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Neurofunctional correlates of behavioral inhibition system sensitivity during attentional control are modulated by perceptual load

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ABSTRACT

Although the Behavioral Inhibition System (BIS) is associated with threat-sensitivity, little is known about its neurofunctional correlates during cognitive control over task-irrelevant threat distractors. Thirty non-clinical participants, who ranged in BIS sensitivity, completed an attentional control paradigm during fMRI. The paradigm varied in cognitive demand with low perceptual load comprising identical target letters and high perceptual load comprising a target letter in a mixed letter string; each superimposed on threatening and neutral face distractors. Whole-brain results indicated that individuals with higher, relative to lower BIS sensitivity, exhibited enhanced dorsolateral prefrontal cortex activation to angry (vs. neutral) and enhanced dorsal anterior cingulate cortex activation to fearful (vs. neutral) face distractors under low load whereas no differences in activation were observed under high load. These findings are consistent with literature indicating that the BIS is involved in conflict processing, including between cognitive and emotional or motivational goals.

Cognitive control is a process wherein top-down resources are allocated to goals, when salient, task-irrelevant stimuli compete for neural representation (MacDonald, Cohen, Stenger, & Carter, 2000; Pessoa, Kastner, & Ungerleider, 2002). This process reflects a balance between aims to accomplish goals while maintaining sensitivity to 'bottom-up' information (Whalen et al., 2006). Prior findings indicate frontal regions implicated in cognitive control (e.g., anterior cingulate cortex [ACC], medial prefrontal cortex [MPFC], dorsolateral PFC [DLPFC]]) are recruited to resolve the conflict that arises when different streams of information compete for processing resources (e.g., emotional *conflict resolution*) (Bishop, Duncan, Brett, & Lawrence, 2004; Duncan & Owen, 2000; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Kanske & Kotz, 2010; MacDonald et al., 2000; Vuilleumier & Driver, 2007). Individual differences in neurofunctional activity in these regions may be related to the behavioral inhibition system (BIS), which is associated with conflict processing in the presence of threat.

The BIS is part of an architecture of defensive systems, which involve the Behavioral Activation System (BAS), the BIS, and the Fight/Flight/Freeze System (FFFS). According to the most recent formulation of the Reinforcement Sensitivity Theory, specific aspects of the defensive system rest on functional distinctions between behaviors (McNaughton & Corr, 2004). For example, behaviors that remove an organism from a source of danger (e.g., flight, fight, or freezing); a function governed by the FFFS, are different from those that allow it to assess a source of potential danger to determine and engage in an appropriate response; a function governed by the BIS (McNaughton & Corr, 2004; McNaughton & Gray, 2000). Specifically, the BIS is a conflict detecting, monitoring, and resolving system that functions as a *comparator* of inputs (McNaughton & Gray, 2000) to determine course of action (McNaughton & Corr, 2004; McNaughton & Gray, 2000). As per the Theory (McNaughton & Corr, 2004; McNaughton & Gray, 2000) if the BIS receives input from only one highly activated goal, it monitors this fact but produces no functional output. If and when a second goal becomes similarly activated, summation of these activities may pass a threshold that warrants production of output from the BIS (McNaughton & Gray, 2000). When more than one goal is such activated, the BIS produces output that includes inhibition of current responses (aimed at the competing goals) and increase of gain of any negatively affective associations with competing goals. This process continues recursively and incrementally either until a specific goal becomes predominant or until exploratory behavior yields new, affectively significant information which causes some response (not necessarily one of those originally in conflict) to become predominant. Accordingly, although termed the

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'behavioral inhibition system', the BIS both *inhibits pre-potent behavior* and *generates additional outputs of attention and arousal* to support exploratory behavior designed to resolve conflict (McNaughton & Corr, 2004). Therefore, a function of the BIS is making assessments in situations involving approach-avoidance, approach-approach, and avoidance–avoidance conflicts (McNaughton & Corr, 2004; McNaughton & Gray, 2000).

Approach and avoidance motivations purportedly interact with cognitive control to guide goal-directed behavior (Gray & Braver, 2002). Yet, despite the pertinence of the BIS to cognitive control, the relation between the two has been surprisingly neglected. Neuroimaging studies of threat sensitivity have largely focused on anxiety − a relevant but not synonymous phenomenon − as non-clinical and clinically anxious individuals exhibit an automatic, preferential attention to threat (i.e., attentional bias) (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007). In this aspect, there is overlap between individuals with BIS hyperactivity and excessive anxiety, as BIS hyperactivity may result in excessive focus on environmental threat and, as an *indirect* consequence, increased focus on threatening associations with previous stimuli (McNaughton & Gray, 2000). Indeed, symptoms of clinical anxiety are associated with high activity of the broader defense system of which the BIS is part and the syndrome of clinical anxiety is associated with hyper-reactivity of such a system (Corr et al., 2012). Despite this overlap, as noted, the response of the defense system of which the BIS is part is *context- or state-dependent*. In contrast, individuals with elevated levels of anxiety *stably* perceive the environment as dangerous; as such, elevated trait anxiety is associated with negative schema, hyper-vigilance to threatening information, and at the memory level, hyper-recall of threatening information (Gidron, 2013).

Given general absence of research on the association between the BIS and cognitive control (but see below for exceptions) but the relevance of the BIS to anxiety, drawing on the anxiety literature may prove helpful in generating hypotheses about neurofunctional correlates of the relation between the BIS and cognitive control over emotional distractors. In studies of anxiety, accumulating evidence indicates an association between attenuated frontal recruitment in the face of threat distractors and attentional bias to threat, particularly when perceptual load on cognitive control mechanisms is low (Bishop, Jenkins, & Lawrence, 2007; Wheaton, Fitzgerald, Phan, & Klumpp, 2014). Specifically, data obtained across studies suggest that when cognitive goals are relatively easy to execute, leftover resources are available to process motivationally-relevant (but task-irrelevant) distractors. For example, Bishop and colleagues (Bishop et al., 2007) observed a negative association between activation in the anterior cingulate cortex (ACC) to threat distractors and trait anxiety but only when load on cognitive control processes was nominal (i.e., low perceptual load) in non-clinical adults. Conversely, no relationship was observed between activation in higher-order functions to threat distractors and trait anxiety when load on cognitive control processes were maximized (i.e., high perceptual load). Results are consistent with the notion that emotional interference is greater when demands on processing resources are minimal (i.e., low load). Interestingly, at the behavioral level, high and low trait anxious participants performed similarly in the low, but not high, perceptual load condition suggesting accuracy and reaction time did not track neurofunctional activity (Bishop et al., 2007).

In a separate study, our group found less ACC activation to task-irrelevant threatening faces under low perceptual load in clinically anxious participants relative to healthy controls. Yet, under high load, ACC activity to threat distractors was greater in the anxious group, potentially indicating a compensatory mechanism. In support of a compensatory function, no group effects were observed in behavioral performance (Wheaton et al., 2014).

Although these data implicate attenuated or compensatory frontal activation in excessive, selective attention to threat in anxiety, far less is known about the neurofunctional correlates of the BIS. To date, limited research in non-clinical individuals indicate a positive association between BIS and conflict detection. Relevant findings include an association between BIS and the N2 (inhibition related to 'No-Go') and error-related negativity (ERN) evoked response potential (ERP) components (both of which reflect enhanced conflict detection-related ACC activity) (Amodio, Master, Taylore, Yee, & Taylor, 2008) and associations between heightened childhood BIS and enhanced ERN (McDermott et al., 2009) as well as temperamental shyness and an enhanced N2 (Henderson, 2010) to errors in non-affective conflict detection paradigms. The findings of the only pertinent fMRI study indicate that adults with heightened childhood BIS[2] relative to adults without heightened BIS sensitivity, exhibited enhanced dorsomedial PFC (DMPFC) activation to conflict detection (Jarcho et al., 2012). Notably, across these studies, behavioral performance was not associated with BIS (Amodio et al., 2008) and group differences between high and low BIS individuals, based on median split, were not observed in behavioral performance (Jarcho et al., 2012; McDermott et al., 2009). These results suggest neural measures, relative to behavioral ones, may be more sensitive to BIS effects.

Collectively, ERP and fMRI data support the function of the BIS in conflict detection, monitoring, and resolution (McNaughton & Corr, 2004; McNaughton & Gray, 2000), to engage response processes to align performance with goals (Gratton, Coles, & Donchin, 1992; Schneider & Shiffrin, 1977). Extending this work, Dennis and Chen (2007) examined the impact of BIS on attentional control over threat distractors with a modified[3] version of the Attention Network Test (ANT) (Fan, McCandliss, Sommer, Raz, & Posner, 2002). The ANT is an experimental paradigm of alerting and orienting (associated with automatic attentional systems) and executive attention (associated with voluntary attentional systems related to the ACC) (Derryberry & Rothbart, 1997). In the modified ANT, task-irrelevant fearful, sad, and happy faces were presented *before* the task, therefore, emotional interference was relatively mild. Results revealed participants with low, relative to high BIS, had reduced cogntive control to fearful face distractors signified by an enhanced N200 response during executive attention. Again, no BIS group differences emerged at the behavioral level.

Together, theory and empirical findings indicating a positive association between the BIS and conflict detection support conceptualization of the BIS as not only inhibiting prepotent behavior but also generating additional outputs of attention and arousal to support exploratory behavior to resolve conflict (McNaughton & Corr, 2004). However, it is unknown whether the enhanced top-down functioning exhibited by individuals with elevated BIS is maintained when cognitive goals directly compete with threat distractors.

Accordingly, the aim of the present study was to examine the association between BIS sensitivity and neural activation to cognitive control during a validated threat-interference paradigm that varied in perceptual load. Threat distractors consisted of angry and fearful faces and were examined separately for the following reasons. First, although both anger and fear are related to threat, there are considerable differences between the two, including with regard to behavioral and communicative function as well as underlying neural processing circuitry. Regarding the former, anger and fear signals are different as far as elicited behaviors in the observer: anger, in contrast to fear, is a more interactive signal (e.g., indicative of interpersonal aggression) often displayed to alter the behavior of the addressed agent. On the other hand, the source of threat related to fear is more ambiguous thus requiring additional contextual information on part of the addressed

[2] Assessed at ages four, 24, and 48 months and indexed by emotional and motor reactivity to novel auditory, olfactory, and visual stimuli; inhibited behavior in response to novel auditory and visual stimuli; and socially reticent behavior when confronted with unfamiliar peers, respectively.

[3] Task-irrelevant face distractors were included in the task.