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# Regulatory behavior and frontal activity: Considering the role of revised-BIS in relative right frontal asymmetry

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**Abstract**

Essential to human behavior are three core personality systems: approach, avoidance, and a regulatory system governing the two motivational systems. Decades of research has linked approach motivation with greater relative left frontal-cortical asymmetry. Other research has linked avoidance motivation with greater relative right frontal-cortical asymmetry. However, past work linking withdrawal motivation with greater relative right frontal asymmetry has been mixed. The current article reviews evidence suggesting that activation of the regulatory system (revised Behavioral Inhibition System [r-BIS]) may be more strongly related to greater relative right frontal asymmetry than withdrawal motivation. Specifically, research suggests that greater activation of the r-BIS is associated with greater relative right frontal activity, and reduced r-BIS activation is associated with reduced right frontal activity (greater relative left frontal activity). We review evidence examining trait and state frontal activity using EEG, source localization, lesion studies, neuronal stimulation, and fMRI supporting the idea that r-BIS may be the core personality system related to greater relative right frontal activity. In addition, the current review seeks to disentangle avoidance motivation and r-BIS as substrates of relative right frontal asymmetry.

**KEYWORDS**

cognitive control, executive function, hemispheric differences/laterality, motivation

## 1 | INTRODUCTION

Fundamental to organism behavior is the drive to move toward or away from a stimulus. Approach, withdrawal, and regulatory control lie at the heart of major theories of personality and temperament (Carver, 2008; Depue & Collins, 1999; Elliot & Thrash, 2002; Gray, 1970; Gray & McNaughton, 2000; Rothbart, Ahadi, & Evans, 2000). These systems are thought to underlie human behavior as stable individual differences (Carver, 2008; Depue & Collins, 1999; Elliot & Thrash, 2002; Gray, 1970). As a personality trait, these systems appear to be stable from early childhood into adulthood (Kochanska & Knaack, 2003; Luengo Kanacri, Pastorelli, Eisenberg, Zuffianò, & Caprara, 2013; Rothbart, Ahadi, & Evans, 2000). Although differences exist in the labels of these systems between theoretical models, there is agreement on the triumvirate nature of approach motivation, avoidance motivation, and regulatory control supervising the motivational systems. Past biological models have linked approach and avoidance motivation with left and right frontal activity, respectively. However, we review a large body of evidence suggesting that regulatory control is associated with right frontal activity.

## 2 | DEFINITIONS OF MOTIVATIONAL AND REGULATORY SYSTEMS

Approach motivational responses have been theorized to be part of a behavioral approach system (BAS; Gray, 1970, 1987; Gray & McNaughton, 2000), behavioral activation system (also BAS; Fowles, 1987), behavioral facilitation system (Depue & Collins, 1999), and goal-approach system (Carver & Scheier, 2008; Elliott, 2008). For the current review, the system governing approach motivation will be labeled the Behavioral Approach System (BAS), based on Gray and McNaughton's Revised Reinforcement Sensitivity Theory (RST; Gray & McNaughton, 2000). BAS is posited to be sensitive to reward signals and averting punishment (Gray, 1970). Activation of BAS is thought to engage goal pursuit and generate anticipated positive affect of goal attainment (Carver & Scheier, 2008). Broadly, the BAS has been related to optimism, reward responsiveness, and extroversion. Hyperactivation of the BAS has been linked with psychopathologies such as addictive behaviors, high-risk impulsive behaviors, and mania (Black et al., 2014; Harmon-Jones, 2004; Nusslock, Walden, & Harmon-Jones, 2015). In contrast, hypoactivation of the BAS has been linked with unipolar depression (Davidson, Pizzagalli, Nitschke, & Putnam, 2002; Diego, Field, & Hernandez-Reif, 2001; Stewart, Bismarck, Towers, Coan, & Allen, 2010).

Withdrawal motivational responses have been theorized to be part of an avoidance system and has been referred to as a behavioral inhibition system (BIS; Carver & White, 1994; Gray, 1970, 1987), fight-flight system (Gray, 1970), flight-fight-freeze system (Gray & McNaughton, 2000), and threat avoidance system (Carver & Scheier, 2008; Elliott, 2008). Gray substantially revised his conceptualization of the behavioral inhibition system and fight-flight systems, proposing the fight-flight-freeze (FFFS) and the revised-BIS systems (r-BIS; Gray & McNaughton, 2000). For the current review, the system governing withdrawal motivation will be labeled the Flight-Fight-Freeze System (FFFS), based on Gray and McNaughton's RST Theory (Gray & McNaughton, 2000). FFFS responds to signals of punishment and nonreward by increasing readiness for action (arousal level) and increasing attention to threatening environmental stimuli (Gray, 1987). Thus, it is thought to respond to potential punishment, nonreward, and fear-related stimuli in order to direct active avoidance, defensive behaviors, and increased attention to aversive stimuli. As such, FFFS was posited to be associated with negative affect (Gray, 1970). Hyperactivation of the FFFS is thought to be linked with phobias, as well as unipolar depression (Carver, Johnson, & Joorman, 2008).

Biological models of approach, avoidance, and regulatory systems have focused primarily on the system of approach/BAS and avoidance/FFFS (Carver, Johnson, and Joorman, 2008; Caspi, Roberts, & Shiner, 2005; Depue & Collins, 1999; Elliott & Thrash, 2002; Fowles, 1993; Gray, 1994; Harmon-Jones, Gable, & Peterson, 2010; Rothbart & Hwang, 2005; Rutherford & Lindell, 2011). Well-established models investigating BAS and FFFS have investigated asymmetrical activation of the frontal cortex. This work suggests that the left and right frontal cortical regions are asymmetrically related to approach and avoidance motivational and emotional (emotive) tendencies. Greater trait approach is associated with greater left frontal activation (Amodio, Master, Yee, & Taylor, 2008; Coan & Allen, 2003; De Pascalis, Cozzuto, Caprara, & Alessandri, 2013; Gable & Harmon-Jones, 2008; Harmon-Jones, 2006; Harmon-Jones & Allen, 1997; Harmon-Jones et al., 2010; Harmon-Jones, Peterson, & Harris, 2009; Harmon-Jones & Sigelman, 2001; for review, see **Harmon-Jones & Gable, 2018**) and greater trait inhibition/withdrawal is associated with greater right frontal activation (Balconi, 2011; Balconi & Mazza, 2009; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009; Sutton & Davidson, 1997).

## 2.1 | Revisions to BIS and FFFS

In Gray and McNaughton's revised theory, they proposed three systems: BAS as the approach system, FFFS as the withdrawal system, and a revised-BIS as the regulatory system resolving conflicts between these two systems. BAS remained mostly unchanged. FFFS was proposed to engage in response to fear, facilitate escape and avoidance behavior, and relate to clinical disorders such as phobia and panic (Gray & McNaughton, 2000). Gray and McNaughton's revised RST has received significant attention in the literature and has been widely supported as a more accurate model than his original model (Berkman, Lieberman, & Gable, 2009; McNaughton & Corr, 2004; Smillie, Pickering, & Jackson, 2006).

The revised-BIS system underwent the biggest changes in revised RST. Gray's original theory did not emphasize the function of the BIS as controlling urges of approach and avoidance motivations. However, in Gray and McNaughton's updated theory, the revisions made to BIS repositioned the system to "control not only behavioral inhibition, but also risk analysis" (Gray & McNaughton, 2000, p. 44). The revised BIS was theorized to be responsible for detection and resolution of conflicts between various systems. Predominantly, the revised BIS was responsible for resolving conflict between the approach (BAS) and withdrawal (FFFS) systems, but it can also resolve BAS versus BAS conflicts and FFFS versus FFFS conflicts. The revised BIS was proposed to mediate these conflicts by enhancing negativity. Gray (2000, p. 291) noted that "So long as there is no goal conflict, the system does nothing directly to influence ongoing behaviour." To distinguish between the substantial differences between revised BIS and original BIS, this review will label revised BIS as "r-BIS" and the old BIS as "original BIS" (Jackson, 2009).

## 2.2 | The regulatory system

The theoretical changes made to r-BIS positioned it as a regulatory system governing conflicts between motivational systems. Activation of r-BIS results in enhanced attention to, memory for, and detection of affectively negative information. R-BIS is thought to alleviate tension between approach and avoidance systems by enhancing aversion of one behavior or the other (Heym, Ferguson, & Lawrence, 2008).

R-BIS is theorized to be essential to the BAS and FFFS in order to supervise, govern, and regulate motivation. Gray hypothesized that r-BIS regulates BAS and FFFS to orchestrate functional behavior (Carver, 2008; Gray, 1970; Gray & McNaughton, 2000; Rothbart et al., 2000). As such, r-BIS is related to behaviors of effortful control, constraint, self-control, inhibition, conflict monitoring, and error detection (Carver & Connor-Smith, 2010; Carver et al., 2008; Derryberry & Rothbart, 1997; Gray & McNaughton, 2000; Kochanska & Knaack, 2003; Nigg, 2006; Rothbart & Rueda, 2005). Although theorists have used different labels to describe regulatory behaviors governed by r-BIS, these regulatory behaviors relate to the control of motivational processes and fit within the scope of r-BIS functioning. In the current review, the term *r-BIS* will refer to the general scope of behaviors regulating motivational functions (Gray & McNaughton, 2000).

Broadly, r-BIS is thought to govern cognitive constructs of executive control and inhibitory function. This may result in suppression of a behavioral response or overriding motivational impulses (Aron, Robbins, & Poldrack, 2004, 2014; Carver & Connor-Smith, 2010; Hester & Garavan, 2004, 2009). The regulatory system is presumably superordinate to both approach and withdrawal systems (Ahadi & Rothbart, 1994). Low functioning r-BIS is thought to relate to reactive responsivity related to impulsive behavior, deficits in inhibitory control, and externalizing disorders such as substance abuse (Enticott, Ogloff, & Bradshaw, 2006; Logan, Schachar, & Tannock, 1997). On the other end, hyperfunctioning regulatory control is thought to relate to anxious inaction, passive avoidance, and internalizing disorders such as generalized anxiety disorder (Carver et al., 2008; DeYoung, 2015; Eisenberg et al., 2004; Rothbart, Ellis, & Posner, 2004; Strack & Deutsch, 2004; Valiente et al., 2003). Work by NcNaughton and colleagues (McNaughton, Swart, Neo, Baes, & Glue, 2013; Neo, Thurlow, & McNaughton, 2011) has focused on the anxiolytic properties of r-BIS. This work suggests that r-BIS is related to biological mechanisms activated during conflict-specific situations (e.g., stop signals in a Stop Signal Task). Also, r-BIS functioning is specifically impaired by a range of antianxiolytic drugs, suggesting specific biological mechanisms behind r-BIS.

Activation of r-BIS is consistent with past research outlining proactive and reactive control (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, 2012; Braver, Paxton, Locke, & Barch, 2009; Schmid, Kleiman, & Amodio, 2015). Reactive control refers to unconscious conflict monitoring processes. The reactive system manages conflict between goals and responses and is conceptually similar to Gray and McNaughton's r-BIS conflict detection function (Amodio et al., 2008). Proactive control is similar to reactive control. However, proactive control is thought to engage in top-down regulation and conscious deliberation. Proactive control is driven by goals and is associated with high-order capacities of effortful control. Despite the differences between reactive and proactive control, both processes regulate motivational urges and can be engaged when deciding between conflicting potential actions.

## 3 | FAILURES LINKING RIGHT ASYMMETRIC ACTIVITY AND FFFS

Despite evidence linking trait frontal activity with FFFS, many studies fail to replicate the finding that withdrawal is associated with greater trait or state right frontal activity (Amodio et al., 2008; Berkman & Lieberman, 2010; Coan & Allen, 2003; Coan, Allen, & Harmon-Jones, 2001; De Pascalis et al., 2013; Henriques & Davidson, 2000; Hewig, Hagemann, Seifert, Naumann, & Bartussek, 2004, 2006; Jackson et al., 2003; Keune, Bostanov, Kotchoubey, & Hautzinger, 2012; Kline, Blackhart, Woodward, Williams, and Schwartz, 2000; Pizzagalli, Sherwood, Henriques, & Davidson, 2005; Quirin, Gruber, Kuhl, & Düsing, 2013; Wacker, Chavanon, Leue, & Stemmler, 2008; Wacker, Chavanon, & Stemmler, 2010).[1] Indeed, recent models of frontal asymmetric activity have questioned the link between Gray's original conception of BIS as an avoidance system and greater right frontal activity (Coan & Allen, 2003; Düsing, Tops, Radtke, Kuhl, & Quirin, 2016; Wacker et al., 2010).

Failures to replicate the link between withdrawal motivation and greater right frontal activity have led researchers to speculate what might be causing these null relationships in human EEG studies. Some have suggested that the theoretical complexity of withdrawal motivation may confound experimental paradigms used to activate withdrawal

[1]Despite the numerous studies associating greater left frontal activity with approach motivation at the state level, there have also been some published failures to replicate the link between trait BAS and greater left frontal activity (Gable, Mechin, Hicks, & Adams, 2015; Neal & Gable, 2016, in press; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009; Wacker, Chavanon, & Stemmler, 2010). Some past research demonstrates that greater left frontal activity evoked by approach-motivated emotional states is related to individual differences in approach motivation (Gable & Poole, 2014; **Harmon-Jones & Gable, 2018**). The consistent relationship between state approach and left frontal activity suggests that the link between BAS and left frontal activity may be largely driven by situational context, such as emotional/motivation states. The relationship between individual differences in left frontal activity and BAS may be more pronounced in the context of emotional responses (Coan, Allen, & McKnight, 2006).

motivation (Amodio et al., 2008; Coan & Allen, 2004). This confound could be causing null relationships between greater right frontal activity and FFFS. For example, it is experimentally difficult to determine when active avoidance goals away from a threat may lead to approach goals toward safety. As such, pure avoidance states may rarely occur, making it difficult to evoke such states (Wacker, Heldmann, & Stemmler, 2003). However, it could also be the case that another personality system could underlie greater right frontal activity. The current review presents evidence suggesting that right frontal activity may be strongly related to regulatory processing of the r-BIS.

## 4 | EMPIRICAL EVIDENCE LINKING RIGHT FRONTAL ACTIVITY AND r-BIS

Despite much research examining the relationship between frontal asymmetric activity and motivational systems, few studies have examined the relationship between regulatory control (r-BIS) and frontal asymmetric activity (Gable, Mechin, Hick, & Adams, 2015; Grimshaw & Carmel, 2014; Neal & Gable, 2016; Wacker et al., 2003). R-BIS is superordinate to the motivational systems and regulates approach and withdrawal behaviors. Because motivational systems appear to be linked with frontal activity, r-BIS may share a similar association with frontal activity. The current review examines past evidence suggesting that r-BIS is asymmetrically related to frontal cortical activity. Specifically, greater functioning of r-BIS appears to be related to greater relative right frontal activity. In contrast, reduced functioning of r-BIS appears to be related to reduced relative right frontal activity.

In addition, the current article seeks to disentangle FFFS and r-BIS as substrates of relative right frontal activity. Similar to the perspective that r-BIS is closely related to relative right frontal activity, Wacker and Stemmler have suggested that right frontal activity is associated with a regulatory system they call BIS Anxiety (Wacker et al., 2008; Wacker et al., 2003). However, their model asserts that FFFS is unrelated to right frontal activity and is instead related to left frontal activity (Wacker et al., 2008). Based on the evidence we review below, we do not link avoidance with left frontal activity. The current article will discuss the relative contributions of r-BIS and FFFS as neural correlates of greater relative right frontal activity.

### 4.1 | Trait r-BIS and frontal EEG activity

Functioning of r-BIS is a stable individual difference measured by personality traits such as impulsivity, sensation seeking, and inhibition. Hyperactivation of r-BIS is marked by neuroticism and anxiety caused by passive avoidance, most commonly resulting from approach-avoidant conflicts (DeYoung, 2015). Hypoactivation of r-BIS is marked by unregulated approach or withdrawal behavior. Personality traits associated with inability to inhibit motivational tendencies are reflective of deficient r-BIS functioning. In particular, trait and behavioral impulsivity is thought to index inverse functioning of r-BIS because of its strong relation to deficits in inhibition, effortful control, and overall executive functioning (Bari & Robbins, 2013; Bickel, Jarmolowicz, Mueller, Gatchalian, & McClure, 2012; Eisenberg et al., 2004).

Research within our lab sought to determine whether impulsive personality traits were associated with trait frontal activity. Positive urgency is a measure of impulsivity reflecting failure of r-BIS to inhibit approach urges, thereby resulting in rash action during intense positive states (Cyders et al., 2010; Zapolski, Cyders, & Smith, 2009). Gable et al. (2015) collected resting EEG data from 126 participants to examine the association between positive urgency and frontal activity. Resting frontal EEG activity was recorded for eight minutes. A fast Fourier transformation extracted the alpha band (8–13 Hz), and a difference score was created between homologous frontal sites. Results revealed a robust relationship between positive urgency and greater relative left frontal activity. This evidence suggests that reduced relative right frontal activity is associated with diminished functioning of r-BIS. Using standardized low-resolution brain electromagnetic tomography (SLORETA; Pascual-Marqui, 2002), source localization results determined that the reduced relative right frontal activity was caused by diminished activity in the right inferior frontal gyrus (rIFG). Thus, reduced right frontal activity, rather than enhanced left frontal activity, was responsible for the observed asymmetrical activity.

One concern linking positive urgency and left frontal activity is that impulsivity may have been confounded with positive affect and approach motivation. Much past work has related positive affect and approach motivation to greater left frontal activity (see **Harmon-Jones & Gable, 2018**). Neal and Gable (2016) sought to address this confound by examining the relationship between frontal activity and facets of impulsivity unrelated to positive affect or approach motivation.

The authors sought to test the relationship between impulsive traits with resting frontal activity in 150 participants. Participants completed the UPPS-P scale assessing negative urgency, lack of premeditation, and lack of perseverance, as well as positive urgency (Cyders & Smith, 2007; Whiteside, Lynam, Miller, & Reynolds, 2005). Negative urgency (rash behavior in negative emotional contexts) related to greater resting left frontal activity (reduced right frontal activity), suggesting that positive emotionality was not driving the relationship between impulsivity and hemisphere asymmetry. Additionally, nonemotional impulsive traits (i.e., lack of premeditation and lack of perseverance) were associated with reduced right frontal activity. Controlling for trait approach motivation, the relationship between impulsivity and right frontal activity was unchanged. These results suggest that impulsivity, independent of affective valence, relates to reduced right frontal activity. Source localization for the relationship between these facets of impulsivity (positive urgency, lack of premeditation, and lack of perseverance) revealed reduced activity in right cingulate gyrus and right medial frontal gyrus.

In this sample, trait sensation seeking was not related to frontal activity. However, this null effect was likely the result of the type of sensation-seeking scale used in the study. The study used the UPPS-P measure of trait sensations seeking, which includes items like, "I would enjoy water skiing." The sensation-seeking scale often does not correlate well with the other subscales of the UPPSP, and other researchers have suggested that it may reflect a construct distinct from impulsivity (Simons, Dvorak, Batien, & Wray, 2010). However, another study (Santesso et al., 2008) measured trait sensation seeking using the Zuckerman Sensation Seeking Scale and found sensation seeking was related to greater left frontal (reduced right frontal) activity. This scale may be more conceptually related to the other UPPS-P subscales than the sensation-seeking subscale.

Together, these findings suggest that deficits in persistence and inhibiting behavior are related to reduced right frontal activity. Source localization of the relationship between frontal activity and r-BIS reveals that diminished activity in right medial and lateral frontal areas appears to be the source of the relationship between reduced right frontal activity and reduced r-BIS activity. Multiple areas of the right prefrontal cortex appear to be involved in reduced right frontal activity and r-BIS deficits.

### 4.2 | Evidence of r-BIS functioning in frontal EEG activity

Localization studies of r-BIS have not been limited to personality traits. Source localization studies have also sought the source of activity relating to behavioral measures of control. Gianotti and colleagues (2009) recorded resting baseline EEG activity and then had participants complete a behavioral risk task. Greater risk-taking behavior was localized to diminished baseline activity of the right lateral prefrontal cortex. Individuals with less stable trait activation of the right prefrontal cortex appear to demonstrate less supervisory control of risky behavior. In another study, resting EEG was recorded and compared to subsequent acceptance of unfair offers in the ultimatum game (Knoch, Gianotti, Baumgartner, & Fehr, 2010). Acceptance of unfair offers reflects an ability to exercise control over an emotional response to punish the opponent for the unfair offer in order to maximize economic benefits. Higher baseline right frontal activity was correlated with increased acceptance of the most unfair offers in order to maximize long-term gain. This relationship was also localized to the right lateral prefrontal cortex.

Greater left frontal (reduced right frontal) activity has been related to drug-cue reactivity, such as cocaine cravings (van de Laar, Licht, Franken, & Hendriks, 2004) and alcohol exposure (Myrick et al., 2004). Left frontal activity to substance cues is thought to emanate from appetitive responses evoked from substance-related stimuli (Carter & Tiffany, 1999). However, failure of r-BIS may also result in greater reactivity toward alcoholic substances. Mechin, Gable, and Hicks (2016) sought to investigate whether greater relative left frontal activity to alcohol cues derived from trait impulsivity or trait approach motivation. Participants completed the UPPS-P Behavioral Impulsivity Scale (Cyders & Smith, 2007; Whiteside et al., 2005;), the BIS/BAS scales (Carver & White, 1994), and questions about drinking habits. Then, they viewed alcohol and neutral pictures while EEG was recorded. Results revealed that trait impulsivity but not trait approach motivation related to reduced right frontal activity toward alcohol cues. Relationships between impulsivity and alcohol cue reactivity held when adjusting for drinking behaviors and frontal activity to neutral pictures. These results suggest that r-BIS, but not BAS, moderates frontal activity to alcohol cues.

Other EEG research lends support that the right frontal cortex is related to aspects of r-BIS such as error detection, emotion regulation, and self-control. Detecting and correcting wrong or inappropriate behavior is an important function of r-BIS. The error-related negativity (ERN) is an evoked potential in response to committing an error. Greater ERN amplitudes have been found in those higher in behavioral inhibition, anxiety, and emotion regulation ability, suggesting that those higher in r-BIS functioning demonstrate greater neural responses associated with conflict monitoring (Amodio et al., 2008; Proudfit, Inzlicht, & Mennin, 2013; Teper & Inzlicht, 2013). Nash, Inzlicht, and McGregor (2012) found that baseline right frontal activity related to enhanced ERN amplitudes. In contrast, baseline left frontal activity predicted smaller ERNs. Heightened right frontal activity appears to relate to greater r-BIS as it relates to conflict detection in response to errors.

Emotion regulation and self-control are two important aspects of r-BIS (Carver et al., 2008). As such, these control processes should be related to greater right frontal activity. In the study by Zinner, Brodish, Devine, and Harmon-Jones (2008), white participants were pressured to act in a politically correct manner for an ostensibly upcoming interaction with a Black participant. The social pressure was designed to enhance anger before the interaction. However, because of the social pressure to be appropriate, participants who felt angry over this social pressure would have to control their anger. EEG was assessed while participants prepared for the interracial interaction. Then, they reported their affective state in anticipation of the upcoming interaction. Results revealed that the more anger individuals felt about the interaction, the greater their relative right frontal activity. These results can be interpreted to suggest that the more anger individuals experienced, the more they had to regulate or inhibit their anger, which related to greater right frontal activity. Individuals high in anger may have experienced the most conflict between wanting to aggress and inhibiting these behaviors in order to act appropriately. In support of this interpretation, individuals who reported more anger also had higher skin conductance and more spontaneous eye blinking, suggesting they were engaging in greater emotion regulation. These results suggest that regulation of emotion by not acting on anger may relate to enhanced right frontal activity.

Similarly, r-BIS functioning may be enhanced when conflicting emotions are activated. Activation of sympathy with someone angering you should engage r-BIS. Anger is associated with the approach system and accordingly elicits left frontal activity (Harmon-Jones & Allen, 1998; Harmon-Jones & Sigelman, 2001; Poole & Gable, 2014). Harmon-Jones, Vaughn-Scott, Mohr, Sigelman, and Harmon-Jones (2004) activated high or low sympathy in individuals by instructing them to imagine how another person might feel (high) versus remain completely objective (low). Then, participants received insulting feedback. After receiving the insult, the high sympathy group showed greater right frontal activity as compared to the low sympathy group. The conflict between the urge to aggress and sympathize may have activated r-BIS and consequently right frontal activity.

In a study by Schmeichel, Crowell, and Harmon-Jones (2016), the authors depleted participants' self-control and examined frontal activity. For individuals relatively higher in trait behavioral approach (BAS) than behavioral inhibition (BIS), the researchers found that depleted (vs. nondepleted) self-control increased left frontal activity to positive pictures. In contrast, depleted individuals with no relative difference in BIS and BAS showed decreased left frontal activity to positive pictures as compared to those who were not depleted. These results suggest that when r-BIS is depleted, those who are higher in approach motivation show greater left frontal activity to rewarding stimuli.[2] An enhanced r-BIS may serve to tamp down approach motivation in individuals with overactive functioning of the BAS and underactive functioning of the inhibition system.

These studies suggest that enhanced right frontal activity may relate to emotion regulation and reduced right frontal (greater relative left frontal activity) may relate to depleted self-control and reduced error monitoring. Both personality traits related to control and situational contexts where control must be exercised have been related to right frontal activity. Other evidence suggesting that reduced right frontal activity may be causally related to reduced functioning of r-BIS comes from evidence examining manipulation of right frontal activity.

### 4.3 | Evidence of r-BIS functioning in lesion studies

EEG evidence discussed previously has been primarily correlational. However, lesion studies suggest a causal role of the right frontal cortex in r-BIS functioning. Research examining individuals with frontal damage has found that individuals with lesions to the rIFG have more trouble inhibiting actions during a stop-signal task, compared to controls (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003). Additionally, individuals with damage to the right, but not left, ventromedial prefrontal cortex showed frequent disturbances in social conduct, leading to inability to sustain employment, as well as making riskier decisions in a gambling task (Tranel, Bechara, & Denburg, 2002). Moreover, patients with damage to the right prefrontal cortex preferred riskier options in a gambling task than those with left prefrontal cortical lesions or controls (Clark, Manes, Antoun, Sahakian, & Robbins, 2003). In particular, this study observed a significant correlation between lesion volume in the right prefrontal cortex and risky decision making. Greater lesion volume related to greater risky decision making. These studies provide evidence that damage to the right frontal cortex is related to reduced functioning of r-BIS.

### 4.4 | Evidence of r-BIS functioning in transcranial electromagnetic stimulation studies

Other research has used physical manipulation techniques, such as transcranial direct current stimulation (tDCS) and transcranial magnetic stimulation (TMS), to investigate the functional significance of regional frontal cortical activity. These studies were based on the previously reviewed work involving individuals with brain damage. However, manipulating r-BIS by impairing (or enhancing) the right frontal cortex using temporary lesions (stimulation) suggests a causal role of the right frontal cortex. tDCS is a brain stimulation

[2]Based on previous evidence linking greater r-BIS activation with greater right frontal activity, a main effect of condition on frontal activity would be predicted. However, it seems likely that viewing positive pictures after ego depletion enhanced BAS, thereby eliminating the main effect of condition on frontal activity and resulting in the observed interaction.

technique that either increases or decreases neuron excitability by using electrical stimulation at anodal or cathodal sites, respectively. Predominantly, studies using tDCS have examined the role of the frontal cortex in r-BIS on motor inhibition (Ditye, Jacobson, Walsh, & Lavidor, 2012; Jacobson, Javitt, & Lavidor, 2011; Stramaccia et al., 2015). In these studies, tDCS stimulation enhanced or decreased the excitability of neuron over the right frontal cortex. Then, participants engaged in a stop-signal task. After stimulation of the rIFG to increase neuron excitability, participants demonstrated better motor inhibition, relative to a sham condition (Jacobson et al., 2011; Stramaccia et al., 2015). Furthermore, participants given tDCS stimulation to increase neuron excitability over the rIFG during training on a stop-signal task showed better performance overall than participants in the sham condition (Ditye et al., 2012). Consistent with research using tDCS, research has shown that temporarily lesioning the rIFG using repetitive transcranial magnetic stimulation (rTMS) impairs the ability to inhibit a response during a stop-signal task (Chambers et al., 2006, 2007). Together, these studies suggest that increased activity in rIFG produces better response inhibition.

While these studies suggest that motor impulsivity is influenced by activity of the rIFG, stimulation of the right dorsolateral prefrontal cortex (DLPFC) and inhibition of the left DLPFC appear to engage aspects of r-BIS related to more cognitive aspects of r-BIS. Fecteau et al. (2007) had participants perform a gambling task measuring decision making in risky situations. Results indicated that individuals who received right DLPFC stimulation chose the less risky option more often than those who received left DLPFC stimulation or those in the sham condition. Using a similar tDCS stimulation paradigm, Hecht, Walsh, and Lavidor (2010) found that enhancing activation of the left DLPFC activity was more likely to lead to heuristic processing to make decisions, while enhancing activation of the right DLPFC activity caused more deliberative decision making. Temporarily lesioning the right DLPFC using rTMS leads to riskier decision making in a gambling task (Knoch et al., 2006). tDCS stimulation also influences temporal discounting of monetary rewards. Hecht, Walsh, and Lavidor (2013) found that participants who received anodal (excitatory) stimulation over the left frontal cortex and cathodal (inhibitory) stimulation of right frontal activity tended to choose smaller, immediate rewards over greater delayed rewards in a delay discounting task. Enhancing left relative to right frontal activity led to disadvantageous and impulsive choices.

Typically, tDCS studies have demonstrated that increasing or decreasing neuronal excitability in the right frontal cortex either facilitates or interferes with inhibition of approach-motivated behaviors. Less work has demonstrated that the right frontal cortex is also involved in inhibition of avoidance behavior. Kelley and Schmeichel (2016) had 217 participants complete an Approach-Avoidance Task (AAT) with either approach-motivating or avoidance-motivating stimuli after receiving one of three tDCS stimulation treatments: increased right frontal activity, decreased right frontal activity, or sham. Participants who received tDCS to increase right frontal activity demonstrated faster responses to motivation-incongruent trials compared to participants in the decreased right frontal activity or sham conditions. Participants who received increased stimulation of the right frontal cortex were faster to approach negative avoidance-motivated images and faster to avoid positive approach-motivated images. Faster responses to motivation-incongruent trials suggest that greater right hemispheric activation enhanced regulation of habitual (motivation congruent) behaviors. Consistent with r-BIS, this work suggests that the right frontal cortex is involved in the inhibition of both approach and avoidance motivational urges.

As illustrated by the lesion and temporary lesion studies, inhibiting the right frontal cortex reduces functioning of r-BIS. In addition, inhibiting or exciting the left frontal cortex enhances or reduces r-BIS functioning. It is important to note that asymmetry was not explicitly measured by some of these studies, as only one hemisphere (not both) received stimulation or lesion. However, lesioning (exciting) one hemisphere should cause an asymmetry due to relatively greater (less) activity in the contralateral hemisphere. The asymmetry created by the lesion or stimulation may play a role in r-BIS functioning. Greater r-BIS functioning seems to be the result of the right frontal cortex becoming more active than the left frontal cortex. In sum, this research suggests that manipulations enhancing relative right frontal activity appear to enhance r-BIS functioning. In contrast, manipulations decreasing right frontal activity or enhancing relative left frontal activity appear to diminish r-BIS functioning.

## 4.5 | Evidence of r-BIS functioning in MRI studies

Lesion and temporary lesion studies have identified the right frontal cortex as a key brain region for inhibition and behavioral impulsivity. Recent MRI evidence backs up these claims with both measures of brain volume and brain function. Broadly, studies investigating brain structure indicate that diminished volume in the right prefrontal cortex impacts regulatory processes. Additionally, fMRI studies have identified areas of the right prefrontal cortex as active during tasks involving inhibition and behavioral impulsivity.

In a sample of cocaine-addicted individuals, trait impulsivity was correlated with gray matter volume of the left inferior frontal gyrus (lIFG), such that more impulsive participants had more gray matter in the lIFG (Moreno-

Lopez et al., 2012). Thus, individuals high in impulsivity had heightened volume in the left frontal cortex. This heightened volume in the lIFG may have created an asymmetry of greater left than rIFG activity. Additionally, in healthy boys aged 7–17, low impulse control was associated with decreased volume in the right ventromedial prefrontal cortex (vmPFC; Boes et al., 2009). Low impulse control was measured by ratings of parents and teachers, and reflected an inability to plan or exhibit control over motor impulses. Reduced volume in the right vmPFC may have created an asymmetry of greater left than right frontal activity. In sum, diminished functioning of r-BIS may be driven by an asymmetry of reduced right frontal volume.

Extensive research over the last two decades has identified the rIFG as a region critical for inhibition, specifically in terms of response inhibition and motor inhibition (Aron et al., 2014). Response inhibition is often linked to impulsive tendencies, suggesting that those with diminished functioning of r-BIS may experience an inability to inhibit behavior (Logan et al., 1997). Early fMRI and PET studies investigating response inhibition paradigms implicated the right prefrontal cortex, including IFG and inferior frontal sulcus, as essential for inhibition (Garavan, Ross, & Stein, 1999; Kawashima et al., 1996; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Konishi et al., 1999). More recent research supports this early work and suggests that rIFG, along with fronto-basal-ganglia networks, is essential for the inhibition of behavior (Aron et al., 2014). Most notably, a recent large-scale fMRI study of 1,896 adolescents found greater rIFG activity is associated with faster inhibition in a stop signal task (Whelan et al., 2012).

Other areas of the right prefrontal cortex have also been implicated in inhibition paradigms. Activation of the right cingulate gyrus is associated with response inhibition during Go/No-Go tasks (Garavan, Ross, Murphy, Roche, & Stein, 2002; Horn, Dolan, Elliot, Deakin, & Woodruff, 2003). Others have found a negative correlation between trait impulsivity and activation of the right dorsolateral prefrontal cortex during No-Go trials (Asahi, Okamoto, Okada, Yamawaki, & Yokota, 2004). These results suggest that individuals with greater impulsive control show greater right frontal activity during a behavioral inhibition task.

Other research has examined self-regulatory processes involving exercising control over automatic or unwanted behaviors. This evidence suggests that self-regulation processes may be rooted in the right prefrontal cortex. For example, attempting to inhibit sexual arousal while viewing erotic stimuli activated right superior frontal gyrus and right anterior cingulate gyrus (Beauregard, Lévesque, & Bourgouin, 2001). Similarly, individuals attempting to stop smoking with greater activation of the rIFG demonstrate greater control over cravings and lead to less subsequent smoking behavior during a 3-week period (Berkman, Falk, & Lieberman, 2011).

Some fMRI studies have identified the right prefrontal cortex as preferentially involved in control processes. However, lateralized hemispheric activity may not always be reported in fMRI studies. fMRI studies investigating processes related to r-BIS often incorporate the use of whole-brain analyses. As such, these studies typically examine contrasts across the entire brain to detect differential activation between the experimental task and a comparison task. Both the right and left frontal cortices may be activated to a greater extent in an experimental task than the comparison condition, resulting in the observation of bilateral activation in tasks requiring control processes (Brown, Manuck, Flory, & Hariri, 2006; Watanabe et al., 2002). However, further analyses into whether the right or left frontal areas are asymmetrically activated are rarely done in fMRI studies (Berkman & Lieberman, 2009). Thus, lateralized hemispheric activity could be masked in the fMRI literature.

## 5 | DISENTANGLING r-BIS AND FFFS IN RIGHT FRONTAL ACTIVITY

Enhanced functioning of r-BIS appears to be reflected in greater right frontal activity. However, some past research has also linked greater relative right frontal activity with greater withdrawal motivation—thought to reflect FFFS functioning. Taken together, the evidence may seem to suggest that the right frontal cortex is related to both FFFS and r-BIS. This raises an important question: How can a right lateralized r-BIS regulate a right lateralized FFFS? To answer this question, some models have separated FFFS functioning from right frontal activity and linked FFFS with greater left frontal activity (Wacker et al., 2008). Instead of separating FFFS functioning from right frontal activity, we examine two possibilities: (1) whether FFFS and r-BIS stem from different cortical structures in the right hemisphere, and (2) whether right frontal activity reflects coactivation of r-BIS and FFFS. We also discuss the potential role of r-BIS in past studies finding right frontal activation to FFFS-related tasks and traits. Finally, we discuss whether r-BIS causes right frontal activity through greater activation of the right hemisphere or inhibition of the left hemisphere.

### 5.1 | Do r-BIS and FFFS stem from different cortical structures in the right hemisphere?

fMRI studies investigating frontal hemispheric activation in manipulations of approach motivation tend to localize BAS-related processes to the left frontal cortex (Berkman & Lieberman, 2009; Canli, Desmond, Zhao, Glover, & Gabrielli,

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1998; Eddington, Dolcos, Cabeza, Krishnan & Strauman, 2007; Herrington et al., 2005). In contrast, fMRI studies investigating frontal hemispheric activation in manipulations of withdrawal motivation and FFFS-related processes tend to be mixed. While four studies have found greater left frontal activation in approach/positive manipulations (Berkman & Liberman, 2009; Canli et al. 1998; Eddington et al., 2007; Herrington et al., 2005), only one study has observed greater right frontal activation in withdrawal/negative manipulations (Canli et al., 1998). More consistently, FFFS-related processes localize to subcortical areas such as amygdala and insula (Dilger et al., 2003; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Schienle et al., 2002). Little fMRI evidence supports that FFFS functioning is localized to areas of right frontal cortex.

Research assessing hemispheric lesions suggests that hemispheric asymmetry may play an important role in r-BIS and FFFS functioning. Lesions to the right hemisphere result in deficits in r-BIS activation, while lesions to the left hemisphere result in greater r-BIS activation (Aron et al., 2003; Aron et al., 2014; Clark et al., 2003; Tranel et al., 2002). This work suggests that the left frontal cortex may have an inhibitory influence on the right frontal cortex. However, if the right frontal cortex is related to both r-BIS and FFFS functioning, then inhibition from the left hemisphere would suppress both r-BIS and FFFS functioning. In addition, greater relative right frontal activity would result in both greater r-BIS and FFFS activity.

Other evidence does not support that both r-BIS and FFFS are simultaneously enhanced by activation of the right frontal cortex. Kelley and Schmeichel's (2016) well-powered tDCS study revealed that greater activation of the right frontal cortex enhanced avoidance-incongruent behavior on an Approach-Avoidance Task (AAT). That is, participants were faster to move *toward* aversive stimuli and *away* from appetitive stimuli after right hemispheric activation. Greater activation of the right hemisphere enhanced regulatory control of both approach and avoidance motivational urges. It appears that activation of the right frontal cortex is related to r-BIS regulation, but not FFFS motivation, suggesting that both systems do not stem from the right frontal cortex—at least not the same areas of the right frontal cortex stimulated by tDCS.

In summary, the idea that r-BIS and FFFS are localized to separate substrates in the right hemisphere is not well supported by past findings. Based on past fMRI and lesion studies, FFFS does not appear to be localized to specific regions of the right frontal cortex. In contrast, the reviewed evidence suggests that r-BIS functioning localizes to areas of the right frontal cortex such as the right inferior frontal cortex, right dorsolateral prefrontal cortex, and right cingulate gyrus. It appears that r-BIS and FFFS are not localized to similar regions of the frontal cortex. However, the frontal cortex is a large brain region that it important for a multitude of psychological processes. The absence of consistent findings localizing withdrawal motivation to the frontal cortex is insufficient to determine that avoidance motivation does not stem from right frontal cortical substrates. For example, the theoretical and experimental complexity of measuring and activating withdrawal motivation could be confounding localization of FFFS to substrates in the right hemisphere (Amodio et al., 2008; Coan & Allen, 2004).

### 5.2 | Does right frontal activity reflect coactivation of r-BIS and FFFS?

Another possibility to understand which system is predominant in right frontal activity is whether studies linking right frontal activity with r-BIS or FFFS may have reflected coactivation of r-BIS and FFFS. This brings up two competing hypotheses: (1) studies linking greater right frontal activity to FFFS also activated r-BIS; as such greater r-BIS activation (but not FFFS) enhances right frontal activity, or (2) studies linking greater right frontal activity to r-BIS also activated FFFS; as such greater FFFS activation (but not r-BIS) enhances right frontal activity. The first explanation assumes that FFFS causes right frontal activity because most instances in which FFFS is assessed still entail some residual BAS activation, thereby triggering conflict and activating r-BIS. The second explanation assumes that r-BIS causes relative right frontal activity only because it requires some activation of FFFS.

Based on the reviewed evidence, it seems most likely that r-BIS is the predominant system related to right frontal activity. Activation of FFFS may have automatically activated r-BIS because FFFS is in conflict with BAS. According to Corr (2011), BAS is the predominantly active state. One function of r-BIS is to resolve conflict and return the organism to the preconflict state of approach. In some instances, the original output of r-BIS may involve inhibition, but inhibition is in service of eventual return to clear and vigorous approach. Past work showing greater right frontal activity to aversive stimuli may have been evoking greater conflict between BAS and FFFS.

### 5.3 | Could r-BIS be activated in aversive tasks?

Past work has questioned whether the experimental paradigms intending to activate greater right frontal activity through withdrawal motivation, actually manipulated withdrawal motivation (Amodio et al., 2008). Right frontal activity observed in some past studies may have been due to r-BIS activation from conflicting urges between BAS and

FFFS that arise when the FFFS system is activated. Experimental paradigms using aversive stimuli may have activated r-BIS. For example, some research using affective pictures and videos has found greater relative right frontal activity to fear- or disgust-provoking stimuli (Canli et al., 1998; Tomarken, Davidson, & Henriques, 1990; Wheeler, Davidson, & Tomarken, 1993). Although this would seem to suggest that FFFS activation led to greater relative right frontal activity, it may be that these paradigms were creating conflict and therefore activating r-BIS. For example, these studies required participants to attend to aversive stimuli, despite the aversive motivation pushing them to look away. The conflict between trying to maintain attention to negative stimuli and the urge to look away from the negative stimuli could activate r-BIS. If these individuals continue to attend to the stimuli, then r-BIS activation was likely greater than FFFS activation, resulting in greater right frontal activity.

In sum, some studies associating withdrawal motivation with greater right frontal activity may have inadvertently activated r-BIS. Avram, Balteş, Miclea, and Miu (2010) found that individuals exhibited greater right frontal activity to fearful faces in an emotional stroop task. However, fearful faces were presented intermixed with neutral and happy faces, and this may have produced conflicts between BAS and FFFS as the trials quickly switched from fearful to happy. Additionally, relative right frontal activity was moderated by anxiety levels; more anxious individuals exhibited greater right frontal activity, which suggests that greater anxiety about the conflict may have been responsible for the observed right frontal activity. The many past studies failing to find an association between withdrawal motivation and greater right frontal activity further suggest greater right frontal activity may not be driven by withdrawal motivation, per se. Future research should specifically focus on disentangling the influence of r-BIS and FFFS on right frontal activity.

## 5.4 | Could r-BIS be underlying some aversive traits?

R-BIS activation may be related to anxiety or inaction as the organism attempts to resolve conflicts between BAS and FFFS. Some of the past experimental manipulations of right frontal activity may be due to anxiety, or inaction caused by activation of r-BIS. For example, anxiety or worry provoking contexts have been found to elicit right frontal activity, especially for those high in trait anxiety (Balconi & Pagani, 2014; Cole, Zapp, Nelson, & Pérez-Edgar, 2012; Crost, Pauls, & Wacker, 2008). Additionally, increasing relative right frontal activity through tDCS stimulation leads to greater self-reported rumination (Kelley, Hortensius, & Harmon-Jones, 2013). Gray and McNaughton's theory posits that those high in r-BIS are also high in neuroticism. Past work has linked neuroticism to right frontal activity, further suggesting that r-BIS and not FFFS relates to greater right frontal activity (Schmidtke & Heller, 2004; Uusberg, Allik, & Hietanen, 2015).

Consistent with the hypothesis that r-BIS is related to anxiety and right frontal activity, Crost, Pauls, and Wacker (2008) assessed EEG frontal activity in individuals high in trait anxiety—measured using the State Trait Anxiety Inventory (Spielberger, 2010). Greater right frontal activity was heightened in these individuals in an anxiety-provoking context. Greater right frontal activity in anxiety may reflect enhanced functioning of r-BIS to manage conflicts between BAS and FFFS and decide on the appropriate action.

## 5.5 | Does r-BIS cause right frontal activity through activation or inhibition?

The frontal cortices may interact through asymmetric inhibition (Grimshaw & Carmel, 2014). Increased activation in the left hemisphere inhibits activation of the right hemisphere and vice versa. Based on the reviewed evidence in the current article linking r-BIS with greater right frontal activity, asymmetric inhibition could be causing the reduced right frontal activity associated with r-BIS. That is, left frontal activation could be inhibiting structures in the right hemisphere such as the inferior frontal gyrus (Gable, Mechin, & Neal, 2016). Inhibition of the right hemisphere could result in greater trait impulsivity.

Consistent with the asymmetric inhibition model, Cunillera, Fuentemilla, Brignani, Cucurell, and Miniussi (2014) used tDCS to increase right and decrease left frontal activity. After tDCS administration, individuals demonstrated greater response inhibition. These results suggest that inhibition of the left hemisphere may enhance r-BIS and result in greater behavioral control. Additionally, increased right frontal and decrease left frontal activation using tDCS appears to decrease risk taking on a gambling task (Fecteau et al., 2007), suggesting asymmetric inhibition could be bidirectional. Activation of structures in one hemisphere may inhibit activation in the contralateral hemisphere.

In contrast to the asymmetric inhibition model, greater r-BIS functioning may result from activation of the right hemisphere per se. Much fMRI work reviewed here demonstrates that increased activation of structures in the right hemisphere enables greater r-BIS functioning (Aron et al., 2004, 2014; Garavan et al., 2002; Horn et al., 2003; Whelan et al., 2012). Increasing right frontal activation using tDCS stimulation appears to decrease food cravings and consumption (Fregni et al., 2008; Goldman et al., 2011) and decrease aggressive behavior (Dambacher et al., 2015). Based on this conflicting evidence, it is unclear whether inhibition of the left frontal cortex or activation of the right frontal cortex drives greater relative right frontal activity associated with r-BIS. However, all of these studies support the hypothesis that r-BIS is linked to the right frontal cortex.

## 6 | LINKING BIS ANXIETY WITH RIGHT FRONTAL ACTIVITY

One issue with past work examining frontal activity and trait withdrawal is the confound between FFFS and r-BIS in Carver and White's (1994) BIS scale. These scales were created and validated prior to Gray and McNaughton's (2000) revision to RST, and therefore reflect earlier conceptions of BIS that confound withdrawal motivation with behavioral inhibition. Thus, correlations between Carver and White's BIS subscale and frontal activity cannot parse out whether r-BIS or FFFS is driving this relationship.

Based on Gray and McNaughton's (2000) revised-BIS, Carver and White's (1994) original behavioral inhibition sensitivity scale has been shown to load onto two separate factors: items relating more to avoidance motivation, and items relating more closely to conflict monitoring (Heym et al., 2008). These two factors suggest that Carver and White's BIS scale seems to be capturing FFFS in some items but r-BIS in other items. In a recent study (Neal & Gable, 2017), we sought to determine if the r-BIS items of Carver and White's BIS scale would relate to greater relative right frontal activity. In addition, we sought to replicate whether trait impulsivity related to reduced right frontal activity. In the study, 182 participants completed Carver and White's (1994) BIS/BAS scales and the UPPS-P measure of impulsivity. Then, 8 minutes of resting EEG activity were collected with eyes open and closed.

The BIS subscales were calculated according to those proposed by Heym, Ferguson, and Lawrence (2008). One BIS subscale reflects avoidance, called the FFFS scale, and the other reflects r-BIS functioning called BIS-Anxiety. Results revealed that greater BIS-Anxiety related to greater relative right frontal activity. Impulsivity related to less relative right frontal activity. BAS and FFFS were unrelated to frontal activity. Controlling for BAS or BIS did not influence the relationships between BIS-Anxiety (r-BIS functioning) and frontal activity. In sum, these results found that enhanced trait r-BIS functioning relates to greater relative right frontal activity, and trait control deficits relate to less relative right frontal activity. Notably, it was r-BIS–related items that were associated with right frontal activity, but FFFS related items were unassociated with right frontal activity.

Because items of Carver and White's (1994) BIS scale relate to separate factors reflecting r-BIS and FFFS, some of the past relationships between greater right frontal activity and the BIS scale could have been the result of greater r-BIS activation, not FFFS. Because these two subscales assess separate personality systems, some past work finding relationships between the original BIS scale and right frontal activity may have been tapping r-BIS. In addition, the confound between FFFS and r-BIS may be one reason why a number of studies have failed to replicate the relationship between Carver and White's BIS and right frontal activity.

## 7 | r-BIS FUNCTIONING IN PSYCHOPATHOLOGY AND RIGHT FRONTAL ACTIVITY

This review has predominantly focused on evidence associating r-BIS with right frontal activity in healthy samples. However, much past research has examined frontal asymmetry in populations with clinical disorders. Below, we discuss how psychological disorders related to right frontal activity may relate to r-BIS activation.

Anxiety has been characterized as overactive r-BIS sensitivity (Gray & McNaughton, 2000; Johnson, Turner, & Iwata, 2003). An overactive BIS sensitivity may reflect a hyperactive control system. Consistent with past work linking r-BIS with anxiety (Wacker et al., 2003), individuals with greater trait (Davidson, 2002; Tomarken & Davidson, 1994) and state (Petruzzello & Landers, 1994) anxiety exhibit greater right frontal activity. Additionally, individuals with disorders related to subtypes of anxiety, such as worry and threat vigilance in posttraumatic stress disorder (Meyer et al., 2015), also exhibit greater right frontal activity. It may be the case that greater right frontal activity in some types of anxiety disorders is related to a hyperactive r-BIS system.

Work by McNaughton and colleagues has revealed an r-BIS sensitive biomarker in the right frontal cortex. Based on much past work linking antianxiolytics to reduced theta band activity in rodents, they investigated human "theta" in the same frequency range as rodents (4–12 Hz) as a biomarker for reduced r-BIS (McNaughton, Kocsis, & Hajos, 2007; Neo et al., 2011). To evoke greater r-BIS, McNaughton and colleagues used a stop signal task (Aaron et al., 2003) and examined presentations of stop signal cues. Antianxiolytic drugs triazolam and buspirone reduce right frontal "theta" during stop signals. These results suggest that antianxiety drugs targeting r-BIS functioning specifically reduce right frontal "theta" activity occurring during a conflict-specific state.

Frontal asymmetric activity in individuals with bipolar disorder may also relate to r-BIS. A dysfunctional r-BIS may be unable to bridle a hyperactive BAS. This reduced r-BIS could manifest as reduced right frontal activity, especially in situations where r-BIS is necessary. Harmon-Jones and colleagues (2008) had participants engage in a difficult anagram task requiring persistence. Individuals with bipolar disorder showed greater left frontal activity than controls during the difficult anagram task. Additionally, research focusing on the onset of manic symptoms in bipolar disorder has found that greater left frontal activity in individuals with bipolar disorder predicts the onset of manic symptoms (Harmon-Jones et al., 2002; Nusslock et al., 2012). Underactive control coupled with overactive approach may be contributing to the relationship between bipolar disorder and greater left frontal activity.

Along these lines, research has suggested that psychopathy is characterized by reduced right frontal activity in the frontal cortices (Hecht, 2011). Reduced right frontal activity may reflect unregulated approach motivation in psychopathic individuals. Others have speculated that reduced right to left hemisphere communication may result in less regulation of automatic impulsive behaviors in psychopathic individuals (Hiatt & Newman, 2007). In sum, this literature suggests that some psychopathologies may be related to dysfunctional r-BIS. Future research should elucidate the role of r-BIS in frontal activity research in individuals with psychological disorders.

## 8 | CONCLUSION

A growing body of research suggests that r-BIS is asymmetrically related to greater right frontal activity. Decades of research have investigated the biological underpinnings of personality systems. As such, approach and avoidance motivation systems have been theorized to relate asymmetrically to frontal cortical activity. This review supports that right frontal activity is associated with r-BIS in order to manage conflicts from the motivational systems. Evidence from a variety of measures and methods suggest that both trait and state greater right frontal asymmetry relates to r-BIS processes. Much work remains to disentangle r-BIS and FFFS functioning from right frontal activity. However, based on a large and growing body of research, the right frontal cortex appears to be a neural substrate of r-BIS.

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