

Review

Frontal Asymmetry as a Neural Correlate of Motivational Conflict

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Abstract: Motivational systems of approach, avoidance, and inhibition are fundamental to human behavior. While past research has linked approach motivation with greater relative left frontal asymmetry, many attempts to link avoidance motivation with greater relative right frontal asymmetry have been mixed. These mixed effects could be due to coactivation of the avoidance and behavioral inhibition system (BIS). Much recent evidence indicates that the behavioral inhibition system may be associated with greater relative right frontal activation. The current review examines evidence linking traits associated with the behavioral inhibition system with resting right frontal asymmetry. Other research links individual differences associated with the behavioral inhibition system with state changes in relative right frontal asymmetry. Moreover, activation of the behavioral inhibition system, but not activation of withdrawal motivation, increases greater relative right frontal asymmetry. Together, this work highlights the role of relative frontal asymmetry as a neural correlate in motivational conflict and helps to disentangle behavioral inhibition from avoidance motivation.

Keywords: motivation; frontal asymmetry; cognitive control



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1. Introduction

Motivational drives to move towards and away are part of all human behavior. Gray's [1] Reinforcement Sensitivity Theory (RST) is one model of motivation that has received much attention in the literature, laying the groundwork for much of our current understanding of motivation. While Gray initially conceptualized two main motivational systems: a behavioral approach system and a behavioral inhibition system, later revisions expanded the theory [2,3]. Early revisions introduced a fight–flight system [2], but it was not until later work that Gray and McNaughton [3] introduced a more fully developed revised reinforcement sensitivity theory which conceptualized three main systems: a behavioral approach system (BAS) thought to facilitate approach motivation, the flight–fight–freeze system (FFFS) thought to facilitate behavioral avoidance and the revised behavioral inhibition system (revised from Gray's [1] original conceptualization; BIS) which is considered a supervisory control system. The BIS system is seen as superordinate to FFFS and BAS and is thought to be activated during times of motivational conflict [3,4].

Given the relevance of the Revised Reinforcement Sensitivity Theory to human behavior, it is not surprising that these motivational systems of approach and avoidance have been investigated in conjunction with psychological measures. Much work has investigated how BAS and FFFS may be related to asymmetric cortical activity over the prefrontal cortex [5]. Many studies investigating this asymmetric cortical activity have utilized electroencephalography (EEG) to examine the relative activity of the right and left hemispheres at homologous frontal sites [6,7]. This process, frequently referred to as “frontal asymmetry,” has been used to examine physiology as both a predictor and an outcome variable [8]. One finding well supported in the literature is a relationship between BAS and greater relative left frontal asymmetry [9]. A number of studies have provided

evidence that individuals who are high in trait aspects of the behavioral approach are more likely to have increased relative left frontal activity, even while resting [10,11]. Furthermore, evidence suggests that subjects who experience state approach motivation are also likely to exhibit increased relative left frontal activity [12,13].

Although prior research has reliably associated greater relative left frontal activation with approach motivation, attempts to link greater relative right frontal activation with avoidance motivation have been mixed [5,14], and recent meta-analyses have suggested caution when considering a relationship between relative right frontal asymmetry and avoidance motivation, as some studies have found null effects [15]. Gable and colleagues [5] reviewed literature failing to support a relationship between the FFFS system and relative right frontal activity and posited that instead of avoidance motivation, it may be the BIS that is associated with increased relative right frontal activity.

It has been argued that one reason for these ambiguous findings may be due to the conflation of FFFS and BIS [16]. Original conceptualizations of Gray's [1] Reinforcement Sensitivity Theory did not differentiate between BIS and FFFS, instead categorizing them as one component. Early work investigating the relationship between motivational systems and frontal asymmetry was largely based on Gray's [1] original theory and failed to make this distinction. For example, early work by Sutton and Davidson [17] linked relative right frontal asymmetry with the behavioral inhibition system; however, as this work predates revisions to the current understanding of the revised behavioral inhibition system, it failed to differentiate between the supervisory role of BIS and the avoidance motivation now associated with FFFS. However, even studies attempting to activate the FFFS may have failed to do so due to coactivation of FFFS and BIS.

Experimental designs seeking to manipulate avoidance motivation frequently use aversive stimuli (e.g., frightening pictures). Participants are asked to engage (i.e., view) the aversive stimuli. One possibility is that participants may disengage from these kinds of stimuli entirely [18]. However, some may have maintained engagement with the aversive stimuli. The motivation to continue to engage with the aversive stimuli would have required approach motivation. Participants simultaneously had the motivation to avoid (i.e., look away) the stimuli and approach (look towards) them. Coactivation of approach and avoidance motivation would have caused motivational conflict, thus activating BIS. The possibility that the participants disengaged from aversive situations entirely, or had motivational conflict from continuing to engage with the stimuli, could account for the ambiguity in the research that has sought to link relative right frontal asymmetry and avoidance motivation. This raises the possibility that instead of greater relative right frontal activity being associated with avoidance motivation, motivation conflict is associated with greater relative right frontal asymmetry.

2. Trait BIS Relates to Resting Frontal Asymmetry

A large number of EEG frontal asymmetry studies examine EEG in individuals while they are sitting without stimulation. This resting EEG is assumed to reflect trait-like attributes, and it has been related to personality traits and individual differences. In typical populations, these studies revealed that greater relative right frontal activity is associated with more negative affect [19]. However, a number of studies have failed to replicate the relationship between individual differences related to FFFS and resting frontal asymmetry [5]. If BIS is associated with greater relative right frontal asymmetry, one would expect to see trait measures of BIS associated with relative right frontal asymmetry at rest, but not trait measures of FFFS.

In order to investigate trait-level differences in predispositions towards the BIS, Neal and Gable [20] examined associations between participants' relative right frontal asymmetry (measured over homologous lateral frontal sites F3/F4) and BIS-Anxiety, a measure of the BIS supervisory control system. Participants completed the BIS/BAS scales [21]. Then, they alternated between resting with eyes closed and resting with eyes open for eight minutes. Heym and colleagues' [22] guidelines were used to compute two distinct subscales of

behavioral inhibition: FFFS, which measures sensitivity to the flight fight freeze system, or withdrawal motivation, and BIS-Anxiety, which measures sensitivity to the revised behavioral inhibition system.

Participants' trait personality scores on BIS-Anxiety, FFFS, and BAS were correlated with their relative frontal asymmetry scores. Results revealed that BIS-Anxiety was associated with participants' relative right frontal asymmetry. Importantly, however, no relationship emerged between FFFS and participants' frontal asymmetry scores. These results suggest a relationship between BIS and greater relative right frontal asymmetry but not between greater relative right frontal asymmetry and avoidance motivation.

The inability to inhibit motivational tendencies is reflective of the hypoactivation of BIS. Trait impulsivity measures are associated with deficient BIS functioning [23,24]. Two large studies [25,26] found a relationship between increased levels of impulsivity and greater relative left frontal activity. This relationship occurred for multiple facets of impulsivity: positive urgency, negative urgency, lack of premeditation, and lack of perseverance. Impulsivity, independent of affective valence, seems to relate to reduced right frontal activity. Neal and Gable [26] conducted source localization for the observed relationships measured at an index of frontal sites (F3, F5, F7/F4, F6, F8) and found that the relationship seemed to stem from reduced activity in the right cingulate gyrus and right medial frontal gyrus. These findings suggest that deficits in persistence and inhibition are related to reduced right frontal activity.

3. Activating Motivational Conflict Relates to Individual Differences of BIS

In order to explore these relationships between individual differences in motivational control and physiology further, Lacey et al. [16] conducted two experiments to directly contrast relationships in frontal asymmetry (measured over homologous lateral frontal sites F7/F8) between the BIS and FFFS systems. In Study 1, participants were asked to listen to an emotional sound clip designed to incite feelings of anxiety or a neutral sound clip [27]. Sound clips were used instead of images because the researchers expected that engaging with an aversive sound is reflexive. That is, it would not require effortful control to listen to an aversive sound.

Participants listened to an anxiety-inducing sound clip and a neutral sound clip under conditions engaging effortful control or experiencing avoidance motivation. In one condition, participants were asked to listen to the sound clips as they normally would. In the other condition, participants were asked to suppress their emotional responses to the sounds so that someone watching them would not know that they were feeling anything at all. This design presented opportunities to directly contrast frontal asymmetry when engaging effortful control and frontal asymmetry when experiencing avoidance motivation.

Participants who reported using high amounts of effort to suppress their emotional responses to the anxiety-inducing sound clip exhibited greater relative right frontal activation while attempting to suppress their responses during the sound clip. Experiencing high levels of anxiety when listening to the sound clip normally was not associated with participants' relative right frontal asymmetry. Increased right frontal activity was associated with the engagement of BIS and not FFFS. Additionally, effort suppressing reactions to neutral sound clips was not associated with increased right frontal asymmetry, indicating that it was not suppression itself but rather the motivational conflict that led participants to exhibit increased relative right frontal activation.

In Study 2, Lacey et al. [16] investigated whether sustained engagement with an aversive image, an action requiring motivational control, or escaping an aversive image, an action which does not require motivational control, would be more closely associated with greater relative right frontal activity (measured over homologous lateral frontal sites F7/F8). Participants were told they would look at both neutral images (rocks) and aversive images (injured bodies) under reward and non-reward conditions. In 80% of the trials, participants were presented with an escape cue halfway through image presentation. The

escape cue indicated to the participant that they had the option to terminate the trial early and forgo any reward associated with the trial.

Results revealed that increased relative right frontal activity was associated with making fewer escapes from aversive images when reward points were available. In other words, when participants were able to exert sufficient motivational control to engage with aversive images to receive a positive outcome, they exhibited greater relative right frontal asymmetry. Conversely, participants' relative right frontal activity was not correlated with escapes to negative images when no points were available, indicating that aversion to interacting with the negative images was not associated with their right frontal asymmetry scores. These results provide evidence that greater relative right frontal activity may be linked with individual differences in the effortful control of motivation, not with individual differences in avoidance motivation [16].

4. Activating BIS Increases Relative Right Frontal Asymmetry

In one paradigm, Lacey and Gable [28] modified a unique version of the approach-avoidance conflict task [29], as experiencing approach-avoidance conflict is thought to engage the revised behavioral inhibition system [28,30,31]. In this paradigm, participants were instructed to make a decision between viewing a very aversive picture (e.g., mutilated bodies) for 0, 1, 3, or 6 reward points, or viewing an appetitive picture (e.g., dessert) for no points. Deciding to engage with an aversive image for points was expected to exert motivational conflict, whereas engaging with an appetitive picture should not. After making the decision of which picture to view, participants then viewed the pictures. It was anticipated that viewing an aversive picture for a high number of points would require low effortful control, whereas viewing an aversive picture for no reward points to high effortful control (i.e., when viewing an aversive image for no reward points). Viewing aversive images for 6 points was predicted to be less effortful than conditions where participants received 0 points for viewing aversive images. The reason for this is that participants received more compensation for engaging in a disagreeable task.

Results revealed that when participants were in the decision-making phase, they exhibited greater relative right frontal activity (measured over an index of homologous lateral frontal sites: F3, F5, F7/F4, F6, F8) during the states of motivational conflict (i.e., when deciding between viewing the aversive image for reward points) relative to the states without motivational conflict. Additionally, participants also exhibited greater relative right frontal activity when viewing aversive images under the highest levels of motivational conflict (i.e., when attempting to sustain engagement with an aversive stimulus for no benefit) relative to the lowest level of motivational control (i.e., when attempting to sustain engagement with an aversive stimulus for a high number of reward points). In both the decision and viewing phases, participants exhibited greater relative right frontal activity when motivational conflict was the highest. These results suggest that activation of BIS through motivational conflict enhanced relative right frontal activity as compared to low or no activation of conflict [28].

Other experimental studies investigating the relationship between states activating BIS and frontal asymmetry have revealed similar patterns of results. In one study, Neal and Gable [32] measured shifts in participants' asymmetric frontal activity over homologous lateral frontal sites F7/F8 during a modified balloon analog risk task (BART; [33]). During the task, participants inflated a virtual balloon by pressing a button on the keyboard. Each time participants inflated the balloon more, the risk of popping the balloon increased. After each inflation pump, participants had the opportunity to cash out of the trial by pressing a different key. If they chose to cash out, they would retain all of the money earned so far during the trial and begin a new trial. If the balloon popped while they inflated it, however, they would lose all of the money accumulated for that trial. All trials ended in either the balloon popping or the participant cashing out. To enhance approach motivation, balloons were superimposed with an appetitive alcohol cue or a neutral comparison cue.

Exercising the motivational control necessary to stop inflating the balloon, thereby reducing the chances of it popping, should reflect activation of the BIS system. Neal and Gable [32] computed frontal alpha asymmetry scores separately for the first half and last half of each trial. Results revealed that participants' frontal asymmetry shifted during the course of the course of each trial. Participants exhibited shifts toward greater relative right frontal asymmetry from the first half of the trial to the second half of the trial on trials in which they exercised control and cashed out. Participants exhibited shifts toward greater relative left frontal asymmetry on trials in which they did not exercise control, popping the balloon and losing their accumulated money for that trial. This study provides further evidence that behavioral shifts consistent with BIS activation relate to increased relative right frontal asymmetry.

Other recent studies have examined the relationship between regulatory control processes and relative right frontal asymmetry during the context of experiencing boredom. When participants experience boredom during a task, they have motivational conflict to quit the task or to continue engaging with the task. To continue with the task, the behavioral inhibition system must override the motivation to quit the task [34,35]. In one study, Perone and colleagues [35] had participants complete an air traffic control task in which they were asked to indicate whether planes would collide under an easy condition and an optimally challenging condition. It was predicted that completing the easy condition after completing the hard condition would enhance boredom.

Results revealed this pattern of results. Participants who completed the easy condition after completing the optimal condition reported that the easy condition was more boring as compared to participants who completed the easy condition first. In addition, the participants who completed the optimal condition first and the easy condition second exhibited greater relative right frontal activation during the easy trial compared to the optimal trial. Importantly, this relationship between the block and frontal asymmetry (measured over homologous frontal sites F3/F4) did not exist for participants who completed the easy trial first and the optimal trial second (i.e., those participants who found the easy trial less boring; [35]). These results provide further evidence that activation of the BIS system to persist in a boring task is related to increases in relative right frontal asymmetry.

5. Imaging and Magnetic Stimulation Research Implicate Right Prefrontal Cortex in BIS

The potential that the BIS, and not the FFFS, may be related to relative right frontal asymmetry is supported by evidence from many psychophysiological measures investigating the right prefrontal cortex independently. Recent findings utilizing functional magnetic resonance imaging (fMRI) techniques have implicated the right dorsolateral prefrontal cortex (dlPFC) in the experience of approach–avoidance conflict, which reflects the engagement of the behavioral inhibition system [31]. In one study, Aupperle and colleagues asked participants to complete the approach–avoidance conflict task while fMRI was recorded [30]. Participants responded along a spectrum to choose the likelihood they would engage with a pleasant image for zero reward points or an aversive image for a variable number (two, four, or six) reward points. Images in this version of the task were also associated with an affective sound matching the valence of the trial type.

Results revealed that during the conflict trials, compared to the avoidance-only trials, participants exhibited greater activation in the right dlPFC (Brodmann area 6, 9). Additionally, this increased activation in the right dlPFC was associated with reductions in approach behavior during conflict, an additional indicator of increased BIS functioning [30]. While these fMRI results cannot speak to the relative cortical activity of the right and left prefrontal cortex, they do provide additional support implicating that the right prefrontal cortex is increasingly more active during the experience of motivational conflict.

Additionally, work investigating transcranial magnetic stimulation (TMS) has also implicated the right prefrontal cortex in inhibitory control processes [36]. In one study, Knock and colleagues [37] administered inhibitory TMS pulses during a risk-taking task.

Administering inhibitory TMS pulses over the right dorsolateral prefrontal cortex led to significant increases in risk-taking behavior during the task when compared to the risk-taking behavior of participants who received TMS pulses over the left dorsolateral prefrontal cortex or those who received sham stimulation. This pattern of responding suggests that the right dlPFC may be responsible for controlling impulsive risk-taking behaviors. Research with TMS has also been extended to consider motivational control processes and BIS more specifically with similar results. For example, Rolle et al. [38] applied TMS to demonstrate the influence of the dlPFC in approach–avoidance conflict. Results demonstrated that disrupting the right dlPFC during approach–avoidance conflict reduced approach-motivated decision making, suggesting the right dlPFC was causally related to motivational conflict, but not FFFS.

Similarly, work with transcranial direct current stimulation (tDCS) has implicated the right prefrontal cortex in control processes generally and motivational control during motivational conflict more specifically [39]. Recent work by Chen et al. [40] found that increased neuronal excitability over the right dlPFC led to better performance during a response inhibition task. This work provides additional support that the right prefrontal cortex plays an important role in inhibitory processes.

Work investigating motivational processes more specifically has also revealed the importance of the right frontal cortex in motivational control and BIS functioning in particular. Chrysikou et al. [41] utilized an approach–avoidance conflict task and found that when neuronal excitability was increased over the right dlPFC, participants who were high in trait anxiety exhibited decreases in behavioral approach behavior. This is especially interesting as trait anxiety has been repeatedly associated with the behavioral inhibition system [42,43]. In other words, increasing relative right frontal activity led to increased inhibition during the task, suggesting that right frontal activity may be associated with BIS.

In one study utilizing tDCS, Kelley and Schmeichel [44] asked participants to complete an approach–avoidance task. During the task, participants viewed either a mix of negative and neutral images (avoidance condition) or a mix of appetitive and neutral images (approach condition). In the first block, participants in the avoidance condition were asked to use a joystick to push away from the negative images and to use the joystick to pull in response to neutral images. For participants in the approach condition, these instructions were flipped to remain congruent with dominant response tendencies (i.e., participants were asked to pull the joystick towards themselves in response to appetitive images and to push the joystick away from themselves in response to neutral images).

Following this block, tDCS was administered for 15 min over homologous frontal sites F3/F4. Participants were randomly assigned to conditions where tDCS was used to increase relative left frontal activity to increase relative right frontal activity or to receive sham stimulation. Then, in block two, participants were asked to respond to images in the opposite pattern they had responded to in block one (for example, participants in the aversive condition would pull the joystick toward themselves during aversive images and push it away from themselves during neutral images). Results revealed that participants who had received tDCS in order to increase their relative right frontal activation had faster reaction times when engaging in non-dominant responses during block two. That is to say, participants who had increased relative right frontal activity were better able to control their motivational responses when compared to participants who had received tDCS to increase their relative left frontal activity and those who had received sham stimulation. This pattern of results provides additional support for the idea that BIS, which facilitates motivational control, may be most closely tied to increased relative right frontal activity than the FFFS system. These results have implications for research on frontal asymmetry, as inhibiting or activating one side of the frontal cortex may shift patterns of asymmetric cortical activity [44].

6. Neural Correlates of FFFS

There is copious evidence linking increased neural activity in the right prefrontal cortex with behavioral inhibition system functioning as opposed to flight–fight–freeze system functioning. This may, however, raise questions regarding the neural correlates of the fight–flight–freeze system. How can we interpret past work linking avoidance motivation and FFFS with relative right frontal asymmetry? One possibility is that some past studies coactivated FFFS and BIS. This may have led to the mixed association between avoidance motivation and right frontal asymmetry. Perhaps activation of BIS could explain why some prior research has found a link between greater relative right frontal asymmetry and FFFS and why some research has failed to find an association between FFFS and greater relative right frontal asymmetry. In addition to this possibility, some models have suggested ways in which FFFS may be associated with frontal asymmetry.

First, some researchers have looked outside of the right prefrontal cortex entirely, suggesting that instead of increases in relative right frontal asymmetry, FFFS may instead be associated with greater relative left frontal asymmetry [45].

There is, however, some contradictory work investigating frontal asymmetry and motivational systems that have linked FFFS, and not BIS, with increased relative right frontal activity. For example, DePascalis et al. found that FFFS was associated with greater relative right frontal activity for female participants paired with female experimenters [46]. It is important to note that this relationship did not emerge for the total group of participants, so it is unclear how generalizable the findings from this study may be. One possibility may be that both BIS and FFFS are associated with increased right frontal asymmetry but that the source of the increased activity may localize to different areas in the right prefrontal cortex. While some past research does not support this theory, the mixed results between FFFS and relative right frontal asymmetry make it difficult to rule this out as a possibility [5]. Finally, yet another possibility may be that it is not only BIS or FFFS alone, but coactivation of the BIS and FFFS systems that results in increased right frontal asymmetry [5]. At present, there is not enough research investigating this potential to determine if this may be the case. Future investigations should seek to compare coactivation of BIS and FFFS with activation of the BIS or FFFS systems on their own to determine if this coactivation may be driving right frontal asymmetry.

7. Limitations

While we find the arguments presented here to be the most persuasive explanation of the previous findings investigating the relationship between motivation and greater relative right frontal asymmetry, it should be noted that other work has proposed differing models. For example, Wacker et al. [45,47] have also proposed a relationship between a regulatory control system and the right prefrontal cortex; however, our model differs from theirs in that their BIS-BAS model of anterior asymmetry links the FFFS system with increased relative left frontal activity, while we do not. Other theories have posited a bilateral behavioral activation system in which behavioral activation is responsible for both approach and avoidance responses [14,48,49]; however, in this bilateral behavioral activation system model approach is still seen as linked with left frontal activity and avoidance is still seen as linked with right frontal asymmetry. It is possible that these findings could relate to other networks, such as those investigated by midfrontal theta [50–52].

One potential limitation to prior work investigating relationships between trait measures of BIS at rest is that participants may not experience the same strength of motivation at rest as when in an emotional context [53]. The relationship between state approach and left frontal activity suggests that the link between BAS and left frontal activity may be driven by situational contexts, such as emotional/motivation states. Coan et al. [53] proposed that the relationship between individual differences in left frontal activity and BAS may be more pronounced in the context of emotional responses. More recent work builds on this model to suggest the linear relationship between traits and frontal asymmetry may be an inverted-U [49]. Further ambiguity may be created by the use of different questionnaires to attempt

to measure similar constructs [21,22,54], or the use of different reference montages [49]. Another broad concern with work investigating individual differences is that studies examining individual differences may frequently be underpowered, a factor that may further contribute to the mixed findings in the literature. It should be noted, however, that many studies reviewed here investigating individual differences have relatively large samples, especially in comparison to other work utilizing neurophysiological measures [20,25,26,44].

Another potential concern is that experiencing motivational conflict may itself be inducing avoidance motivation. That is, participants may experience negative affect during conflict, leading them to want to avoid the conflicting situation. If this were the case, however, we should not see increased relative right frontal asymmetry in situations where participants report experiencing increased negative effects under avoidance conditions relative to conflict conditions. For example, participants in Lacey and Gable [16] reported greater anxiety when listening naturally than when suppressing, but it was effortful control of motivation, and not the experience of that negative affect, that was associated with participants' relative right frontal asymmetry scores. Based on the evidence, it is unlikely that experiencing conflict induces avoidance motivation to an extent greater than internal avoidance only states.

8. Conclusions

The current article reviews recent research examining relationships between the behavioral inhibition system and relative frontal asymmetry. Traits related to BIS activation predicted greater relative right frontal asymmetry, whereas traits related to less BIS activation predicted reduced right frontal asymmetry. Individual differences in BIS states were associated with greater relative right frontal asymmetry, but individual differences in FFFS states were not. Moreover, manipulations increasing BIS caused greater relative right frontal asymmetry, but manipulations of FFFS did not. Together, this work reviewed here is part of a growing body of research highlighting the relationship between relative right frontal asymmetry and the behavioral inhibition system [55]. The updated evidence presented in this article supports the idea that relative right frontal asymmetry is closely associated with BIS.

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