


## RESEARCH ARTICLE

# Meta-analytic evidence for a joint neural mechanism underlying response inhibition and state anger

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## Abstract

Although anger may weaken response inhibition (RI) by allowing outbursts to bypass deliberate processing, it is equally likely that RI deficits precipitate a state of anger (SA). In adolescents, for instance, anger occurs more frequently and often leads to escalating aggressive behaviors. Even though RI is considered a key component in explaining individual differences in SA expression, the neural overlap between SA and RI remains elusive. Here, we aimed to meta-analytically revisit and update the neural correlates of motor RI, to determine a consistent neural architecture of SA, and to identify their joint neural network. Considering that inhibitory abilities follow a protracted maturation until early adulthood, we additionally computed RI meta-analyses in youths and adults. Using activation likelihood estimation, we calculated twelve meta-analyses across 157 RI and 39 SA experiments on healthy individuals. Consistent with previous findings, RI was associated with a broad frontoparietal network including the anterior insula/inferior frontal gyrus (al/IFG), premotor and midcingulate cortices, extending into right temporoparietal areas. Youths showed convergent activity in right midcingulate and medial prefrontal areas, left al/IFG, and the temporal poles. SA, on the other hand, reliably recruited the right al/IFG and anterior cingulate cortex. Conjunction analyses between RI and SA yielded a single convergence cluster in the right al/IFG. While frontoparietal networks and bilateral al are ubiquitously recruited during RI, the right al/IFG cluster likely represents a node in a dynamically-

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adjusting monitoring network that integrates salient information thereby facilitating the execution of goal-directed behaviors under highly unpredictable scenarios.

#### KEYWORDS

activation likelihood meta-analysis, anterior insula, inferior frontal gyrus, frontoparietal, monitoring network, response inhibition, state anger, temporoparietal

## 1 | INTRODUCTION

State anger (SA) expression is defined as a transient psychobiological reaction characterized by emotional outbursts that vary in intensity and magnitude (Spielberg, 1999) and that usually emerge in response to goal obstruction (Carver & Harmon-Jones, 2009). To ensure goal attainment, state anger temporarily displaces response inhibition. The latter refers to successfully withholding or canceling routinized, ongoing, or prepotent responses to enable goal-oriented behaviors (Aron, Behrens, Smith, Frank, & Poldrack, 2007; Luna, Padmanabhan, & O'Hearn, 2010). The degree to which one can inhibit their responses seems to be the strongest predictor of state anger expression when accounting for working memory, cognitive flexibility, and attentional control mechanisms (Tonnaer, Cima, & Arntz, 2016), with impairments in inhibition being a significant predictor of violent crime (Meijers, Harte, Jonker, & Meynen, 2015).

In adolescents anger tends to occur frequently, oftentimes resulting in escalating aggressive behaviors (i.e., expressing anger). A failure to suppress anger may thus be sufficient to initiate a sequence of aggressive actions. Although such transient behaviors marked by mood volatility are typical of normative adolescent development, to counter a habitual response tendency would require one's conscious awareness of the action and a successive need to voluntarily inhibit it. Yet inhibitory abilities are heterogeneous and develop throughout adolescence and up to late adulthood (Burnett & Blakemore, 2009). Nonetheless, although the experience of anger may weaken response inhibition by allowing emotional outbursts to bypass deliberate processing (Dambacher et al., 2015; LeDoux, 2000), it is equiprobable that response inhibition deficits precipitate anger through frustration (Dambacher et al., 2015). Notwithstanding that response inhibition is a core component of state anger (Denson, DeWall, & Finkel, 2012) and that deficits in both processes are present in most neurodevelopmental and psychiatric conditions impairing social functioning, we are still lacking an integrative understanding of their joint neural representations.

Laboratory proxies of SA expression index retaliatory responses to interpersonal provocation. Such responses vary from inflicting unpleasant psychophysiological stimulation such as pain or noise blasting varying in intensity and/or duration (i.e., Taylor aggression paradigm; Taylor, 1967) or administering spicy sauce/drinks (i.e., Hot sauce; Lieberman, Greenberg, Sheldon, & McGregor, 1999). Other tasks include monetary punishments such as unwarrantedly deducting money from an alleged opponent (i.e., Point subtraction aggression game; Cherek, 1981) or unfair monetary splits between cooperating

parties (i.e., Ultimatum or Dictator games; Güth, Schmittberger, & Schwarze, 1982)). These paradigms are rigged to participants' disadvantage allowing the expression of anger-driven behaviors. SA expression is operationalized in terms of punishment intensity or monetary sanctions administered to real or alleged opponents. Unexpectedly interfering with goal-directed behaviors usually elicits spiteful or altruistic anger expressions. While spiteful punishment is the most common proxy of laboratory-induced state anger (Taylor, 1967), denotes an impulsive reaction to expectation violations, and inflicts harm on recipients (Janssen & Bushman, 2008), altruistic punishment promotes the greater good by sanctioning trust violations and aims to establish trust, cooperation, and rule enforcement (Crockett, Clark, Hauser, & Robbins, 2010; Fehr & Fischbacher, 2004; Güth et al., 1982). Spiteful punishment has been associated with hypoactivity of dorsolateral and dorsomedial prefrontal cortices (DLPFC, DMPFC) and hyperactivity of the ventral striatum, cingulate, and insular cortices (Beyer, Münze, Göttlich, & Krämer, 2015; Buades-Rotger, Brunnelieb, Münze, Heldmann, & Krämer, 2016; Dambacher et al., 2015; Lotze, Veit, Anders, & Birbaumer, 2007; Repple et al., 2017). Similarly, altruistic punishment has been associated with activity in the anterior, mid-cingulate, and dorsolateral prefrontal cortices, as well as in the anterior insula and adjacent inferior frontal gyrus (al/IFG; Feng, Luo, & Krueger, 2015; Gabay, Radua, Kemplton, & Mehta, 2014). These two punishment modalities enable a dynamic anger state in which reflexive-intuitive and reflective-deliberate systems interact (Wu, Luo, & Feng, 2016) under heterogeneous inhibitory abilities and highly unpredictable scenarios.

Suppressing ongoing or prepotent responses is critical for goal-directed behaviors including state anger. Experimentally, response inhibition is typically assessed by go/no-go (GNG) or stop-signal (SST) tasks. While the former requires selecting between inhibiting ("no-go") and executing ("go") a motor command, the latter demands withholding an ongoing behavior already under selection or preparation (see Puiu et al., 2018; Schachar et al., 2007 for ample discussions). Both tasks, however, enforce top-down frontoparietal control to suppress prepotent responses (Luna et al., 2010). Although oftentimes treated interchangeably (Lenartowicz, Kalar, Congdon, & Poldrack, 2010) and despite considerable neural overlap (Criaud & Boulinguez, 2013; Rae, Hughes, Weaver, Anderson, & Rowe, 2014), meta-analytic evidence shows distinct "stopping" and "not going" neural networks (Criaud & Boulinguez, 2013; Nigg, 2017; Swick, Ashley, & Turken, 2011). Specifically, findings showed that "not-going" engages a frontoparietal network mediating adaptive online control, while "stopping"

activates a cingulo-opercular network responsible for salience detection (, Mueller, Eickhoff, Langner, & Eickhoff, 2015; Dosenbach et al., 2006; Simmonds, Pekar, & Mostofsky, 2008; Swick et al., 2011). Functional overlap is reliably found in the presupplementary motor area (pre-SMA) and aIFG (Guo, Schmitz, Mur, Ferreira, & Anderson, 2018; Rae et al., 2014; Swick et al., 2011), which have been thought to form a *core inhibition* network mediating task-set (Dosenbach et al., 2006; Rae et al., 2014).

Emotional stimuli are thought to be more salient and thus automatically capture attention (Schimmack & Derryberry, 2005). They likely interrupt ongoing inhibitory activities and require increased effort to inhibit habitual responses. Emotional processing may, therefore, hijack cognitive control and reduce the allocation of attentional resources available for control strategies (Chen et al., 2016). Meta-analytical findings showed that resolving cognitive conflict due to emotional interference on cognitive control is attained through a network comprising the dorsolateral and medial prefrontal cortices, the IFG, and dorsal ACC (Song et al., 2017), with activations contingent on the magnitude of the emotional conflict. To maintain cognitive performance, intrusive emotional processing must be suppressed or altered through alternative regulatory processes (for a comprehensive review of behavioral and cognitive regulation of emotional control, see Ochsner & Gross, 2005). The ability to effectively regulate the thoughts, feelings, or behaviors emerging from negative emotional states (with anger representing one basic negative emotion that can interfere with control abilities) is paramount for normative development. Multiple studies link deficits in response inhibition and inhibitory control to anger and aggression (Dambacher et al., 2015; Repple et al., 2017; Xia, Zhang, & Wang, 2018). For instance, aggressive individuals show behavioral deficits in emotional stop-signal tasks (i.e., increased reaction time latencies) and hypoactivity in core inhibition brain areas (i.e., pre-SMA; Pawliczek et al., 2013). Similarly, state anger in adolescents alters connectivity patterns in frontoparietal regions (Cohn et al., 2015). Self-control training, however, decreases impulsive aggression and normalizes prefrontal and amygdala activity (Denson, Capper, Oaten, Friese, & Schofield, 2011; Zotev et al., 2016). Altogether, these findings suggest that impaired top-down control of prefrontal networks over cortico-limbic areas likely increases aggressive outbursts in aggressive psychopathology and is linked to poor modulation of anger outbursts, in general (Blair, 2012; Denson et al., 2011; Lievaart, van der Veen, Huijding, Hovens, & Franken, 2018; Wong et al., 2019).

From a developmental perspective, the efficiency of inhibitory control changes across the lifespan. Performance on basic cognitive control tasks, including response inhibition, sharply improves during childhood (Crone & Dahl, 2012; Luna et al., 2010; Luna, Marek, Larsen, Tervo-Clemmens, & Chahal, 2015) followed by a somewhat slower albeit ongoing improvement until mid-to-late adolescence (Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Dumontheil, 2016). The development of response inhibition during childhood and adolescence has been related to the protracted maturation of frontoparietal networks (Casey,

Tottenham, Liston, & Durston, 2005). Specifically, unlike adults who recruit rather focal right-lateralized regions, youths rely on more distributed prefrontal activity during response inhibition (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002). Moreover, behavioral and imaging studies report that deliberative processes such as state anger show an even more protracted developmental trajectory than basic response inhibition, with continuous changes throughout adolescence up to early adulthood (Burnett & Blakemore, 2009). This is in line with observations that, unlike adults, youths are more likely swayed by their emotions and that they need longer to regain composure after anger outbursts (Guyer, Silk, & Nelson, 2016).

Taken together, while response inhibition is typically associated with a right-dominant midcingulate-insular-frontoparietal network extending into the basal ganglia and the thalamus (Cieslik et al., 2015; Corbetta & Shulman, 2002; Dosenbach et al., 2006; Guo et al., 2018; Rae et al., 2014; Swick et al., 2011), negative emotional states seem localized to portions of the ventromedial and ventrolateral prefrontal cortex extending into the insular cortex (Blair, 2012; Kragel et al., 2018). Although these findings epitomize the functional links between response inhibition and state anger, we are lacking a quantitative overview of the neural networks supporting response inhibition, state anger, and their neural overlap. While former meta-analyses have examined either the neural correlates of response inhibition (Criaud & Boulinguez, 2013; Rae et al., 2014; Swick et al., 2011; Wu et al., 2016), emotion regulation (Cromheeke & Mueller, 2014; Langner, Leiberg, Hoffstaedter, & Eickhoff, 2018; Ochsner, Hughes, Robertson, Cooper, & Gabrieli, 2009), or different executive functions separately (Cieslik et al., 2015; Worringer et al., 2019), here we selectively focused on quantitatively describing the neural link between state anger and basic response inhibition. Despite a general agreement on the shift from diffuse to more focal response inhibition activity throughout development, comparatively less attention has been paid, however, to disentangling the neural mechanisms of youth versus adult response inhibition. A quantitative overview of the neural architecture of basic response inhibition in youths and adults has important implications for understanding the organization of state anger neurocircuitry. This might further account for the hypothesized inverse relationship between anger and response inhibition (Lievaart et al., 2018; Xia et al., 2018).

To this aim, we first meta-analyzed all basic successful and failed motor response inhibition fMRI studies that assessed go/no-go and stop-signal tasks to update the existent findings (Cieslik et al., 2015; Criaud & Boulinguez, 2013; Rae et al., 2014; Swick et al., 2011). Second, we performed sub-analyses to identify the neural correlates of response inhibition in youths versus adults, separately. Third, to the best of our knowledge, we calculated the first activation-likelihood estimation meta-analysis on state anger expression in healthy individuals. Finally, we tested for shared and distinct neural mechanisms of RI and SA by using conjunction and difference analyses. Due to the limited number of studies we were, however, unable to compute age-dependent state anger meta-analyses.

## 2 | METHODS

### 2.1 | Study identification and inclusion criteria

We selected studies through standard searches on PubMed, Web of Knowledge, and Google Scholar until January 2019 using the terms “go/no-go,” “stop-signal,” “aggression,” “anger,” “punishment,” “provocation,” “ultimatum,” and “dictator” in combination with “MRI,” “magnetic resonance imaging” or “imaging.” Additional studies were identified through the BrainMap database (Fox et al., 2005), review articles, and reference tracking. As we focus on basic response inhibition, we excluded other general executive function paradigms (i.e., Flanker, Stroop task) from our analyses as these include neural networks of resistance to distractor interference (Miyake et al., 2000). Furthermore, given that basic response inhibition underlies the experience of state anger (Dambacher et al., 2015), we only included studies typified by go/no-go and stop-signal paradigms that reported results for successfully withholding or canceling a motor action (i.e., contrasts such as “no-go > go/baseline” or “successful > failed inhibition”) irrespective of sensory modality. While theoretically including no-go > go/baseline and successful > failed inhibition in the same analysis is problematic methodologically as multiple contrasts from the same subject set can create dependencies across modelled activation maps (Turkeltaub et al., 2012), we adjusted for within-group effects by pooling the coordinates from all relevant contrasts typifying successfully inhibiting a motor response into one experiment, thus averaging the contrast maps of a sample and adjusting the variance. For this study, we included studies contrasting no-go activation with go/baseline/rest periods which allowed accounting for all potential regions that may be critical in motor response inhibition, including those involved in response selection. Both go/no-go and stop-signal tasks are weighted toward go stimuli in order to build up a prepotent tendency to respond and thereby reflecting an increased inhibitory effort necessary to successfully withhold responding to no-go stimuli.

State anger studies were included when results reflected an intent to aggress (i.e., an anger-driven response to provocation or unfairness such as “punishment > control” or “high punishment > no/low punishment” derived from tasks such as the Taylor Aggression Paradigm, point subtraction aggression game, ultimatum/dictator game, third-party punishment, etc.). The common denominator across these tasks is that they require inhibitory control over a dominant response and that they rely on the context-dependent initiation of a behavioral alternative (i.e., perform nondominant response or not respond at all). Although for SA studies we meta-analyzed experiments reporting proxies of anger expression (i.e., punishment > no punishment), this does not mean that the execution of punishment is identical to failures in affective inhibition given that the decision to punish is self-initiated. The rationale for examining the overlap between successful response inhibition and state anger is twofold. First, despite the described link between response inhibition and state anger, findings do not imply a direct causal relationship between impaired response inhibition and anger expression in healthy individuals. Instead, they emphasize a relationship between response inhibition efficiency and retaliatory behaviors, as response-

inhibition efficiency correlates well with treatment outcome in a range of neurological and psychiatric disorders (Verbruggen et al., 2019). For instance, emotional go/no-go tasks showed that anger-related words increase response latencies compared to neutral words (Xia et al., 2018) and that this is further mediated by trait anger scores (Pawliczek et al., 2013). Other studies, however, report improved inhibitory performance after exposure to negative stimuli (Pessoa et al., 2012) or no inhibitory effects whatsoever (Chamberlain et al., 2007; Gole et al., 2012; Hare et al., 2005). And second, failures in inhibiting prepotent/ongoing dominant responses are associated with post-error slowing followed by a transitory period of reactive adjustment and error-monitoring (Verbruggen & Logan, 2008; Ornstein et al., 2009; Schachar et al., 2004). Therefore, increased latencies and neural activity after inhibition errors in go/no-go and stop-signal tasks are not only related to the inability to withhold a response but also include error monitoring and allocation of additional executive resources (Norman & Shallice, 1986; Schachar et al., 2004). When errors occur, participants likely experience a subjective feeling of failing that is not necessarily present in the expression of state anger. Nonetheless, it is crucial to emphasize that we cannot rule out that false alarms, thus not succeeding in a specific task, might also correspond to feelings of error awareness, failing, mental overcompensation, and negative emotions such as irritation and anger. Altogether, as failed response inhibition contrasts (i.e., no-go/stop) are quite heterogeneous (and oftentimes not reported within the publications) we would likely capture performance monitoring activities during go/no-go and stop-signal tasks that overlap partially yet not completely with brain regions involved in response inhibition (i.e., the right anterior insular cortex and right superior frontal gyrus; Menon et al., 2001). Nevertheless, as a control measure, we calculated a failed RI meta-analysis to check for overlap between successful/failed inhibition and state anger.

We only included findings from healthy individuals and excluded between-group (i.e., clinical group vs. healthy subjects) results if findings were unavailable separately. Consistent with recommendations from Müller et al. (2018), we only included experiments reporting results of whole-brain group analyses corresponding to standard stereotactic reference spaces (MNI, Talairach/Tournoux). TAL-space coordinates were MNI-transformed using the icbm2tal transformation (Laird et al., 2010) and used to estimate voxel-wise activation likelihood. We excluded region-of-interest (ROI) results because the activation-likelihood estimation (ALE) algorithm relies on the *a priori* assumption that each voxel is equally likely activated (Eickhoff et al., 2009). ROI findings would, therefore, bias the results toward user-defined brain regions, restricting highly significant convergent functional activity to predefined anatomical locations. Last, to avoid within-experiment or within-group effects, we treated contrast-specific coordinates derived from the same experimental group as separate experiments (Turkeltaub et al., 2012). Data from 5,249 subjects and nine different tasks were included in the analyses. Tasks used visual or auditory inputs, and several kinds of stimuli including pictures, tones, letters, words, moving scenarios (i.e., video games). An overview of all included experiments, study characteristics, and contrasts employed per each experiment included in the meta-analysis is

available in Table S1 in the supplementary files. Altogether, 194 studies met the inclusion criteria and were included in this meta-analysis (Figure 1 cf., PRISMA guidelines; Moher et al., 2009).

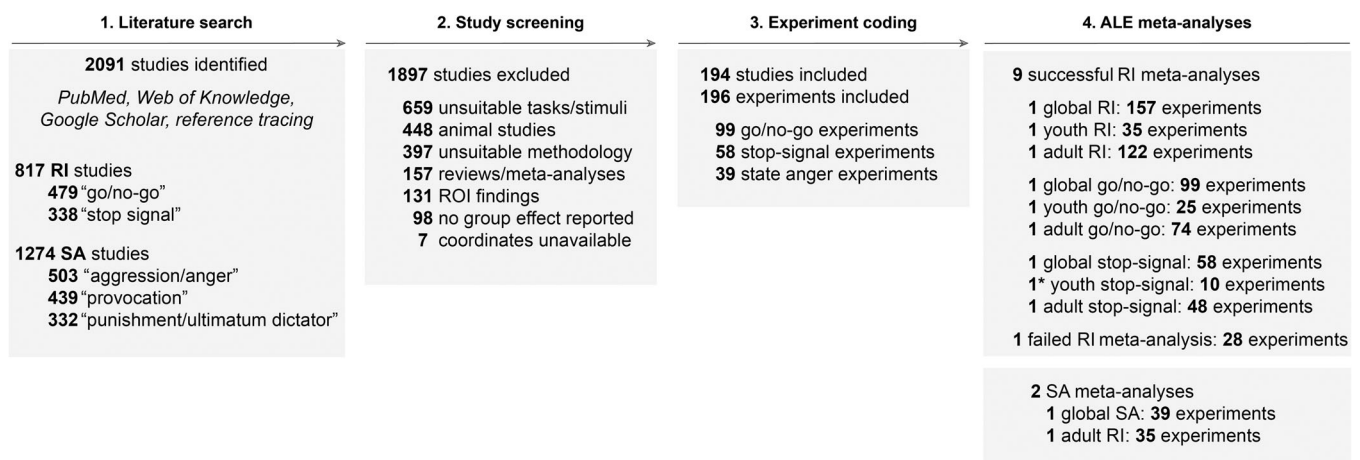
## 2.2 | Meta-analytic design

We computed five main meta-analyses: one global analysis for successful response inhibition across subjects and tasks, one for go/no-go tasks, one for stop-signal paradigms, one for failed response inhibition, and one for state anger. We calculated a separate SA meta-analysis for adults only that we report in the supplementary file. Given dynamic changes in brain maturation characterized by structural and functional reorganization processes taking place throughout adolescence and into early adulthood (Gogtay et al., 2004; Nigg, 2017), we additionally calculated meta-analyses for youths (aged 10–21) and adults (aged 21 and older) globally across all response inhibition experiments as well as separately for go/no-go and stop-signal tasks. This age criterion was selected based on thorough evidence that brain maturation continues to develop until the beginning of the third decade of life (Giedd et al., 1999) and that adolescents aged 18–21 years show diminished cognitive control under brief and extended negative emotional arousal relative to adults aged above 21 years (Cohen et al., 2016). We report the results of the go/no-go and stop-signal analyses separately in the supplementary file. Due to the limited number of studies (Eickhoff et al., 2016) we were unable to compute age-dependent state anger meta-analyses. Twelve meta-analyses were computed in total.

## 2.3 | Activation-likelihood estimation

Topographic convergence was assessed using the revised algorithm for coordinate-based ALE meta-analyses (Eickhoff, Laird, Fox, Lancaster, & Fox, 2017; Turkeltaub et al., 2012). The method identifies

functional convergence across experiments where activation changes differ significantly to an expected random spatial null distribution. Maxima  $x,y,z$  peaks pooled from all included studies are treated as centers of 3D normal probability distributions accounting for inherent neuroimaging spatial uncertainty (Eickhoff et al., 2009, 2016). The three-dimensional probabilities of activation foci are then combined for each voxel yielding a modeled activation map containing voxel-wise ALE scores (Turkeltaub et al., 2012). The union of these maps yields the functional overlap at each voxel which is further tested for true convergence. In other words, it assesses whether between-experiment convergence occurs above chance level by comparing ALE scores against the empirical null-hypothesis of spatially independent brain activations (Turkeltaub et al., 2012). In ALE terminology, an experiment refers to individual results from neuroimaging contrast analyses yielding maxima peaks, while a study denotes a scientific publication reporting at least one experimental result (Laird et al., 2005). Statistical parametric conjunction maps were submitted to statistical significance testing using a cluster-level family-wise error (cFWE) correction ( $p < .05$ ) with an uncorrected cluster-forming threshold of  $p < .001$  using 5,000 permutations. Put differently, ensuing suprathreshold clusters were compared against a null distribution of 5,000 simulated datasets with random foci location but otherwise identical properties as the original foci (i.e., number of foci). The cFWE correction was preferred over the false discovery rate or the overly conservative voxel-wise FWE correction as it provides the best trade-off between sensitivity and specificity in detecting true effects (Chumbley & Friston, 2009; Eickhoff et al., 2016). Last, although we were primarily interested in the overlap between response inhibition and state anger, we additionally performed difference analyses that allowed identifying areas of activation which converged significantly more for either response inhibition or state anger studies and vice-versa. Ensuing clusters were anatomically labeled using the SPM Anatomy Toolbox 2.2c (Eickhoff et al., 2005, 2007).



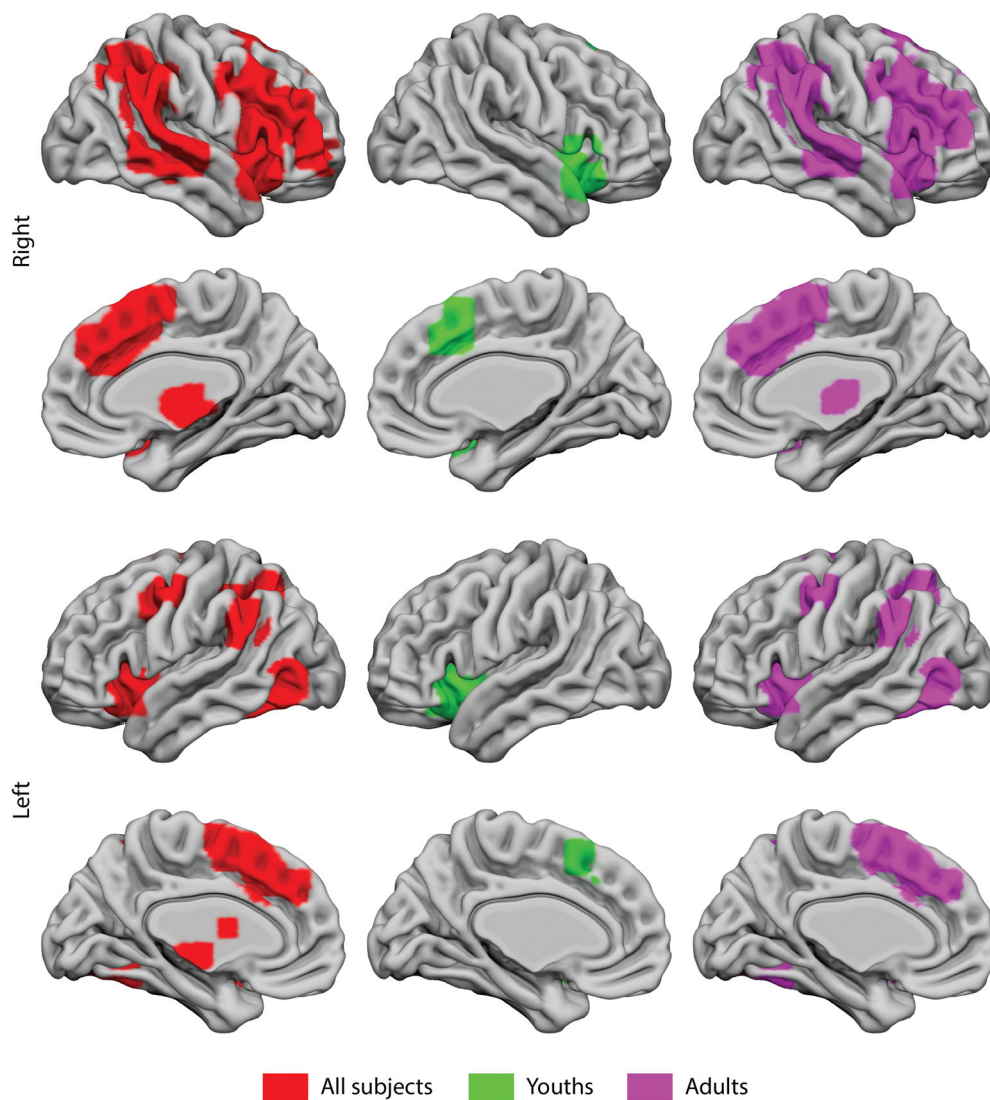
**FIGURE 1** Flowchart of the different meta-analytic steps (cf., PRISMA). In total, 12 meta-analyses including 157 response inhibition and 39 state anger experiments were calculated. \* indicates the meta-analysis fell short of the recommended experiment sample size for detecting true effects. ALE, activation likelihood estimation; RI, response inhibition; ROI, region of interest; SA, state anger

### 3 | RESULTS

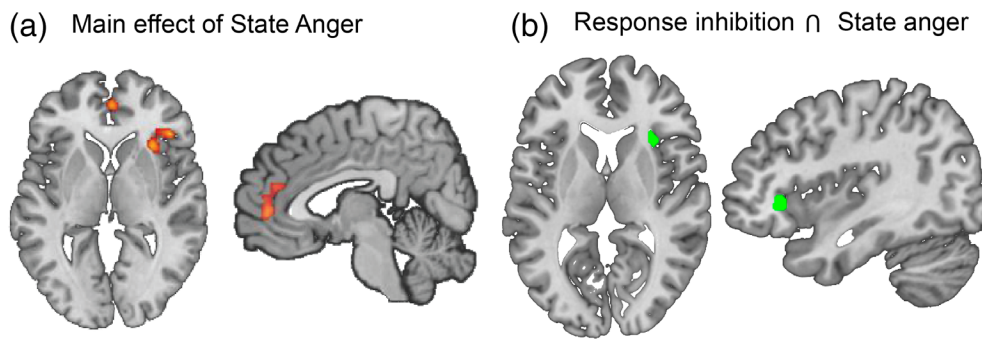
*Main effect of successful response inhibition* (157 experiments, 4,172 subjects). The meta-analysis across all subjects, go/no-go, and stop-signal tasks showed consistent activity in eight clusters comprising a frontoparietal network including the right ventrolateral and right dorsolateral prefrontal cortices (VLPFC, DLPFC), bilateral medial prefrontal and bilateral insular cortices, bilateral inferior parietal lobule (IPL) and bilateral precentral gyrus. Moreover, left-lateralized activity was found in the dorsal striatum, fusiform gyrus, and superior parietal lobule (SPL; Figure 2; Table S1 in the supplementary file). *Youths* ( $M_{\text{age}} = 14.4 \pm 2.3$  years; 35 experiments, 1,218 subjects) showed convergent activity in the right midcingulate and medial prefrontal

cortices, bilateral IFG, temporal poles, and in the left insula. *Adults* ( $M_{\text{age}} = 29.8 \pm 7.4$  years; 74 experiments, 1,525 subjects) rely on a more spread-out network including the right VL/DLPFC, right midcingulate cortex, right superior temporal gyrus (STG), bilateral mPFC and insular cortex, bilateral IPL, and bilateral precentral gyrus. Further convergent activity was found in the left SPL, left occipital and fusiform gyri, as well as in the left putamen. The meta-analytic results of the go/no-go and stop-signal tasks are available in the supplementary file.

*Main effect of failed response inhibition* ( $n = 28$  and 644 subjects) showed consistent activity in four clusters comprising the anterior cingulate gyrus, bilateral anterior insula cortex, the left IFG, supramarginal, and angular gyri (Figure S1).



**FIGURE 2** Convergent response inhibition clusters across subjects and tasks (collapsed across go-no/go and stop-signal tasks). The overall ALE analysis (red) shows a broad frontoparietal network extending into temporo-occipital areas that serves successful response inhibition. Sub-analyses in youths (green) showed convergent activity in midcingulate and medial prefrontal areas, left al/ IFG, and the temporal poles, while adults (magenta) rely on a distributed frontoparietal network responsible for adequate inhibitory control. Results survived cluster level FWE correction for multiple comparisons ( $p < .05$ , cluster forming threshold at voxel level  $p < .001$  using 5,000 permutations; ALE scores ranged from a minimum value of 0.022–0.051). ALE, activation likelihood estimation; FWE, family-wise error (correction)



**FIGURE 3** (a) Main effect of state anger. Meta-analyzing state anger experiments yielded two clusters of convergent activity in the anterior cingulate cortex and the right al/IFG. (b) Conjunction analysis between successful response inhibition and state anger. The right al/IFG was the only ensuing cluster following response inhibition—state anger conjunction analyses. Results survived a cluster-level  $p < .05$  family-wise error-corrected for multiple comparisons, cluster-forming threshold  $p < .001$  at voxel level. al, anterior insula; IFG, inferior frontal gyrus

### 3.1.1. | Main effect of state anger

Consistent activation across 39 experiments typifying state anger ( $n = 1,084$  individuals) was found in two clusters: one cluster (peak MNI: 2, 48, -2;  $k = 273$  voxels) comprising the bilateral anterior cingulate cortex (ACC), paracingulate and superior frontal gyri and a second cluster (peak MNI: 44, 28, -2;  $k = 215$  voxels) in the anterior insula (a) and the pars triangularis division of the IFG (Figure 3A; Table S5).

### 3.1.2. | Conjunction analyses

We ran a minimum conjunction analysis across the main effect ALE maps of response inhibition and state anger. Analyses revealed significant convergence in one cluster ( $k = 177$  voxels) comprising the right insular cortex (peak MNI: 32, 20, 2) and the pars triangularis of the right IFG (peak MNI: 44, 28, -2). The same cluster emerged for the conjunction between state anger and adult response inhibition as well as between state anger and the overall stop-signal sub-analysis. The conjunction analysis between state anger and the go/no-go sub-group revealed a smaller cluster ( $k = 125$  voxels) in the right insular cortex (peak MNI: 32, 20, 2) extending into the pars triangularis of the right IFG (MNI: 40, 30, -4). The same cluster emerged for the conjunction between state anger and go/no-go and stop-signal adult subsample (Figure 3B). As anticipated, the conjunction analysis between failed inhibition and state anger yielded two clusters of convergent activity in the anterior cingulate and paracingulate gyri and in the right anterior insula that partially overlap with the findings from the successful inhibition—state anger conjunction analyses.

### 3.1.3. | Difference analyses

Global response inhibition (across all subjects and tasks) in contrast to state anger tasks revealed stronger convergence for response inhibition in the temporal and frontal poles. For the adult go/no-go in contrast to state anger tasks, the middle frontal gyrus was identified, whereas for the adult stop-signal in contrast to state anger, the super

frontal gyrus was revealed. Table S6 and Figure S2 in the supplementary file show the results of the difference analyses.

## 4 | DISCUSSION

In this study, we used coordinate-based ALE meta-analyses to revisit and update the neural correlates of motor response inhibition, to determine a consistent neural architecture of state anger, and to identify their joint and disparate neural networks. We included data from 196 experiments where 157 investigated response inhibition using go/no-go and stop-signal paradigms and 39 investigated state anger. Our results replicate and extend previous meta-analytic findings on response inhibition revealing a broad bilateral frontoparietal network including the al/IFG, premotor and midcingulate cortices, as well as a strong right-lateralized temporoparietal convergent activity. For youths, the meta-analysis revealed convergent activity in right midcingulate and medial prefrontal areas, left al, and right IFG. The meta-analysis on state anger showed that bilateral ACC and right al/IFG underlie transient anger. Conjunction analyses revealed the right al/IFG as the only consistent cluster of overlap between successful and failed response inhibition and state anger. These results suggest that, while frontoparietal networks and the bilateral al is ubiquitously recruited during generic inhibitory control, the right al/IFG cluster represents a potential node in a network facilitating the execution of goal-directed behaviors under highly unpredictable scenarios.

### 4.1 | Response inhibition

Our updated meta-analysis on experiments reporting brain activity during successful response inhibition (157 experiments relative to 56 experiments in Cieslik et al. 2015 and 102 experiments in Swick et al., 2011) replicated previous meta-analytic findings. We found convergent activity in a frontoparietal network comprising the pre-SMA/MCC, al/IFG, right VL- and DLPFC, right TPJ, right intraparietal sulcus

(IPS), right thalamus, and the left dorsal striatum. This network likely represents a set of mutually interacting regions engaged in domain- and process-general top-down inhibitory control (Camilleri et al., 2018; Müller, Langner, Cieslik, Rottschy, & Eickhoff, 2015). These regions may coordinate the activity of other specialized networks (Smallwood, Brown, Baird, & Schooler, 2012) and are involved in the initiation and adjustment of inhibitory control by processing salient information (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). The involvement of the pre-SMA/MCC and basal ganglia in inhibitory control has been consistently reported across the literature. The former has been associated with higher-level motor control including monitoring and regulating task-specific motor output (Nachev, Kennard, & Husain, 2008). The latter is typically involved in motor execution and forms a putative cortico-basal ganglia-thalamocortical circuit (Wei & Wang, 2016). Recent evidence, however, extends the functional fingerprint of the basal ganglia and argues for its role in multi-domain, somatosensory, cognitive, and motivational processing (Guo et al., 2018).

In youths, our findings highlight a core response inhibition network comprising the bilateral aI/IFG and the right cingulate cortex. Although during stop-signal task performance youths also recruit the left aI, the bilateral aI/IFG hub remains a core node maintained and augmented throughout adulthood. The emergence of these two clusters in youths is likely mediated by a lack of convergence across the included studies reflected in a diffuse network that supports response inhibition across childhood and adolescence. Nonetheless, these findings are consistent with longitudinal data showing developmental changes in prefrontal cortex activity regarding response inhibition (Gogtay et al., 2004; Zhou et al., 2016). Throughout adolescence, response inhibition is supported by diffuse frontoparietal activity that gradually shifts to rather focal prefrontal loci in line with cognitive maturation (Luna et al., 2010). Resting-state functional networks show a functional reorganization with age inasmuch as frontoparietal connections responsible for implementing adaptive control on a trial-by-trial basis strengthen throughout adolescence, while a parallel cingulo-opercular network implementing set-maintenance is still missing most of its connections until early adulthood (Fair et al., 2007). Undergoing constant development throughout childhood and adolescence, these systems are less efficient during response inhibition relative to those of adults and reflect ontogenetic maturation lags (Konrad & Eickhoff, 2010). Although not relying on the strong focal activity observed in adults' canonical inhibition networks, most adolescents still successfully regulate their behaviors (Tompson et al., 2018). Bottom-up processing facilitated by the mPFC and temporal areas with adequate rule-based top-down control gradually support the formation and maintenance of control networks (Dosenbach et al., 2007).

Generally, motor inhibition shows developmental changes in prefrontal activity that coincide with cortical maturation and the ability to adapt to internally generated error-related feedback (McCormick & Telzer, 2018). The latter is associated with MCC activity. Although the anterior MCC has often been labeled as dorsal ACC, the two structures are structurally and functionally distinct (Palomero-Gallagher,

Vogt, Schleicher, Mayberg, & Zilles, 2009). Findings suggest that the MCC is associated with interference in information processing (Laird et al., 2005) and with the evaluation of ongoing performance rather than with executive control *per se*. For example, during Stroop tasks, MCC activity increases first followed by an increase in prefrontal activity triggering a behavioral response (Kerns et al., 2004). Likewise, the higher the cognitive load during stop-signal tasks, the more activity is observed in the inferior frontal cortex but not in the MCC. Instead, the latter likely accounts for error and performance monitoring (Chevrier, Noseworthy, & Schachar, 2007; Matthews, Simmons, Arce, & Paulus, 2005).

## 4.2 | Does the right aI/IFG–ACC network support an anger state?

We found consistent activation for tasks eliciting an anger state in a network comprising the bilateral ACC and right aI/IFG. Although the aI and ACC are jointly activated in response to basic emotions, both are also involved in higher-order emotional processing (i.e., romantic love or social ostracism; Eisenberger, Lieberman, & Williams, 2003; Moor et al., 2012). Rather than merely being involved in emotion processing, the aI and ACC belong to the salience network and are involved in decoding incoming information in preparation for action execution (Menon & Uddin, 2010; Uddin, 2015).

Functionally heterogeneous, the insular cortex is an important node in a network mediating inhibitory control (Cieslik et al., 2015; Nelson et al., 2010). It also plays a role in multimodal sensory information processing as well as in intrinsic homeostatic integration (Uddin, 2015) in a posterior–anterior functional gradient (Craig, 2009). Specifically, while acute emotions are encoded posteriorly, abstract cognitive processes are represented in the most anterior parts of the insular cortex (Uddin, Kinnison, Pessoa, & Anderson, 2014). Basic anterior insula mechanisms include bottom-up detection of cross-modal salient events, switching between task-relevant brain areas to facilitate access to attention and working memory, and coupling with the ACC to allow reflexive access to the motor system (Dosenbach et al., 2007; Menon & Uddin, 2010). Similarly parcellated, the rostral-ventral ACC reportedly encodes top-down emotion regulation, while dorsal-caudal ACC is involved in the (re)appraisal of negative emotion (Etkin, Egner, & Kalisch, 2011). Together with convergent activity in middle frontal and paracingulate gyri, our findings are consistent with literature suggesting that greater integrity and thus higher functional efficiency of the salience network facilitates the processing of unexpected emotionally salient events, thus preparing individuals to take decisions accordingly. Considering our conceptualization of state anger (including spiteful and altruistic anger), the role of the ACC and rAI/IFG goes beyond supporting a reaction to anger elicitation. Instead, this network may facilitate quick cognitive reorganization during unpredictable scenarios loaded with expectancy violations. Alternatively, this cluster might facilitate compensatory actions to ensure goal attainment. Thus, instead of retaliating following provocation, it is likely that we aim to retrieve alternative thoughts, memories,



or behaviors. However, given high unpredictability, these alternatives might be too weak to overrule a “hot” decision (Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Shackman et al., 2011). It is plausible, therefore, that these perception-action loops bias adaptive responding in affective processing and motor execution hubs (Shackman et al., 2011). This idea fits well with earlier models suggesting the AI represents an input hub for a self-awareness system that projects global emotional states into the ACC which then selects and prepares appropriate responses (Medford & Critchley, 2010).

Deficits in adaptively regulating emotional and cognitive responses are prominent in most neuropsychiatric disorders with consequences ranging from personal distress to societal and healthcare implications. Our findings align to ongoing efforts in psychiatry to determine if cognitive markers of brain dysfunction, such as anger expression or response inhibition may be promising candidate endophenotypes (i.e., unaffected siblings of ADHD-diagnosed individuals also show relative inhibitory deficits compared to neurotypical controls; Durston et al., 2003). Furthermore, as self-regulation impairments typically decrease the effectiveness of therapeutic interventions, our findings support the idea of integrative treatment approaches aimed at strengthening executive functions alongside conventional therapeutic strategies (Aupperle et al., 2012). Likewise, inhibitory control training using modified versions of the go/no-go paradigm influenced lead to decreasing alcohol intake in a group of alcohol users (Houben et al., 2011) or decreasing impulsivity in patient groups with eating disorders (Houben & Jansen, 2015). As emotion regulation deficits may originate in a dysfunctional ability to process and attend to incoming stimuli, it remains unclear whether response inhibition and emotion regulation represent a unitary deficit manifested across varying contexts or whether they function synergistically to ensure adequate self-regulation.

### 4.3 | Right AI/IFG: relay station for higher-order cognition?

Conjunction analyses between state anger and (successful and failed) response inhibition modeled activation maps revealed convergent activity in a cluster comprising the right AI/IFG. Early hypotheses argued that the right inferior frontal cortex (IFC incl. the rAI/IFG) is a dedicated response inhibition module (Aron, 2011) downregulating the activity of motor control networks (Aron & Poldrack, 2006). While there is strong evidence supporting the “braking” role of the rIFG when pausing or stopping is required (Aron, 2011; Aron, Robbins, & Poldrack, 2014), other findings link rIFG activity to broader inhibitory processes including response inhibition during speech processing (Neef et al., 2016), word comprehension (Lai, van Dam, Conant, Binder, & Desai, 2015), or working memory control (Marklund & Persson, 2012). Thus, instead of being a dedicated response inhibition hub, the rIFG rather supports general inhibitory processes ensuring quick and dynamic exchanges between domain-general multiple-demand networks (Camilleri et al., 2018; Dosenbach et al., 2007).

Additionally, the rAI/IFG encodes integrated representations of temporary emotional awareness (Craig, 2009) as part of a ventral network that processes incoming sensory information. This ventral network is thought to narrow the spatial and temporal focus, thereby dynamically adjusting processing, action control, and awareness (Tops & Boksem, 2011). In other words, the rAI/IFG might quantify information about resource availability combined with internalizing environmental information (Tops & Boksem, 2011; Tops, Boksem, Wester, Lorist, & Meijman, 2006) to facilitate fast and opportunistic actions. The rAI/IFG, thus, monitors whether ongoing or planned behaviors are still adequate to achieve expected goals and then signals the ACC the need to adapt responses when cognitive schemas are challenged (Tops & Boksem, 2011). The rAI/IFG supports swift computational processes across most if not all goal-directed behaviors and flags salient events in time and space for subsequent processing (Dosenbach et al., 2008). This idea fits well with the orienting function of the rAI/IFG as part of the salience network, ensuring dynamic switching between external and internal control modalities during unpredictable emotionally-laden scenarios (Menon & Uddin, 2010; Tops & Boksem, 2011). Corroborating all evidence, it appears that the rAI/IFG is involved in monitoring cue and target events and ensures updating and executing a corresponding action plan which corresponds with the notion that the rAI/IFG is *de facto* a relay station for higher-order cognition.

### 4.4 | Limitations and recommendations for future research

The current findings should be considered in light of several limitations. First, although minimizing heterogeneity across our input data by applying stringent inclusion criteria (i.e., selecting and including similar paradigms, imaging contrasts), the included fMRI studies varied concerning specific imaging thresholding options, analysis software packages, or degree of smoothing. Second, due to the limited number of studies typifying state anger, we were unable to parse out the state anger results by age group (i.e., youths vs. adults). Likewise, considering the limited availability of studies reporting stereotactic coordinates for spiteful and altruistic punishment separately in healthy individuals, we pooled the two punishment modalities into the expression of state anger meta-analysis. Future endeavors should disentangle the shared and distinct neural correlates of spiteful and altruistic punishment. Similarly, the stop-signal task youth analyses were likely underpowered considering recommendations for performing ALE meta-analyses advise for a minimum of seventeen experiments (Eickhoff et al., 2016). Nevertheless, this meta-analysis yielded a small but reliable AI/IFG cluster that coincides with available literature. Third, both go/no-go and stop-signal tasks do not typically include adequate controls for non-inhibitory demands. Specifically, because the same stimuli are used for go and no-go/stop signals, the “no-go/stop > go” contrast might introduce the confound of subjects’ degree of familiarity to the experimental stimuli. Our analyses, however, aimed to identify the most reliable network of overlap supporting basic response

inhibition irrespective of additional confounds. Furthermore, our findings coincide with previous meta-analytic results indicating a strong role of the al/IFG and confirming the role of the pre-SMA in response inhibition. Fourth, the influence of sex differences in the neurobiology of inhibitory control, however, is less clear, with mixed evidence suggesting either increased inhibitory activity and efficiency in women relative to men (Garavan et al., 2006) or the opposite (Li et al., 2006). Such inconsistencies might be attributable, for instance, to estrogen or menstrual cycle hormonal fluctuations (Amin et al., 2006). As ALE methodology does not currently allow performing meta-regressions and considering that the included studies rarely reported within-sex neural correlates, future studies should strive to highlight sex-specific distinct and shared neural networks of response inhibition and state anger. Last, as computing classical effect-size meta-analyses was beyond the scope of this article, future studies using a mixed coordinate- and image-based meta-analytic approaches are warranted to tease apart study idiosyncrasies that might be the driving force between cross-sectional studies reporting heterogeneous brain activation patterns.

## 4.5 | Conclusions

The present study used ALE meta-analyses to identify the shared and distinct neural correlates of motor response inhibition and state anger in healthy individuals. Response inhibition was associated with a distributed frontoparietal network including ventrolateral and dorsolateral prefrontal cortices, the anterior insula, and inferior frontal gyrus. State anger, on the other hand, reliably recruits the right al/, and anterior cingulate cortex. Conjunction analyses between response inhibition and state anger yielded a convergent activity cluster in the right al/IFG which likely represents a relay station for higher-order cognition. Altogether, these results suggest that a dynamically-adjusting, task-dependent multiple-demand processing network is involved in both response inhibition and state anger.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

Andrei A. Puiu and Kerstin Konrad designed the study. Andrei A. Puiu performed the database search, data analysis, interpretation, and wrote the manuscript. Andrei A. Puiu, Olga Wudarczyk, Gregor Kohls, Danilo Bzdok, Beate Herpertz-Dahlmann, and Kerstin Konrad revised the manuscript critically for intellectual content. All authors contributed to and approved the final manuscript version.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon request from the corresponding author.

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