happy, excited) mood changed from pre- to post-task.

Non-task (e.g., anatomical) scans were interleaved to reduce the carry-over impact of the previous task context. Task stimuli and order can be found in the [Supplemental Methods](#). The order of the following four tasks was counterbalanced across participants:

- *Neutral Task*. GNG target stimuli consisted of a circle for “Go” trials and a square for “NoGo” trials. As depicted in Figure 1, these target stimuli were superimposed on **neutral** IAPS pictures (e.g., chairs, tables, writing utensils). This context was used as a baseline comparison, as it differed from the aversive and appetitive tasks only by the valence/arousal of the stimuli and from the cognitive task only by the lack of the working memory manipulation.
- *Aversive Emotion Task*. GNG stimuli were superimposed on **aversive** IAPS stimuli (e.g., attacking animals, aimed weapons, assaults). A large literature shows that such negatively valenced stimuli activate aversive emotional systems (e.g., Brown et al. 2012, 2015; Urry et al. 2006). Thus, this

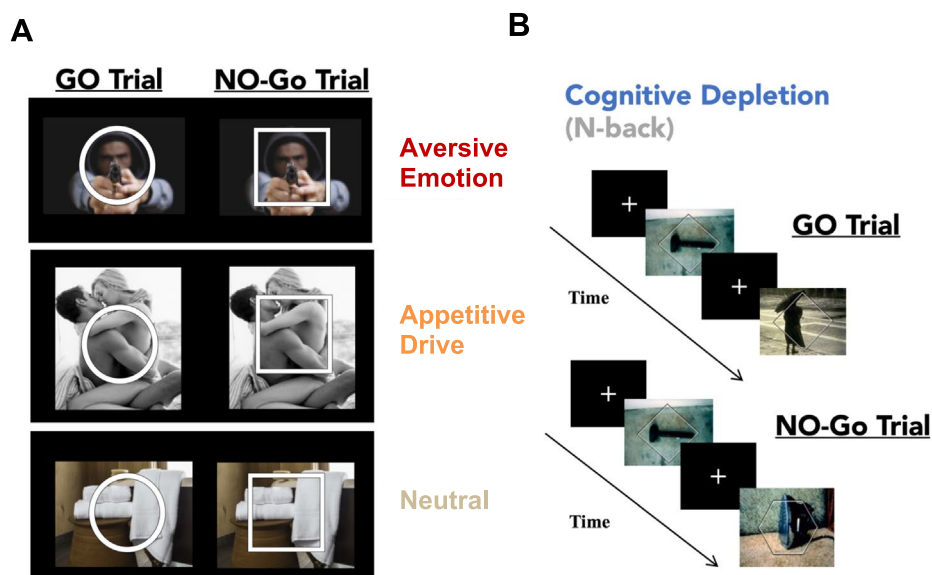


FIGURE 1 | fMRI Task. (A) Depiction of the Go and NoGo trials for the Go/NoGo task across the Aversive Emotion, Appetitive Drive, and Neutral Tasks. (B) Depiction of the Go and NoGo trials in the Cognitive Depletion task, which requires both inhibitory control (Go/NoGo) and working memory (N-Back).

task allowed us to examine the impact of aversive mood on inhibitory control.

- **Appetitive Drive Task.** GNG stimuli were superimposed on **appetitive** IAPS stimuli, specifically erotica and romantic couples. A large literature has demonstrated that such sexually explicit material activates motivational systems involved in appetitive drive and reward processing (e.g., Karama et al. 2002; Stark et al. 2019; Walter et al. 2008), including the IAPS images of erotic couples which were used in this study (Sabatinelli et al. 2007). The selection of appetitive stimuli was driven by the need to use stimuli with high hedonic value for healthy adults. After reviewing the literature, we determined that erotic images were the most arousing positive stimuli available (compared to alternatives like food; Lang, Bradley, and Cuthbert 1997) that reliably activated reward circuitry.
- **Cognitive Depletion Task.** This task is adapted from fMRI studies examining inhibitory control processes using a GNG paradigm with additional, concurrent working memory demands (Barber et al. 2013; Mostofsky et al. 2003). GNG stimuli were superimposed on **neutral** IAPS stimuli that were irrelevant to the task and included to maximize low-level stimulus compatibility across contexts. Participants were instructed to execute a motor response when the shape that appeared on the trial matched the shape from the prior trial. They were told to withhold the motor response when the shape was different from the shape one trial back (N-back design). This task allowed us to examine the impact of cognitive load on inhibitory control.

5.2.2 | MRI Acquisition

Neuroimaging data were collected via a Siemens 3T Magnetom Prisma scanner with a 64-channel head coil. Acquisition parameters were consistent with those currently used in the Human Connectome Project (Van Essen et al. 2012). fMRI: four runs of multiband EPI (MB-EPI) with an MB factor of 8 (TR = 0.829 s, spatial resolution = $2 \times 2 \times 2$ mm, and TE = 40 ms). T1: multiecho MPRAGE (resolution = 1 mm^3 , TR = 2530 ms, TEs = 1.69, 3.55, 5.41, 7.27 ms).

5.3 | Data Analysis

5.3.1 | Behavioral Data

Paired *t*-tests were used to assess task performance, using reaction time (RT) during Go trials and commission errors (CE) during NoGo trials as the dependent variables. Comparisons of interest were each task compared to the neutral baseline (e.g., Aversive Emotion RT vs. Neutral Task RT). To address the potential for outliers to drive findings, a winsorized version of each variable was created by winsorizing all values greater than three standard deviations from the median, using the median absolute deviation method for computing standard deviations.

In addition, to detect the presence of speed-accuracy tradeoffs in task performance, we examined bivariate correlations between

RT and CE within each task. All behavioral data were analyzed in SPSS Version 29 (IBM Corp 2023).

5.3.2 | Preprocessing

Using FSL and ANTS tools, fMRI data were motion and field-map corrected and spatially smoothed (full width at half maximum = 5 mm). The ICA-AROMA tool was used to identify and remove motion-related ICA components. Next, data were high-pass temporally filtered and registered via ANTS to MNI152 2009a space via boundary-based (functional to anatomical) and nonlinear (anatomical to standard) registration.

5.3.3 | Primary Analysis

Separate first-level models were created for each task (aversive, appetitive, cognitive, neutral), with regressors modeling each condition (NoGo, Go), and a NoGo–Go contrast created, which was carried up to second-level fixed-effects models to create the relevant task context contrasts for each participant. For example, the NoGo–Go contrast in the Appetitive Drive Task was compared to that same contrast in the Neutral Task to index neural processes related to motivational reward processes. Next, FSL's RANDOMISE was used to compute a two-tailed *t*-test of the mean difference for each task ($p < 0.05$, 5000 permutations, threshold-free cluster enhancement), which have been shown to provide robust and replicable results (Eklund, Nichols, and Knutsson 2016). Importantly, RANDOMISE corrects for multiple comparisons individually for each voxel. In other words, each voxel that meets the 0.95 (1-*p*) “threshold” is individually significant, rather than significance being determined on a cluster level. This is accomplished by building a joint (permutation-based) distribution across all voxels under consideration, rather than an individual distribution for each voxel. Thus, adding more voxels to the pool examined (and thus to the joint distribution) adds more cases in which strong effects may emerge by chance, thus making it harder for any given voxel to reach significance.

A sample-specific gray matter mask was used to limit the number of voxels under consideration. Specifically, each T1 scan (already warped into MNI 2009a space) was segmented using FSL's FAST tool, after which each partial gray matter mask was binarized, and the resultant masks were averaged to create a sample-specific probabilistic gray matter atlas. Given differences in what areas of cerebellum and brainstem were acquired in the functional data, these regions were edited from the atlas. Finally, a threshold of 80% was applied to the atlas, followed by binarization.

Although each above-threshold voxel is individually significant, it would be unwieldy to discuss each voxel in turn (although statistically acceptable). Thus, we derived contiguous clusters as a way of grouping voxels to aid in interpreting and discussing the findings. We also applied a 100-voxel threshold in order to pare down the number of findings to a more manageable set, while retaining the most meaningful regions. The choice of 100 voxels as a threshold was arbitrary. However, lowering this threshold had no meaningful impact, as the clusters that would

then be retained are in the same areas as the clusters that are currently retained/discussed. To probe significant interactions, we extracted the mean beta across each identified cluster for the relevant conditions and examined each of the lower-level effects (i.e., the main effects for a significant two-way interaction). These analyses were conducted using repeated-measures GLM in SPSS. Only significant effects are reported below.

An additional procedure was performed to segment a very large cluster into smaller ROIs to aid in making inferences. Given that the cluster in question covered a diverse array of regions, it was possible that some of the regions would have exhibited different activation patterns across tasks. Importantly, this segmentation is valid, because correction for multiple comparisons occurred voxelwise (see above). There are several methods with which we could have divided this cluster, the most common likely being creating spheres around local maxima. However, this did not cover most of the cluster, and we felt that it was more meaningful to apply a method that grouped voxels into subregions based on similarity. Thus, we applied the Louvain algorithm commonly used in graph theory for community detection, as implemented in the Brain Connectivity Toolbox (Rubinov and Sporns 2011). First, the data across participants for all voxels in the cluster were reshaped into two 2D matrices (one per hemisphere), with participant as the rows and voxel as the columns, after which a Pearson correlation matrix was created reflecting the correlation between each pair of voxels (across participants). This was entered into the Louvain algorithm with a gamma of 1 (balancing module size) and modularity as the optimized function. The results were reshaped into their original xyz locations, and contiguous clusters were identified within each module (the algorithm was blind to location). Only subclusters with over 1000 voxels were retained, as examining all clusters would have been unreasonable.

5.3.4 | Manipulation Checks

5.3.4.1 | Neural Activation. We conducted a manipulation check to examine whether the *Aversive Emotion Task* would induce greater neural activation in bilateral amygdala compared to the *Neutral Task* and whether the *Appetitive Drive Task* would induce greater neural activation in bilateral nucleus accumbens (NAcc) compared to the *Neutral Task*. Mean betas across amygdala and NAcc were extracted for each participant from the beta-maps for each factor cell (i.e., Appetitive NoGo, Appetitive Go, Aversive NoGo, Aversive Go, Neutral NoGo, Neutral Go). To examine the main effects of task context, we averaged neural activation for NoGo and Go trials in each task separately, and values were entered into repeated-measures ANOVAs to

examine differences in each ROI (i.e., amygdala or NAcc) by task (e.g., *Appetitive Drive* vs. *Neutral*).

5.3.4.2 | Self-Reported Mood. Repeated-measures ANOVAs of self-reported PANAS ratings completed before and after each of the tasks were examined to assess whether the tasks induced changes in negative or positive mood states.

6 | Results

6.1 | Behavioral Performance

Participants responded more slowly in the challenging contexts than the Neutral Task. RT on Go trials was slower on average for the Aversive Emotion ($t_{65}=3.71$, $p<0.001$, Cohen's $d=0.46$, $M/SD=596.52$ ms/139.85 ms), Appetitive Drive ($t_{65}=3.89$, $p<0.001$, Cohen's $d=0.48$, $M/SD=609.28$ ms/146.73 ms), and Cognitive Depletion ($t_{65}=5.34$, $p<0.001$, Cohen's $d=0.66$, $M/SD=620.75$ ms/115.56 ms) tasks than the Neutral Task ($M/SD=562.10$ ms/114.47 ms).

Across tasks, CEs were low, with the challenging tasks eliciting one error or less on average (Appetitive Drive: $M/SD=0.70/0.98$; Aversive Emotion: $M/SD=0.72/0.81$; Cognitive Depletion: $M/SD=1.05/2.00$) and the Neutral Task averaging 1.68 errors ($SD=0.91$), suggesting participants found it relatively easy to inhibit the Go response. Despite a restricted range on accuracy, we explored differences in CEs across the tasks. Participants evidenced slightly more CEs in the Neutral Task ($M/SD=1.68/0.91$) than the Aversive Emotion ($t_{65}=7.23$, $p<0.001$, Cohen's $d=0.89$, $M/SD=0.73/0.81$), Appetitive Drive ($t_{65}=5.91$, $p<0.001$, Cohen's $d=0.73$, $M/SD=0.70/0.98$), and Cognitive Depletion ($t_{65}=2.45$, $p=0.016$, Cohen's $d=0.306$, $M/SD=1.05/2.00$) tasks.

6.2 | Self-Reported Mood

As a manipulation check, we examined self-reported mood ratings on the PANAS before and after participants completed each task (see Table 1 for descriptive statistics). For the Aversive Emotion Task, participants' negative mood increased (i.e., sad, upset) [$F_{(1,65)}=9.24$, $p=0.003$, $n_p^2=0.12$] and their positive mood decreased (i.e., excited, happy) [$F_{(1,65)}=5.77$, $p=0.019$, $n_p^2=0.08$] based on their ratings before and after completion of the task. For the Appetitive Drive Task, there was not a significant change in positive mood [$F_{(1,65)}=2.51$, $p=0.118$, $n_p^2=0.04$] or negative mood [$F_{(1,65)}=0.15$, $p=0.698$, $n_p^2=0.00$] based on the self-reported mood ratings.

TABLE 1 | Descriptive statistics for the PANAS mood ratings by task.

	Negative mood ratings		Positive mood ratings	
	Pre-task (M/SD)	Post-task (M/SD)	Pre-task (M/SD)	Post-task (M/SD)
Neutral Task	1.12/0.46	1.21/0.54	2.00/0.73	1.70/0.57
Aversive Emotion Task	1.23/0.71	1.46/0.86	1.69/0.75	1.53/0.71
Appetitive Drive Task	1.22/0.54	1.25/0.60	1.69/0.57	1.58/0.67
Cognitive Depletion Task	1.42/0.85	1.37/0.83	1.49/0.69	1.69/0.69

Although we did not expect mood changes on the Cognitive Depletion or Neutral Tasks, we examined PANAS ratings before and after these tasks as well to assess if these contexts impacted self-reported mood. On the Cognitive Depletion task, there was an increase in positive mood [$F_{(1,65)} = 12.38, p < 0.001, \eta_p^2 = 0.16$] from pre- to post-task completion but no change in negative mood [$F_{(1,65)} = 0.37, p = 0.548, \eta_p^2 = 0.01$]. For the Neutral Task, there was a decrease in positive mood [$F_{(1,65)} = 20.27, p < 0.001, \eta_p^2 = 0.24$] from pre- to post-task completion but no change in negative mood ratings [$F_{(1,65)} = 2.29, p = 0.135, \eta_p^2 = 0.03$].

Together, these results indicate that only the Aversive Emotion Task induced negative mood states in participants. Additionally, the Cognitive Depletion task was associated with an increase in positive mood, while the Neutral Task led to a decrease in positive mood. This may suggest that participants found the Cognitive Depletion task engaging, whereas they perceived the Neutral Task as monotonous.

6.3 | Neural Activation

6.3.1 | Aversive Emotion Task

First, we conducted a manipulation check to examine whether the aversive emotional distractors in this task would induce greater neural activation in bilateral amygdala and bilateral NAcc (compared to the Neutral Task). Repeated-measures ANOVAs comparing activation in right amygdala showed a significant difference between the tasks ($F_{(1,65)} = 9.33, p = 0.003, \eta_p^2 = 0.13$), such that activation was greater for the Aversive Emotion Task ($M/SD = 27.04/20.32$) than the Neutral Task ($M/SD = 17.36/17.36$). Left amygdala showed a similar pattern with the Aversive Emotion Task showing relatively greater activation ($M/SD = 22.48/20.40$) than the Neutral Task ($M/SD = 16.85/18.68$); however, the difference in activation was not significant ($F_{(1,65)} = 3.21, p = 0.078, \eta_p^2 = 0.05$). Interestingly, left NAcc showed relatively reduced activation during the Aversive Emotion Task ($M/SD = -4.14/23.89$) compared to the Neutral Task ($M/SD = 2.08/20.73$); however, the difference in activation was not quite significant ($F_{(1,65)} = 3.10, p = 0.083, \eta_p^2 = 0.045$). There were no significant differences in activation in right NAcc ($F_{(1,65)} = 0.26, p = 0.615, \eta_p^2 = 0.004$) between the Aversive Emotion Task ($M/SD = -5.16/24.36$) and Neutral Task ($M/SD = -3.03/24.63$).

Second, we conducted voxelwise analysis of the cortical and subcortical gray matter to examine whether the emotional context of the Aversive Emotion Task moderated neural activation during inhibitory control processes. This analysis revealed a significant two-way emotional context (Aversive Emotion vs. Neutral contrast) \times inhibitory control (NoGo vs. Go contrast) interaction in 12 clusters spanning frontal, temporal, and occipital cortices (see Table 2, Figure 2). To interpret these interactions, we examined inhibitory control (NoGo vs. Go contrast) separately in the Neutral and Aversive Emotion Tasks. Results of these follow-up analyses are presented in Table 2.

Across all 12 clusters, the inhibitory control contrast was significant in the Neutral Task, such that there was greater neural activation during NoGo trials than Go trials. In contrast, the

significance of the inhibitory control contrast for the Aversive Emotion Task differed across the clusters. For most of the clusters (i.e., left Agranular OFC/Insula, left Temporal Occipital Fusiform Gyrus, right ITG, right Superior Lateral Occipital Cortex, left Parahippocampal Gyrus, left Paracingulate Gyrus, bilateral Lateral Orbital Sulci), activation in NoGo trials was *less than* activation in Go trials. Whereas, in the remainder of the clusters (i.e., left inferior lateral occipital cortex, left superior lateral occipital cortex, bilateral posterior orbital gyrus/agranular OFC/insula), there was not a significant difference in neural activation as a function of inhibitory control demands (see Figure 5). These results suggest reduced inhibitory control activation across several frontal, temporal, and occipital regions bilaterally for the Aversive Emotion Task compared to the Neutral Task.

6.3.2 | Appetitive Drive Task

First, we conducted a manipulation check to examine whether the appetitive distractors in this task would induce greater neural activation in subcortical regions linked to affective processing, including salience detection, indicated by the amygdala, as well as reward processing, indexed by the NAcc, compared to the Neutral Task. Repeated-measures ANOVAs comparing activation in NAcc revealed no significant differences between the Appetitive Drive Task (right NAcc: $M/SD = -0.57/21.11$; left NAcc: $M/SD = 0.44/21.92$) and Neutral Task (right NAcc: $M/SD = -3.03/24.63$; left NAcc: $M/SD = 2.08/20.73$) for right NAcc ($F_{(1,65)} = 0.50, p = 0.48, \eta_p^2 = 0.008$) or left NAcc ($F_{(1,65)} = 0.18, p = 0.67, \eta_p^2 = 0.003$). Similarly, repeated-measures ANOVAs comparing activation in amygdala revealed no significant differences between the Appetitive Drive Task (right amygdala: $M/SD = 23.08/25.08$; left amygdala: $M/SD = 19.52/21.87$) and Neutral Task (right amygdala: $M/SD = 17.35/17.36$; left amygdala: $M/SD = 16.85/18.68$) for right amygdala ($F_{(1,65)} = 1.94, p = 0.168, \eta_p^2 = 0.029$) or left amygdala ($F_{(1,65)} = 0.50, p = 0.483, \eta_p^2 = 0.008$).

Second, we conducted voxelwise analysis of the cortical and subcortical gray matter to examine whether the appetitive distractors in the Appetitive Drive Task moderated neural activation during inhibitory control processes. This analysis revealed a significant two-way appetitive context (Appetitive Drive vs. Neutral contrast) \times inhibitory control (NoGo vs. Go contrast) interaction in 10 clusters (see Table 3, Figure 3) spanning frontal, occipital, and motor cortices. To interpret these interactions, we examined inhibitory control (NoGo vs. Go contrast) separately in the Neutral and Appetitive Drive Tasks. Results of these follow-up analyses are presented in Table 3.

Across all 10 clusters, the inhibitory control contrast was significant in the Neutral Task, such that there was greater neural activation during NoGo trials than Go trials. In contrast, the significance of the inhibitory control contrast for the Appetitive Drive Task differed across the clusters. Across six clusters (i.e., bilateral Inferior/Superior Lateral Occipital Cortex, right Superior Parietal Lobule, left IFG pars opercularis, right Cuneus/Precuneus), activation in NoGo trials was *less than* activation in Go trials, and in the remainder of the clusters (i.e., left Frontal Operculum, right IFG pars opercularis, left OFC/Insula) there was not a significant difference as a function of inhibitory control demands (see Figure 5). These results suggest reduced

TABLE 2 | Aversive versus Neutral × No-Go versus Go.

Cluster		BA	Size (mm ³)	MNI (x, y, z) coordinates			Aversive No-Go vs. Go	Neutral No-Go vs. Go
1	L Agranular OFC/Agranular Insula/Frontal Operculum/IFG pars opercularis/IFG pars triangularis/MFG/dlPFC	44, 45, 6, 47, 9, 46	11,770	133	160	69	0.011	<0.001
2	L Inferior Lateral Occipital Cortex/ITG/MTG	37, 19	3512	149	67	63	0.153	<0.001
3	L Superior Lateral Occipital Cortex	7, 39, 18	3444	123	61	110	0.258	<0.001
4	R Posterior Orbital Gyrus (Agranular OFC)/Insula	13, 45, 47	1850	62	164	66	0.214	<0.001
5	L Temporal Occipital Fusiform Gyrus	37, 19, 35, 36	1606	127	84	57	0.001	<0.001
6	R ITG/Inferior Lateral Occipital Cortex	19, 37	1354	52	75	61	0.044	<0.001
7	R Superior Lateral Occipital Cortex	7, 39	434	70	63	106	0.029	0.005
8	L Parahippocampal Gyrus/Posterior Temporal Fusiform Cortex	28, 35, 36	426	133	106	51	<0.001	0.001
9	L Posterior Orbital Gyrus (Agranular OFC)/Insula	47	198	126	144	56	0.297	<0.001
10	L Paracingulate Gyrus/SFG	8, 9	192	102	173	101	0.001	0.016
11	R Lateral Orbital Sulci (OFC)	47	131	63	169	58	0.003	0.002
12	L Lateral Orbital Sulci (OFC)	47	108	133	168	53	0.002	0.002

Note: $N = 66$. Cluster labels refer to the location of the peak cluster value.

Abbreviations: BA, Brodmann Area; IFG, Inferior Frontal Gyrus; ITG, Inferior Temporal Gyrus; L, Left Hemisphere; MFG, Middle Frontal Gyrus; Neu, Neutral; OFC, Orbital Frontal Cortex; R, Right Hemisphere; SFG, Superior Frontal Gyrus.

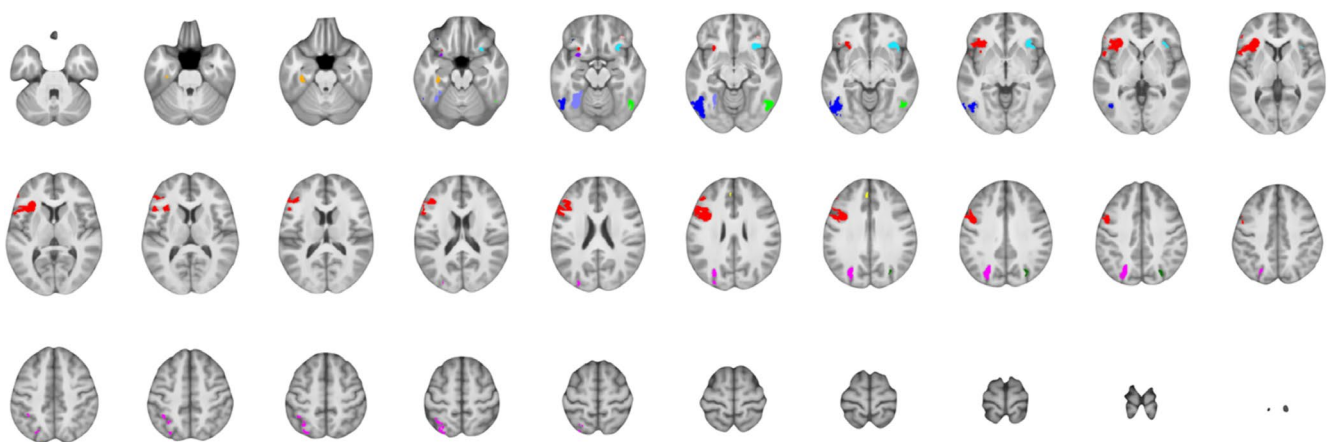


FIGURE 2 | Location of each cluster that showed a significant Aversive versus Neutral × No-Go versus Go interaction effect. Each color represents one of the 12 clusters reported in Table 2. R = Right hemisphere; L = Left hemisphere. L Agranular OFC/Agranular Insula/Frontal Operculum/IFG pars opercularis/IFG pars triangularis/MFG/dlPFC (red), L Inferior Lateral Occipital Cortex/ITG/MTG (blue), L Superior Lateral Occipital Cortex (pink), R Posterior Orbital Gyrus (Agranular OFC)/Insula (light blue), L Temporal Occipital Fusiform Gyrus (periwinkle), R ITG/Inferior Lateral Occipital Cortex (lime green), R Superior Lateral Occipital Cortex (dark green), L Parahippocampal Gyrus/Posterior Temporal Fusiform Cortex (orange), L Posterior Orbital Gyrus (Agranular OFC)/Insula (purple), L Paracingulate Gyrus/SFG (yellow), R Lateral Orbital Sulci (light pink), L Lateral Orbital Sulci (navy blue).

TABLE 3 | Appetitive versus Neutral \times No-Go versus Go.

Cluster		BA	Size (mm ³)	MNI (x, y, z) coordinates			Appetitive No-Go vs. Go	Neutral No-Go vs. Go
1	L Inferior/Superior Lateral Occipital Cortex/MTG	37, 19, 39, 21, 22	16,529	149	60	72	<0.001	0.001
2	R Inferior/Superior Lateral Occipital Cortex/MTG	37, 19, 18, 39	12,490	53	64	63	<0.001	0.003
3	R Superior Parietal Lobule/Superior Lateral Occipital Cortex	7, 40, 39, 2, 19, 5	10,389	133	88	121	<0.001	0.009
4	L IFG pars opercularis/MFG	6, 44, 9, 45	2287	137	142	99	0.018	<0.001
5	L Frontal Operculum/IFG, pars triangularis	45, 44, 47	1988	135	159	80	0.060	<0.001
6	R IFG pars opercularis/MFG/Precentral Gyrus	44, 6, 8, 9	1204	55	143	97	0.848	<0.001
7	R Superior Parietal Lobule	7, 5	1044	62	83	130	0.040	<0.001
8	R Cuneus/Precuneus	7, 39	947	70	59	106	0.003	0.005
9	L OFC/Insula	22	219	49	118	63	0.477	<0.001
10	L OFC/Insula	13, 47	162	125	143	56	0.061	<0.001

Note: $N=66$. Cluster labels refer to the location of the peak value. Cluster labels refer to the location of the peak cluster value.

Abbreviations: BA, Brodmann Area; IFG, Inferior Frontal Gyrus; L, Left Hemisphere; MFG, Middle Frontal Gyrus; MTG, Middle Temporal Gyrus; Neu, Neutral; OFC, Orbital Frontal Cortex; R, Right Hemisphere.

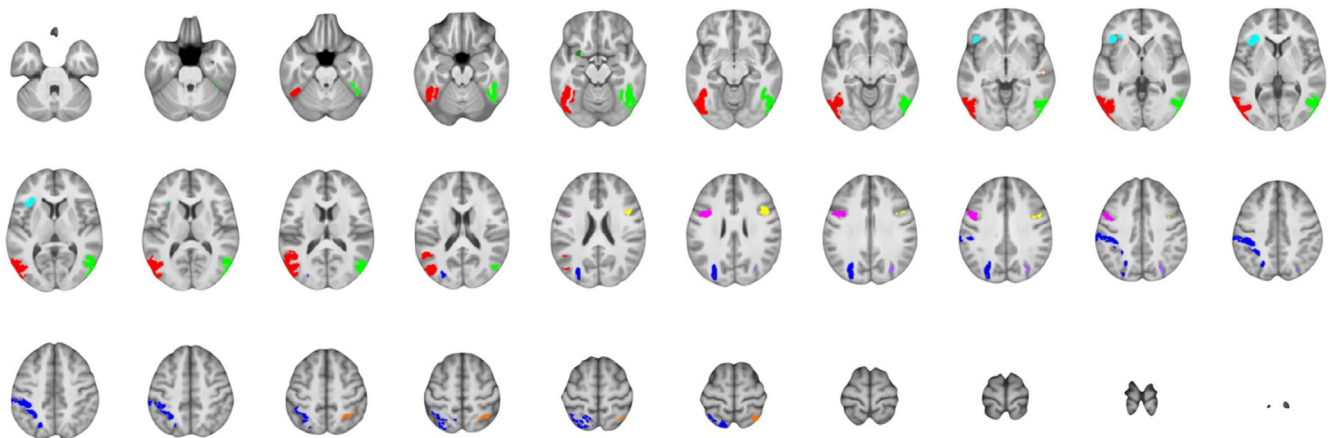


FIGURE 3 | Location of each cluster that showed a significant Appetitive versus Neutral \times No-Go versus Go interaction effect. Each color represents one of the 10 clusters reported in Table 3. R = Right hemisphere; L = Left hemisphere. L Inferior/Superior Lateral Occipital Cortex/MTG (red), R Inferior/Superior Lateral Occipital Cortex/MTG (lime green), R Superior Parietal Lobule/Superior Lateral Occipital Cortex (blue), L IFG pars opercularis/MFG (pink), R Frontal Operculum/IFG, pars triangularis (light blue), R IFG pars opercularis/MFG/Precentral Gyrus (yellow), R Superior Parietal Lobule (orange), R Cuneus/Precuneus (purple), L OFC/Insula (peach), R Posterior MTG/STG (dark green).

inhibitory control activation across several clusters bilaterally for the Appetitive Drive Task compared to the Neutral Task.

6.3.3 | Cognitive Depletion Task

Next, we assessed whether the working memory load in the Cognitive Depletion Task moderated neural activation during inhibitory control processes. Voxelwise analysis of the cortical and subcortical gray matter revealed a significant two-way

cognitive context (Cognitive Depletion vs. Neutral contrast) \times inhibitory control (NoGo vs. Go contrast) interaction in six regions spanning the majority of cortex (see Table 4, Figure 4). To interpret these interactions, we examined inhibitory control (NoGo vs. Go contrast) separately in the Cognitive Depletion and Neutral Tasks. Results of these follow-up analyses are presented in Table 4.

In contrast to the other challenging contexts, neural activation during the Cognitive Depletion Task was significantly greater

during inhibitory control (NoGo vs. Go contrast) for all six clusters that showed moderation effects. In three of these clusters (i.e., Cross-Cortex Cluster, bilateral Posterior Cingulate Gyrus, right MTG), neural activation did not differ as a function of inhibitory control in the Neutral Task, and in the other three clusters (i.e., right Thalamus, left Caudate, left Putamen; see Figure 5), activation was *diminished* in NoGo compared to Go trials in the Neutral Task.

Given that one of the clusters showing a cognitive context \times inhibitory control interaction was very large and incorporated much of the cortex, we conducted an additional procedure to segment this cluster into smaller units to aid in making inferences. We identified 25 subclusters within this large cluster and examined the activation patterns in each (see Supplemental Table 1 for details). This analysis indicated that the activation patterns across all examined subclusters were extremely similar to each other and the overall cluster.

7 | Discussion

Converging lines of research indicate that inhibitory control is likely to be compromised in contexts that place competing

demands on emotional, motivational, and cognitive systems. The objective of this study was to develop a battery of neuroimaging tasks that can be used to investigate the brain regions and networks that support inhibitory control across contexts that pose challenges to impulsive responding. In a sample of 66 healthy adults, we investigated patterns of cortical activation during inhibitory control (Go/NoGo) tasks that differed in the competing demands imposed by aversive emotional distractors, appetitive cues, and working memory demands. Voxelwise analysis revealed several clusters in each task where the emotional, motivational, or cognitive demands of the context interacted with inhibitory control processes to explain neural activation. Compared to a simple GNG task with neutral distractor pictures, the two GNG tasks with distractor pictures selected to be highly arousing and either aversive (*Aversive Emotion Task*) or appetitive (*Appetitive Drive Task*) in nature elicited less activation during inhibitory control (NoGo vs. Go trials) in several regions spanning frontal, temporal, parietal, and occipital cortices. In contrast, the GNG task with a concomitant working memory load (*Cognitive Depletion Task*) elicited greater activation across much of the frontal and parietal lobes compared to the simple neutral GNG task. Together, these findings provide new evidence that the neural regions involved in inhibitory control

TABLE 4 | Cognitive versus Neutral \times No-Go versus Go.

Cluster	BA	Size (mm ³)	MNI (x, y, z) coordinates			Cognitive No-Go vs. Go	Neutral No-Go vs. Go
1 Cross-Cortex Cluster ^a	—	223,421	105	146	124	<0.001	0.633
2 R Thalamus	—	3418	82	113	86	<0.001	0.002
3 B Posterior Cingulate Gyrus	23, 26, 29, 30	2180	96	102	98	<0.001	0.354
4 L Caudate	—	1693	116	147	80	<0.001	<0.001
5 R MTG	37, 22	261	52	79	84	<0.001	0.422
6 L Putamen	—	172	119	146	78	0.008	0.029

Note: N = 66. L = Left Hemisphere; R = Right Hemisphere; B = Bilateral; BA = Brodmann Area; MTG = Middle Temporal Gyrus.

^aThis cluster spanned the entire cortex. Additional clusters within this cluster are reported in Supporting Information to provide additional location specificity. Cluster labels refer to the location of the peak value.

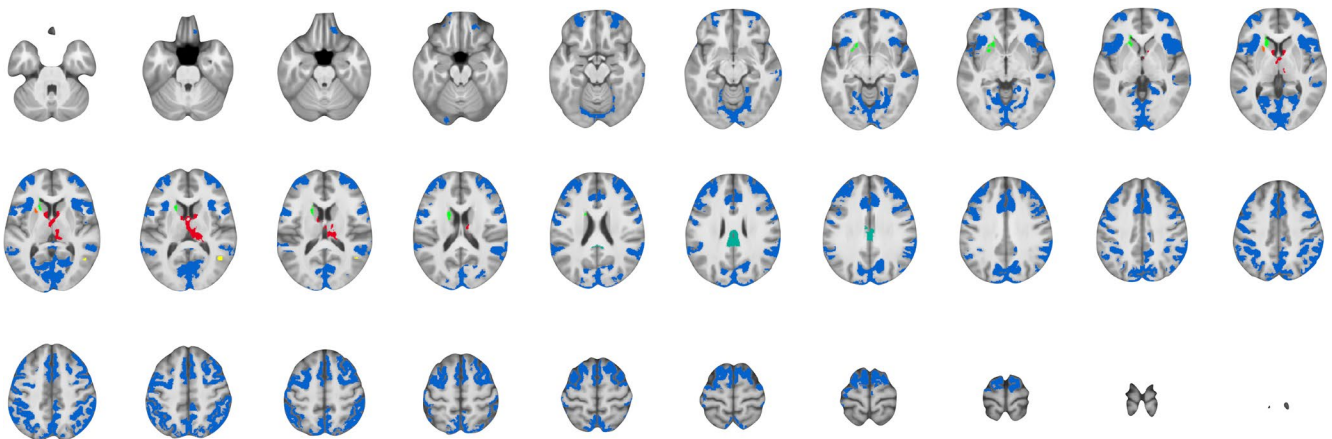


FIGURE 4 | Location of each cluster that showed a significant Cognitive versus Neutral \times No-Go versus Go interaction effect. Each color represents one of the six clusters reported in Table 4. R = Right hemisphere; L = Left hemisphere. Cross-Cortex (blue), R Thalamus (red), B Posterior Cingulate (teal), L Caudate (lime green), R Middle Temporal Gyrus (yellow), L Putamen (orange).

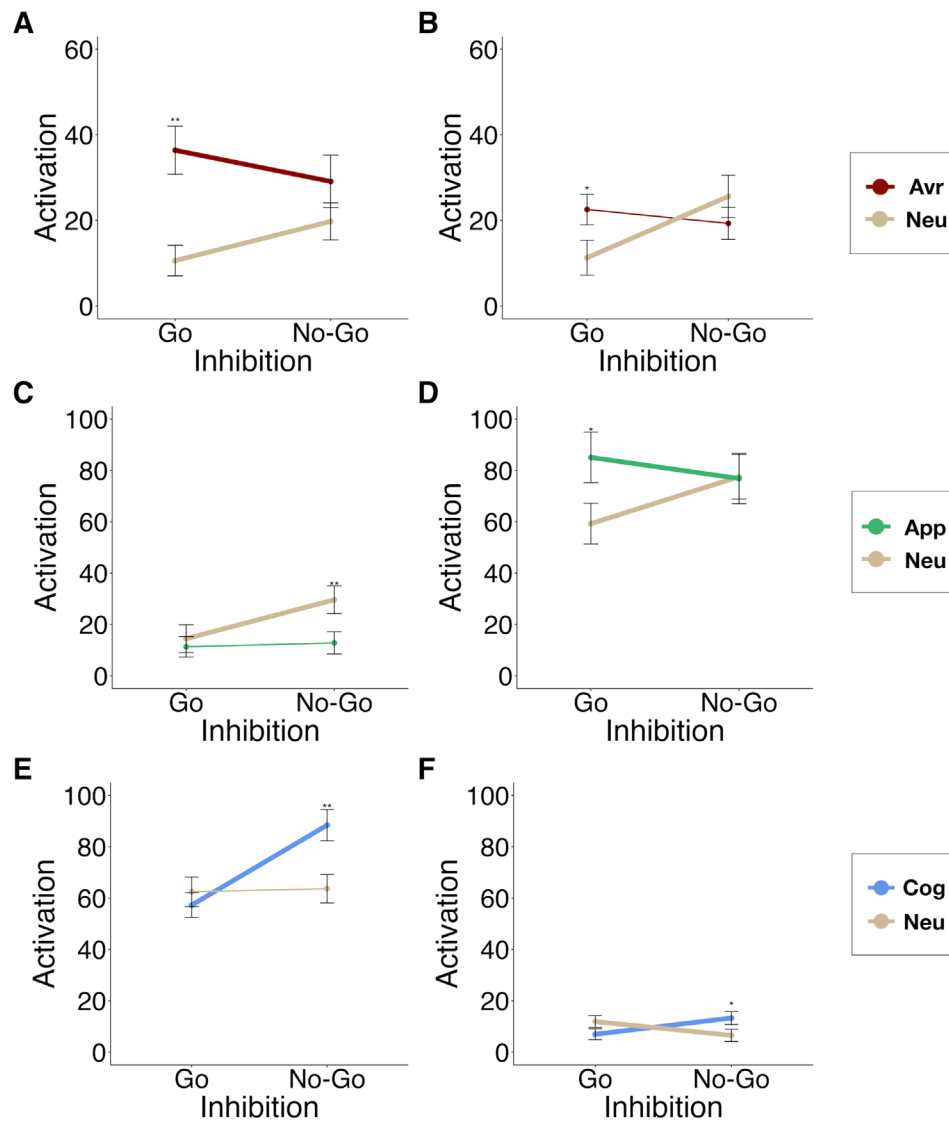


FIGURE 5 | Representative Visual Depiction of the Interaction Effect Patterns in Aversive, Appetitive, and Cognitive Depletion Tasks versus Neutral. Avr = Aversive, App = Appetitive, Cog = Cognitive, Neu = Neutral. Y-axis reflects beta values derived from the GLM that quantifies the mean level activation in each task condition and trial type. Error bars reflect standard error across individuals for each cluster. (A) Left Lateral Orbital Frontal Sulci (cluster 12 in Table 2). A similar pattern of simple slopes was observed in seven clusters (clusters 1, 5–8, 10–11 in Table 2) for the Aversive Emotion contrast. (B) Left Agranular Orbital Frontal Cortex (OFC; cluster 4 in Table 2). A similar pattern of simple slopes was observed in three clusters (clusters 2, 3, and 9 in Table 2) for the Aversive Emotion contrast. (C) Left OFC/Insula (cluster 9 in Table 3). A similar pattern of simple slopes was observed in three clusters (clusters 5, 6, and 10 in Table 3) for the Appetitive Drive contrast. (D) Left IFG, pars opercularis (cluster 4 in Table 3). A similar pattern of simple slopes was observed in five clusters (clusters 1–3, 7, 8 in Table 3) for the Appetitive Drive contrast. (E) Cross-Cortex (cluster 1 in Table 4). A similar pattern of simple slopes was observed in two clusters (clusters 3 and 5 in Table 4) for the Cognitive Depletion contrast. (F) Left caudate (cluster 4 in Table 4). A similar pattern of simple slopes was observed in two clusters (clusters 2 and 6 in Table 4) for the Cognitive Depletion contrast. *Significant cross-valence, within condition effect (e.g., Avr vs. Neu during Go trials). Bolded lines indicate significant within-valence, cross-condition effects (e.g., NoGo vs. Go during Neutral). * $p < 0.05$, ** $p < 0.001$.

vary as a function of the emotional, motivational, and cognitive challenges posed by different situations. They extend previous research by identifying cortical regions where contextual demands intersect with inhibitory control processes to presumably promote self-regulation in challenging situations. Importantly, the present findings from healthy adults can be used as benchmarks for evaluating neural disruptions in inhibition that occur in clinical populations and across mental illnesses.

7.1 | Neural Activation During Inhibitory Control in the Context of Aversive Emotional States

Research has highlighted the importance of understanding the impact of emotional processes on inhibitory control, as stressful and upsetting situations are known to increase engagement in risky behaviors and other adverse health behaviors (e.g., Baumeister et al. 2005; Hartikainen, Siiskonen, and Ogawa 2012; Nelson et al. 2008; Sinha 2008). Given the broad

relevance of negative mood states for understanding impulse control failures, we examined how inhibitory control was modulated by the addition of distracting pictures with aversive content (e.g., mutilated bodies, assaults, disasters) that were meant to evoke a negative mood state. As expected, we found that this Aversive Emotion Task increased self-reported ratings of negative mood and, compared to a simple neutral GNG task, slowed down prepotent behavioral responses and increased amygdala activation. These findings suggest the Aversive Emotion Task manipulation was successful at altering mood, behavior, and neural activation in a manner consistent with previous studies examining emotional processing (Hayes and Northoff 2011).

One primary aim of this study was to uncover brain regions that instantiate the interactive effects of emotional and inhibitory control processes. Results of a voxelwise comparison of inhibition-related activation in the Aversive Emotion and Neutral Tasks revealed 12 clusters, spanning bilateral frontal, occipital, and temporal cortices, where emotional context moderated inhibitory control processes. Across the 12 identified clusters, activation was consistently greater when participants were instructed to withhold rather than to execute a prepotent motor response (NoGo vs. Go trials), but this pattern of findings was only observed in the simple neutral GNG task. In contrast, most of the identified clusters—particularly within the frontal cortex (e.g., bilateral OFC, left SFG, and left dlPFC)—showed the opposite pattern of neural activation during the Aversive Emotion Task, such that there was *less* activation on trials where participants were instructed to inhibit the prepotent motor response (NoGo vs. Go trials).

Our findings converge with previous work showing enhanced recruitment of prefrontal regions during tasks that require inhibiting a prepotent response (e.g., Criado and Boulinguez 2013) and extend this work by identifying cortical regions where neural activation related to inhibitory control is suppressed in emotionally aversive compared to neutral contexts. The current findings build on prior work by Brown et al. (2012) who used a similar fMRI task with emotionally aversive stimuli superimposed on inhibitory control cues in a sample of 20 undergraduate students. This study found greater activation in NoGo versus Go trials in the aversive emotional condition compared to the neutral condition in regions involved in attentional control and conflict resolution (e.g., bilateral posterior MTG and angular gyrus, and right frontal eye field). In contrast to the findings of this study, we found that the difference in activation was smaller in NoGo versus Go trials in the Aversive Emotion Task relative to the simple Neutral Task. The present findings, therefore, advance understanding of emotion modulation of inhibitory control processes by isolating brain regions where activation is diminished or suppressed in emotional contexts (compared to neutral contexts) to facilitate inhibitory control.

Given that neural activation during NoGo trials on the Aversive Emotion Task was either diminished relative to Go trials or nonsignificantly different from Go trials across all 12 clusters suggests activation in these regions was downregulated in the emotionally aversive context compared to the neutral context. These regions may prioritize attentional capture and salience processing, which could either facilitate inhibitory control in

neutral contexts where inhibition cues would be most salient or hinder it in contexts where emotional distractors capture attention. This interpretation is consistent with our finding that neural activation in NoGo trials was suppressed or downregulated (relative to the Go trials) in the Aversive Emotion Task but not the Neutral Task across the identified clusters. Suppression or downregulation of neural activation in these cortical regions in emotional contexts may facilitate self-regulation by helping individuals maintain attentional control and generate adaptive inhibitory responses in the face of competing emotional demands.

7.2 | Neural Circuitry Related to Inhibitory Control in the Context of Appetitive Drive

A second major situational factor that influences impulse control is activation of appetitive motivational systems, which are theorized to disrupt inhibitory control through the activation of reward processes which, in turn, influence top-down executive control processes (Sinha et al. 2007). To examine the interactive effects of appetitive context and inhibitory control, we superimposed distracting pictures with appetitive content, specifically erotic images, that were meant to evoke an approach-oriented appetitive state. To our knowledge, this is the first study to examine neural activation associated with the synergistic effects of appetitive-reward and inhibitory control processes relative to a neutral inhibition context. Contrary to hypotheses, the addition of erotic distractor pictures in the Appetitive Drive Task did not increase self-reported positive mood (i.e., happy or excited) or recruit neural regions associated with reward processing (NAcc) to a greater extent than the Neutral Task. Examination of the RT data did indicate a slowing of behavioral responses on Go trials in the Appetitive Drive Task compared to the Neutral Task, suggesting the picture stimuli were distracting to participants. Overall, these findings suggest that the Appetitive Drive Task may not have evoked reward processing or an appetitive drive state in participants, despite the presentation of erotic stimuli that have been positively associated with NAcc activation in past research (Meseguer et al. 2007). Unlike previous work, however, the Appetitive Drive Task used in this study also included a response inhibition component, and it is possible that cognitive demands imposed by the inhibition task overpowered any weak reward processing induced by the stimuli. Future research examining sensitivity to appetitive stimuli and reward processes using this task may reveal interesting individual differences in neural reactivity to these stimuli.

Despite the apparently weak induction of appetitive drive in this sample, the addition of erotic distractor stimuli to the inhibitory control task altered neural activation in 10 clusters that spanned frontal, occipital, parietal, and motor cortices relative to the simple neutral GNG task. Like the findings for the Aversive Emotion Task, we found significant inhibition-related activation (NoGo vs. Go trials) in the Neutral Task in the identified clusters but did not observe this pattern in the Appetitive Drive Task. For example, results showed inhibition-related activation in a cluster within the right IFG during the Neutral Task (NoGo > Go), a region linked to response inhibition (Aron, Robbins, and Poldrack 2004; Hampshire et al. 2010), but this effect was not found in the Appetitive Drive Task. Similar effects were found

in clusters spanning the left IFG, MFG, and regions of the OFC. Similar to the Aversive Emotion Task, the apparent suppression of inhibition-related activation in these clusters may reflect differences in the attentional demands required for response inhibition in different affective and motivational contexts. The behavioral slowing observed in the Appetitive Drive Task, compared to the Neutral Task, suggests that participants adjusted to the potentially distracting stimuli by responding more cautiously. Therefore, the neural findings may reflect an adaptive response aimed at producing goal-congruent behavior in this context rather than disruptions in inhibitory control processes.

7.3 | Neural Circuitry Related to Inhibitory Control in the Context of Cognitive Depletion

Previous work has cited greater inhibitory control difficulties when cognitive resources are concurrently taxed by other cognitive functions (e.g., Baumeister 2014; Hagger et al. 2010; Hofmann, Schmeichel, and Baddeley 2012). To isolate neural circuits involved in inhibitory control in the context of a competing cognitive load, we introduced a concurrent working memory task (an N-back task) on top of the inhibitory control demands of the classic GNG task. When comparing this Cognitive Depletion Task to the simple neutral GNG task, we found widespread activation differences as a function of the additional working memory load across a swath of clusters spanning the frontal cortex and subcortical regions. Probing of the interactions revealed that there was greater activation in these regions during NoGo trials (vs. Go) when there was an added working memory demand, a pattern that was not observed in these regions during the Neutral Task. This pattern of findings suggests that the addition of a concurrent working memory load when inhibition is required was taxing, given the number of additional regions that were recruited to compensate for the additional cognitive load.

Notably, the swath of activation associated with the Cognitive Depletion Task extended into regions implicated in both inhibitory control and working memory. Specifically, significant activation differences were found in several clusters within the bilateral IFG, OFC, and ventrolateral PFC, all frontal regions linked to inhibition (Aron, Robbins, and Poldrack 2004; Hampshire et al. 2010) and working memory (e.g., SFG, cingulate gyri; Hampson et al. 2006; Wager and Smith 2003). We also found significant effects in the thalamus, caudate and putamen, which have previously been implicated in functions relevant for inhibitory control, including context monitoring, attention allocation, and response preparation (Barbas et al. 2018; Guo et al. 2018). Further, research has also shown that these subcortical regions are functionally and structurally connected to prefrontal regions, and together represent neural circuitry supporting inhibition (Bounoua et al. 2022; Dragan, Sokołowski, and Folkierska-Żukowska 2022). This pattern of findings indicates that the observed activation increases were not simply the result of the working memory demands, per se, but also the impact of such demands on concurrent inhibition processes. Together, the observed widespread neural activation required to concurrently engage inhibitory control and working memory abilities reveals a taxing neural effect across the brain.

7.4 | Future Directions, Strengths, and Limitations

To further conceptualize patterns of neural activation in each of the challenging inhibitory control contexts, future work may benefit from examining relationships among brain regions, such as fronto-limbic functional connectivity. Fronto-limbic circuitry may be particularly helpful in further characterizing the neural mechanisms of inhibitory control across challenging contexts, as this circuitry has been shown to be critical for threat detection and response inhibition (Heatherton and Wagner 2011; Wager et al. 2008). In addition, research has established both functional and structural relationships between prefrontal and limbic regions (Bounoua et al. 2022; Dragan, Sokołowski, and Folkierska-Żukowska 2022), and substantial work has implicated dysregulated fronto-limbic resting-state functional connectivity among individuals with disorders marked by poor self-regulation (Arienza et al. 2020; Jagger-Rickels et al. 2022; Varkevisser et al. 2017). Extending resting-state work by clarifying how inhibition-related fronto-limbic connectivity differs across contextual challenges in a healthy sample has the potential to further our understanding of the functional organization of this clinically relevant neural circuitry.

To our knowledge, this is the first study to test for neural circuitry associated with inhibitory control across three clinically relevant contexts marked by threats to self-regulation. Our examination within the same sample allows for better comparison of relevant neural correlates of inhibitory control across the three contexts. Further, our sample was relatively large compared to other studies examining affective inhibitory control and consisted of psychologically healthy community adults assessed by a gold-standard clinical interview, which extends the generalizability of findings. Finally, our use of voxelwise analyses allowed for a data-driven identification of relevant neural correlates of inhibitory control among healthy adults. Although outside the scope of the current study, these findings may provide a baseline understanding of relevant neural circuits in each of these contexts that can be used in future research among clinical samples.

However, study findings should be interpreted considering study limitations. Although the emotional context was created using well-established, standardized images shown to reliably evoke strong emotional reactions, the laboratory context may not accurately reflect real-world emotional contexts. Moreover, our sample only included psychologically healthy adults. We recruited healthy adults without a history of psychiatric disorders to avoid the potential confounds arising from using clinical samples. For example, the inclusion of a clinical sample may make it difficult to disentangle the effects of mental disorders and risky behaviors (e.g., chronic substance use) on inhibitory-related neural activation patterns from the effects of the contextual challenges. While this provides a foundational understanding of neural correlates of contextual inhibitory control, findings may not be generalizable to younger and/or clinical samples. Additionally, the healthy nature of our sample may have influenced the results by reducing impulsive responding. The finding that participants responded more slowly and made fewer CEs in the challenging contexts, compared to neutral, suggests they adapted to task demands by slowing down and responding more cautiously. This adaptive strategy likely supported more accurate, goal-directed behavior

in the face of environmental challenges. Future studies should examine neural correlates of contextual inhibitory control in other samples, including individuals who exhibit impulse control problems. Additionally, adapting the Go/No-Go task for the MRI scanner required presenting the picture stimuli more slowly (2000 ms) than typical behavioral tasks administered outside the scanner (500–1000 ms). Although this change is standard for the use of such tasks in neuroimaging work, the extended presentation time may not have been fast enough to elicit a strong prepotent response, which aligns with our observation of infrequent CEs across tasks in this study (0–2 errors per task on average). Therefore, the behavioral findings in this study should be interpreted with caution until future research can examine the behavioral effects of the tasks with faster stimulus presentation outside the MRI scanner. Since valence and arousal ratings for the IAPS stimuli were not collected from participants in this study, we cannot assess how well the standardized norms apply to our sample. For instance, the lack of NAcc activation during the Appetitive Drive Task might be due to participants not perceiving these stimuli as particularly pleasurable. However, the lack of the valence and arousal ratings limits our ability to interpret these findings. Finally, we interpreted the interactions based on planned comparisons of neural activation between NoGo and Go trials within different conditions, as our hypotheses focused on how context moderates inhibitory control processes. However, the graphical representations of the interaction effects suggest that differences in neural activation on Go trials across conditions may also exist, which could be valuable to explore in future research.

Despite these limitations, the current study provides a first step in clarifying the neural basis of inhibitory control across multiple contexts for future work to expand upon. The objective of the current study was to identify the neural correlates of response inhibition in three challenging contexts that commonly disrupt inhibitory control. We found that the neural circuitry related to inhibitory control varied as a function of concurrent affective, motivational, and cognitive demands. Findings provide preliminary evidence that these tasks alter neural regions involved in inhibitory control during affectively and cognitively demanding contexts. Thus, these tasks may be of interest to researchers interested in studying the neural correlates of situational lapses in inhibitory control that occur in contexts of negative mood, appetitive cues, and resource depletion (e.g., sleep deprivation, cognitive fatigue) as well as those who wish to probe neural alterations related to inhibitory control deficits among populations who struggle with executive dysfunction and poor impulse control.

Acknowledgments

This work was supported by the National Institute of Mental Health (1R01MH116228 awarded to NS; 1F31MH120936 awarded to NB; F31MH135695-01A1 awarded to AS) and National Institute of General Medical Sciences (2P20GM103653 awarded to NS). It was also supported by an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences (P30GM145765).

Ethics Statement

The University of Delaware's Institutional Review Board approved all protocols and procedures (Protocol No. 1073423-17). The study was

carried out in accordance with the provisions of the World Medical Association Declaration of Helsinki. Study data are available from the corresponding author.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author (N.S.), upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.