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Behavioural Inhibition System (BIS) sensitivity differentiates EEG theta responses during goal conflict in a continuous monitoring task

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ABSTRACT

Previous research has revealed that EEG theta oscillations are affected during goal conflict processing. This is consistent with the behavioural inhibition system (BIS) theory of anxiety (Gray & McNaughton, 2000). However, studies have not attempted to relate these BIS-related theta effects to BIS personality measures. Confirmation of such an association would provide further support for BIS theory, especially as it relates to trait differences. EEG was measured (32 electrodes) from extreme groups (low/high trait BIS) engaged in a target detection task. Goal conflicts were introduced throughout the task. Results show that the two groups did not differ in behavioural performance. The major EEG result was that a stepwise discriminant analysis indicated discrimination by 6 variables derived from coherence and power, with 5 of the 6 in the theta range as predicted by BIS theory and one in the beta range. Also, across the whole sample, EEG theta coherence increased at a variety of regions during *primary goal conflict* and showed a general increase during *response execution;* EEG theta power, in contrast, was primarily reactive to *response execution*. This is the first study to reveal a three-way relationship between the induction of goal conflict, the induction of theta power and coherence, and differentiation by psychometrically-defined low/high BIS status.

1. Introduction

The neurophysiological bases of personality have been long studied and increasing sophistication in theory development and methodologies have started to yield valuable insights. One of the most influential models of emotion, motivation and personality was developed by Jeffrey Gray (1982). This model, now known as *Reinforcement Sensitivity Theory* (RST; Gray and McNaughton, 2000; McNaughton and Corr, 2004, 2008), proposes three major systems of emotion processing; individual differences in the functioning and sensitivity of these systems comprise the foundations of 'personality' within RST.

First, the *Fight-Flight-Freeze System* (FFFS) is responsible for mediating reactions to aversive stimuli; secondly, the *Behavioural Approach System* (BAS) is responsible for mediating reactions to appetitive stimuli; and thirdly, the *Behavioural Inhibition System* (BIS) is responsible for resolving goal conflicts of all kinds, but especially those between the FFFS (avoidance) and BAS (approach) (unresolved goal conflicts potentially contributing to anxiety). These systems have been studied using EEG, with the following general findings. First, resting EEG linked to specific scalp locations has been related to individual differences in psychometrically-defined levels of BIS/BAS sensitivity. Secondly, inter-hemispheric EEG asymmetry response has been associated with emotional and motivational states which are linked to BIS/BAS sensitivity. Thirdly, studies have used EEG to determine the neural processes associated with phasic activation of BIS/BAS circuitry. A brief overview of each of these categories of EEG studies is provided below — the current study falls into the final category.

Regarding the first category, relationships between BIS/BAS sensitivity, as defined by questionnaire, and different resting EEG wavebands and EEG indexes, have been studied most prominently in the laboratory of Gennedy Knyazev (Knyazev and Slobodskaya, 2003; Knyazev et al., 2004, 2003, 2002). In general, these studies demonstrated that higher EEG frequencies (e.g. EEG alpha and above) relate to BIS sensitivity and lower EEG frequencies (e.g. EEG theta and below) to BAS sensitivity. Additionally, data have suggested that the oscillations associated with the BIS system (represented in the alpha EEG range) relate negatively to oscillations associated with the BAS system (represented in the delta EEG range); the strength of that relationship being positively related to psychometrically-defined BIS sensitivity (Knyazev and Slobodskaya, 2003).

Regarding the second category, studies have been reported which describe relationships between frontal EEG (alpha) asymmetries and withdrawal or approach related behaviours; the former linked to BIS

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sensitivity and the latter to BAS sensitivity. For instance, Sutton and Davidson (1997) reported that participants displaying greater relative left prefrontal EEG activity (8–13 Hz) had higher levels of BAS sensitivity; participants with greater relative right prefrontal EEG activity had higher levels of BIS sensitivity. Davidson (1998) argued that an individual's affective style can be partly moderated by their trait anterior frontal asymmetry; that is, a frontal EEG asymmetry which favours greater relative left hemisphere activation would predispose a person to positive approach type emotions, such as happiness (which are emotions thought to be linked to the BAS system).

In contrast, Harmon-Jones (2004, 2007) demonstrated that, whilst the approach motivational aspect of frontal anterior EEG asymmetry appears to hold, approach motivation is not always associated with positive emotion. Harmon-Jones reported data showing that trait anger, considered a negative emotion (and, hence, not traditionally a BAS emotion), had a positive relation with greater relative left hemisphere asymmetry. Therefore, the approach motivational tendencies associated with anger appear to override the negative emotional aspects of anger presenting a challenge to explanations of anterior asymmetry based purely on emotional valence (see Coan and Allen, 2004).

The third category employs experimental tasks likely to provoke activity in neural structures associated with BIS or BAS processing. For example, to activate neural structures and processes linked to the BIS, participants could be placed into a state of goal conflict. These studies often focus on EEG coherence as well as EEG power. Moore et al. (2006) reported scalp-wide theta coherence and power increases during a task stage requiring rapid resolution of a cognitive goal conflict. These theta effects did not extend into the alpha EEG range (Moore et al., 2008). In brief, EEG alpha response followed a different trend and was linked to the overt motor demands of the task rather than linked to BIS or BAS sensitivity per se.

The task used in Moore et al. (2006) was based on the idea that the primary role of the BIS is the detection and resolution of goal conflict (Gray and McNaughton, 2000; McNaughton and Corr, 2004). Moore et al. (2006) argued that the increased widespread theta coherence and power increase resulted from cognitive goal conflict. Specifically, and in accordance with BIS theory, increased theta coherence effects were explained as an effect of the septo-hippocampal system (SHS): limbic-neocortical interplay; the SHS being the neural structure which is regarded as central to the BIS (Gray and McNaughton, 2000). Moore et al. (2006) proposed that simultaneous communication between the SHS and two or more discrete neocortical regions led to the appearance (in terms of theta coherence) of phase consistency between those neocortical regions. This account is consistent with Gray and McNaughton's (2000) view that increased phase locking between the SHS and the neocortex maintains the discreteness of individual cycles of recursive calculations during goal-conflict resolution. Moore et al. (2006) also linked EEG theta power to resetting of the dentate theta rhythm; functionally, this was linked to the clearing of hippocampal circuits just prior to phases of active SHS goal conflict processing. This conclusion is also consistent with proposals made by Gray and McNaughton (2000) in their account of BIS activity, stimulus processing and SHS activity.

Andersen et al. (2009) experimentally explored the links between EEG theta and BIS mediated goal conflict resolution. Participants were induced into a state of internal, personally-meaningful goal conflict (i.e. rumination). The processing of unresolved goal conflict is thought to be experienced as anxious rumination (Gray and McNaughton, 2000; McNaughton and Corr, 2004, 2008). Results showed that EEG theta (coherence and power) were enhanced in the most personal form of rumination compared with a nominal form of rumination not entailing personally-meaningful stimuli. Andersen et al. (2009) concluded that these data show that increased theta coherence is an index of active attempts to resolve goal conflicts during anxious rumination.

In a related study, Neo et al. (2011) reported that right frontal EEG theta (7–8 Hz) power was greater in stop signal trials with an intermediate stop signal delay compared to a short or long delay. Theoretically, the immediate delay was reasoned to be the stage at which (go/stop) goal conflict was maximal (and, presumably, the point at which BIS was maximally activated); the intermediate delay was set individually for each participant to give a stop probability of 50%.

Additionally, Savostyanov et al. (2009) reported data which appeared to show an increase in low frequency EEG during a goal conflict stage. They showed that 1–7 Hz (i.e. delta and theta range) EEG was increased for 800 ms following presentation of a stop signal when participants were suppressing the pre-potent response — this mimics conditions for activation of goal conflict processing and, hence, neural structures inherent in BIS activity. These data are consistent with the results of Moore et al. (2006) and Andersen et al. (2009).

One major limitation of the above studies, specifically when relating observed EEG effects to anxiety, is the absence of psychometric measures of individual differences in BIS sensitivity. Although consistent with BIS theory, observing an association between goal conflict and theta power/coherence is not the same as showing that this association is related specifically to anxiety (which in humans is almost exclusively defined by self-report). In Neo et al. (2011), the revised Eysenck Personality Questionnaire (EPQ-R; Eysenck and Eysenck, 1991) and State Trait Anxiety Inverntory (STAI; Spielberger, 1983) were used to assess levels of threat sensitivity. Neo et al. (2011) reasoned that these questionnaires are more valid as measures of threat related mental disorder. However, trait anxiety and neuroticism are threat-related, but not specifically so (e.g., this anxiety scale includes depression variance) and it is not usual to omit purpose-developed BIS scales from experimental studies exploring BIS processes. The most widely used BIS scale comes from the Carver and White (1994) BIS/BAS scale.

Although questionnaire BIS scores do not provide a direct index of BIS system activity at a neural *state* level, they do provide a measure of the *trait* sensitivity of BIS system activation; that is, the consequences of longer-term activity itself, related (at least, under typical conditions; e.g., not continuous trauma) to *state* BIS sensitivity. This position is endorsed in Neo et al. (2011, p. 2) when they state that higher threat sensitive individuals are more likely to show enhanced activation of the BIS neural response. If true, it follows that there should be a differential EEG response during goal conflict conditional upon psychometrically-defined trait BIS scores.

In Moore et al. (2006) trait BIS was not measured so it could not be compared with state BIS activation, as revealed by EEG. In Andersen et al. (2009), trait BIS was measured, but no relationship was found with state BIS theta during personal goal conflict rumination — this study did not use extreme BIS groups and, in consequences of small sample size and absence of reliable measurement along the entire BIS scale, this study was under-powered. The aim of the current study is to remedy these limitations.

1.1. The current study

The primary goal of this study was to define EEG responses under a condition of goal conflict in low/high trait BIS participants. First, a large sample was surveyed and then two sub-samples at the extreme end of the trait BIS dimension were selected. The task reported in Moore et al. (2006, 2008) was adopted. As well as a conventional ANOVA analysis, a stepwise discriminant analysis (SDA) was applied to data associated with the low/high BIS sensitivity groups using a technique developed by Thatcher et al. (2005). This technique includes a stage which substantially reduces sources of error in the dataset — therefore even very small group differences which are not visible in an ANOVA approach should be apparent. The SDA considered EEG data across a 4–30 Hz spectrum (following Andersen et al., 2009). However, in the main ANOVA analysis, whilst EEG data were also considered from 4 to 30 Hz in the primary stage, follow up ANOVA analyses have only been reported for interactions which suggested modulation of the theta waveband.[1] The main ANOVA analysis only focused on the theta waveband in consideration of previous research which has confirmed a link between goal conflict and EEG theta.

Predictions based on previous research (Andersen et al., 2009; Moore et al., 2006; Neo et al., 2011; Savostyanov et al., 2009) were made. First, theta coherence was expected to increase at task stages which present the participant with a goal conflict. It was also expected that theta power would increase at these task stages too. Since increased theta activity is associated with BIS sensitivity (Gray and McNaughton, 2000), it was also predicted that these responses would be more apparent in high trait BIS participants.

2. Method

2.1. Participants

One hundred and sixty-two first year undergraduates were screened on the Carver and White (1994) BIS/BAS questionnaire. Thirty-six participants (7 males), aged 18 to 48 (M: 23.86; SD: 7.51), were recruited to the study. The 18 top scoring participants were assigned to the high BIS group (M: 26; SD: 1.5), and 18 lowest scoring participants to the low BIS group (M: 16; SD: 1.70). Due to technical problems with EEG recording, 1 participant was removed from each group thus there were 17 participants in each group whose data were entered into statistical analyses. Participants were in good health, had normal or corrected to normal vision and were right handed.

2.2. Procedure

After preparation for EEG recording (see *Physiological and behavioural measures* sub-section), the seated participant monitored a continuous stream of digit sequences containing 4 single integer digits; these were presented on a computer monitor. Each digit in the sequence was presented individually at a rate of 1 digit per second. An X, representing a brief rest period, separated each digit sequence (this was also presented for 1 second). Participants pressed the left key of a computer mouse as quickly as possible each time a digit sequence was comprised of 4 odd digits (i.e. digit sequence OOOO) — the final digit in this digit sequence was, therefore. the stage of *response execution*.

Other digit sequences were: three odd digits followed by one even digit (digit sequence OOOE); two odd digits followed by two even digits (digit sequence OOEE); one odd digit followed by three even digits (digit sequence OEEE); and four even digits (digit sequence EEEE). The even digit that appeared first in each digit sequence (e.g. **E**EEE, O**E**EE, OO**E**E, OOO**E**) was the stage of goal conflict (see Table 1 in Moore et al., 2006) — however, the even digit in digit sequence OOOE was the task stage at which the conflict between response execution and response inhibition was experienced and hence was considered the task stage at which goal conflict was presumed to be most acute — this was, therefore, the *primary goal conflict*. Forty versions of each type of digit sequence were presented.

2.3. Physiological and behavioural measures

Continuous EEG was recorded with a Brain Vision Recorder (version 1.03.0004) from 32 electrodes (Fp1, Fp2, Af3, Af4, F7, F3, Fz, F4, F8, Fc5, Fc1, Fc2, Fc6, T7, C3, Cz, C4, T8, Cp5, Cp1, Cp2, Cp6, P7, P3, Pz, P4, P8, Po3, Po4, O1, Oz and O2 —see Fig. 1). Electrode impedances were kept below 10kΩ for the duration of data acquisition. Afz was used as a subject ground; an average reference was applied offline. Vertical and horizontal electrooculogram (EOG) activity was also recorded, using electrodes placed above and below the left eye, and at the outer canthi of both eyes. EEG and EOG activity were sampled at 500 Hz. Offline, the high pass filter was set to 0.531 Hz and the low pass to 70 Hz (0.3 second time constant). A 50 Hz notch filter was also included. Recording of participant EEG and EOG was continuous through the experimental task.

EEG data were analysed offline with Brain Analyser (version 2.0.0.2701). All EEG data were treated with an eye movement reduction algorithm (Gratton and Coles, 1989; Gratton et al., 1983) and EEG epochs including data that were greater than '+75 μV' or less than '−75 μV' were rejected. This amounted to less than 15% of all epochs for each participant.

Speed of RT and correct detection of target stimuli were recorded along with errors of omission and commission (though errors were sparse so no meaningful analyses could be applied to error data). Participants were exposed to 40 targets; a mean reaction speed per participant was calculated. Missed targets were not included in the calculation of mean reaction speed.

2.4. EEG data reduction

EEG coherence values and power values were extracted for: 4–6 Hz (low theta), 6–8 Hz (high theta), 8–10 Hz (low alpha), 10–12 Hz (high alpha), 12–20 Hz (low beta) and 20–30 Hz (high beta). EEG data were processed according to regions of interest (ROI) (based on Andersen et al., 2009; Bosch et al., 2001) —see Fig. 1.

In deriving ROI specific data, initially, for each waveband, coherence values were calculated for each inter-ROI electrode pair permutation (496 electrode pairs) for each digit within each digit sequence using the equation: $K_{XY}=|C_{XY}|^2/(C_{XX}C_{YY})$ (where C_{XY} is the waveband specific cross power spectra from a pairs of electrodes and K_{XY} is the coherence value of interest). Since each digit sequence was presented on 40 separate occasions, these data were derived from up to 40, 1-second trials. Following Moore et al. (2006, 2008), as a comparison in analyses, the X

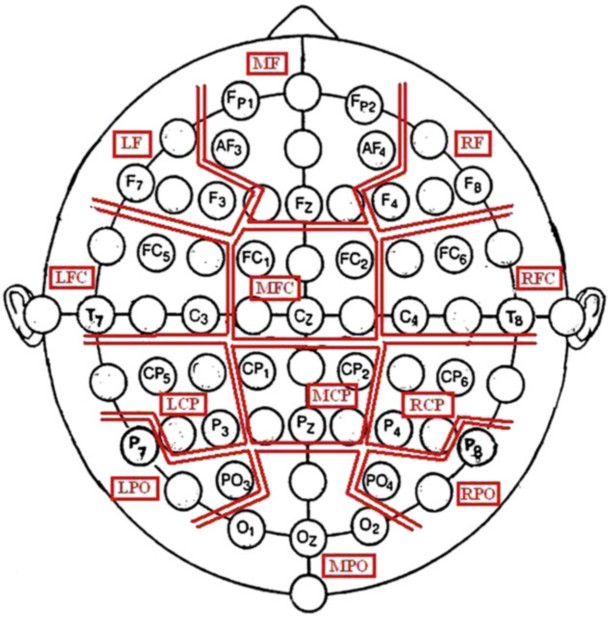

Fig. 1. Regions of interest. The following ROIs were used: left frontal (LF), mid frontal (MF), right frontal (RF), left fronto-central (LFC), mid fronto-central (MFC), right fronto-central (RFC), left centro-parietal (LCP), mid centro-parietal (MCP), right centro-parietal (RCP), left parieto-occipital (LPO), mid parieto-occipital (MPO) and right parieto-occipital (RPO).

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[1] Data associated with alpha and beta from this study will be reported in a separate paper.

presented subsequent to digit sequence EEEE was adapted as a baseline. Thus, coherence values were also derived for the baseline.

To create ROI pair specific coherence values, the mean coherence level associated with pairs of electrodes that bridged two ROIs was calculated. For each pair of ROIs, this yielded a single mean inter-ROI coherence value for each digit within each digit sequence and also for the baseline X. This process was repeated for each waveband.

EEG power was also derived for each digit within each digit sequence and also for each X that followed each digit sequence. To do this, all 1-second trials linked to presentation of each stimulus were treated with a cosine window and a fast Fourier transform (FFT) was applied. An average power value was derived for each individual digit in each digit sequence and each X linked to the digit sequence it followed. Mean power values linked to each ROI were then calculated. This process was repeated for each waveband.

2.5. Statistical analysis

2.5.1. Stepwise discriminant analysis (SDA)

There were 2 stages to the SDA: reduction of the variables to enter into the SDA and applying the SDA.

Stage 1 Reduction of variables

Previous research has shown that EEG effects are most prominently associated with the stimuli linked to *primary goal conflict* and *response execution* (see Section 2.2 for information about these stimuli) (Moore et al., 2006, 2008) so only data associated with these EEG variables were analysed. Following Thatcher et al. (2005), unrelated *t*-tests were conducted on all 1728 EEG variables (144 relating to EEG power and 1584 relating to EEG coherence) — the independent variable was BIS level (low/high BIS group). This identified statistically significant differences at $p<0.05$; thus, separating the most significant from the least significant variables. This *t*-test stage was included as a filter to reduce the number of variables entered into the final SDA; as such, in keeping with Thatcher et al.'s (2005) approach, no alpha adjustment was made for multiple comparisons as no inferential conclusions were drawn at this stage. Next, EEG variables identified as statistically significant were entered into a waveband specific principal components analysis (PCA) (varimax rotated solution) — the highest loading factors for each principal component were identified for entry into the SDA analysis.[2] This resulted in 11 variables as eligible for entry into the SDA, yielding a subject-to-variable ratio of 2.83.

Stage 2 Applying the SDA

Eleven variables were entered; predictors were identified using the Wilk's Lambda method. A conservative criterion of '*F* probability of entry' into, and '*F* probability of removal' from, the SDA equation was adopted; the former was set at 0.05 and the latter to 0.10 (following Brace et al., 2003). From the original set of 11 variables, 6 predictor variables were entered into the discriminant equation (see Table 1). At each stage, these were identified by entering the variable which was both eligible for entry into the equation (i.e. possessing an '*F* to enter' value of less than 0.05) and which most reduced the Wilk's Lambda value. A variable was entered from stages 0 through to 5 (yielding 6 predictor variables) after which no more variables were eligible for entry. A jack-knife cross-validation classification test was deployed to test the validity of the discriminant function.

2.5.2. EEG coherence and power data

All coherence data were Fisher Z transformed (following Sarnthein et al., 1998) to preserve a Gaussian distribution. Analyses for each digit sequence were initiated with an omnibus ANOVA; this incorporated the repeated measures factors inter-region (66 levels: coherence between all possible pairs of ROIs shown in Fig. 1), stimulus (5 levels: digit positions 1–4 or baseline X), waveband (6 levels: defined previously) and the independent groups factor BIS (2 levels: high BIS; low BIS). Alpha levels in subsequent follow-up analyses (justified by resulting interactions) were treated with Bonferroni correction (Rosenthal et al., 2000). ANOVAs performed subsequent to omnibus ANOVAs are shown in Table 4. After the omnibus stage, our focus was main effects and interactions which indicated modulation linked to one of theta wavebands.

For the EEG power data, all data were natural log transformed to normalise distributions prior to being entered for analyses. Analyses of EEG power were initiated with an omnibus ANOVA; the repeated measures factors were waveband (defined previously), digit sequence (5 levels: digit sequence OOOO; digit sequence OOOE; digit sequence OOEE; digit sequence OEEE and digit sequence EEEE), stimulus (5 levels: digit positions 1–4 or X) and ROI (12 levels: see Fig. 1). The independent groups factor was BIS (defined previously). Probability levels in follow up analyses were treated with a Bonferroni correction procedure. Only main effects and interactions which indicated modulation linked to one of the theta wavebands were further reported here.

3. Results

Section 3.1 deals with analyses associated with the behavioural responses of the two groups; Section 3.2 (and its sub-sections) reports analyses addressing differential EEG response in the two groups; Section 3.3 covers EEG effects across the whole sample linked to EEG theta.

3.1. Performance data

3.1.1. Low/high BIS participants performed at a similar level

Participants were exposed to a total of 40 targets. The mean number of these targets detected was 38.05 (SD: 2.75). For the low BIS group, the mean number of targets detected was 37.47 (SD: 3.24) and for the high BIS group, 38.65 (SD: 2.09), $t\ (32) = -1.26$, $p = 0.17$. Mean RT score for the low BIS groups was 483.07 (SD: 63.56) and for the high BIS group 477.43 ms (SD: 57.65), $t\ (32) = 0.27$, $p = 0.38$. There were no significant differences in the degree to which the participants in the two groups engaged with the experimental task.

3.2. EEG differentiation between low/high BIS sensitivity

3.2.1. Low/high BIS participants were primarily discriminated by EEG theta variables in the SDA

There was evidence of differentiation in the discriminant analysis. Table 1 shows that, of the 11 variables which were entered into the SDA, 6 were eligible for entry into the discriminant equation as predictor variables; therefore, 6 EEG variables combine to predict group membership into the high or low BIS group.

The standardised discriminant function coefficients (Table 2) suggest that one of the two groups had a higher EEG level (i.e. coherence or power) for three of the six variables — 'RFC-RPO *RE*' (4–6 Hz); 'MCP *PGC*' (6–8 Hz); 'LCP–LPO *PGC*' (4–6 Hz) — than the other group and a lower EEG level than the other group on the remaining three variables — 'MF-LPO *PGC* (6–8 Hz)'; 'RFC-MCP *RE* (6–8 Hz)'; 'MF-RF *PGC* (20–30 Hz). By scrutinising the means and standard deviations of the groups (Table 2), this trend is confirmed that the high BIS group has higher EEG levels on the first 3 variables mentioned above and the lower EEG levels on the latterly mentioned 3 variables.

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[2] For two wavebands (high alpha and high beta) only one variable was found to be significant at the t-test stage so the PCA stage was omitted for each of these wavebands. Instead, the single significant variable for each of these wavebands was simply entered.

Table 1
Wilk's lambda and '*F* to enter' probability value at steps 0–5 of the SDA. Each predictor variable is defined in terms of region of interest (or 'regions' in the case of coherence predictor variables), waveband and stimulus. For instance, 'MCP *PGC* (6–8 Hz)' represents 6–8 Hz EEG power recorded from the mid-central parietal region of interest associated with *primary goal conflict*; 'RFC–RPO *RE* (4–6 Hz)' represents 4–6 Hz EEG coherence associated with *response execution* between the regions of interest right-frontal central and right-parietal occipital etc. (see Section 2.2 for information about specifically which stimuli link to *primary goal conflict* and *response execution* respectively). Predictor variables which were eligible for entry into the SDA are shown in the top half of the Table. Those shown in the bottom half were not eligible for entry (based on '*F* to enter' value).

Step	Predictor variable	Wilk's λ	*F* to enter
0	MF-LPO *PGC* (6–8 Hz)	0.761	0.003
1	MCP *PGC* (6–8 Hz)	0.598	0.007
2	MF-RF *PGC* (20–30 Hz)	0.459	0.005
3	RFC-RPO *RE* (4–6 Hz)	0.365	0.011
4	LCP–LPO *PGC* (4–6 Hz)	0.271	0.004
5	RFC-MCP *RE* (6–8 Hz)	0.219	0.018
Variables not eligible for entry			
RF-MFC *PGC* (12–20 Hz)			
LFC-RFC *RE* (12–20 Hz)			
LPO *GC* (10–12 Hz)			
RCP-MPO *PGC* (6–8 Hz)			
LCP-LPO *PGC* (4–6 Hz)			

An individual case by case classification test shows that the discriminant equation successfully predicted group membership in 94.1% of the high BIS participants and 100% of the low BIS participants in the original dataset — this is summarised in Table 3a. A separate jack-knife classification test suggests the discriminant equation is reliable as group membership is successfully predicted in 88.2% of the high BIS participants and 100% of the low BIS participants in the original dataset — this is summarised in Table 3b.

3.2.2. *Low/high BIS participants were not differentiated in terms of coherence or power in the main ANOVA analyses*

Though BIS level appeared to be discriminated in the SDA, this was not reflected in the main ANOVA analysis. The omnibus analyses, which were applied to the EEG coherence data, yielded a series of interactions. When making selections for follow up analyses, interactions uncovered at this stage were not considered to be meaningful if they did not collectively involve at least the factors 'waveband' and 'stimulus'. The former confirmed that the interaction was waveband specific and the latter that it was related to the significance of individual stimuli within a digit sequence. Additionally, only those follow up analyses linked to either of the theta wavebands have been reported here. Interactions that complied with these criteria were associated with two digit sequences — OOOE and OOOO (see Table 4, Stage 1).

The results of the omnibus analyses showed that the coherence data were not modulated by BIS level since there were no significant interactions that also involved the 'BIS' factor. However, for digit sequence EEEE alone, there was an interaction between the 'waveband', 'stimulus' and 'BIS' factors which was nearly significant ($F(20,620) = 1.86$, $p = 0.054$, EPS: 0.468). A significant result here would have justified investigating each level of the 'waveband' factor individually in terms of 'stimulus' × 'BIS'. These analyses were performed as an exploratory measure. However, they revealed that 'stimulus' × 'BIS' interactions in individual wavebands were not significant following Bonferroni correction. This result confirmed that coherence data associated with all wavebands were not modulated by BIS level for any of the digit sequences in the ANOVA analyses.

Table 2
Standardised discriminant function coefficients associated with each predictor variable + means (M) and standard deviations (SD) as a function of BIS level (see the description of predictor variables in the legend of Table 1).

Predictor variable	Standardised discriminant function coefficients	Low BIS		High BIS	
		M	SD	M	SD
MF-LPO *PGC* (6–8 Hz)	−0.79	0.18	0.05	0.12	0.04
RFC-MCP *RE* (6–8 Hz)	−0.56	0.08	0.03	0.06	0.02
MF-RF *PGC* (20–30 Hz)	−0.59	0.12	0.05	0.08	0.04
RFC-RPO *RE* (4–6 Hz)	0.82	0.04	0.01	0.05	0.02
MCP *PGC* (6–8 Hz)	0.86	0.31	0.36	0.63	0.29
LCP–LPO *PGC* (4–6 Hz)	0.59	0.21	0.08	0.26	0.29

Table 3a
Classification analysis for BIS level — original data.

		Predicted group			
		Low BIS		High BIS	
Actual group membership	*N*	*n*	%	*n*	%
Low BIS	17	16	94.1	0	0
High BIS	17	1	5.9	17	100

Table 3b
Classification analysis for BIS level — jack-knife method.

		Predicted group			
		Low BIS		High BIS	
Actual group membership	*N*	*n*	%	*n*	%
Low BIS	17	15	88.2	0	0
High BIS	17	2	11.8	17	100

The omnibus analysis applied to the EEG power data also yielded a series of interactions. As before, interactions uncovered at this stage were not considered to be meaningful if they did not collectively involve at least the factors 'waveband' and 'digit sequence' (or were not linked to either of the theta wavebands); the latter confirmed that there would be significant differences in EEG power at levels within at least one digit sequence. These analyses revealed a 'waveband' × 'digit sequence' × 'stimulus' interaction ($F(80, 2560) = 5.93$, $p < 0.001$, EPS: 0.259). However, since there were no interactions which involved the 'BIS' factor, it can be concluded that BIS level was not modulated by EEG power levels associated with any wavebands or digit sequences in the main ANOVA analysis. The reasons for this apparent discrepancy with the SDA approach are discussed in Section 4.1.

3.3. *EEG theta effects across the whole sample*

3.3.1. *Coherence*

3.3.1.1. Increased low/high theta coherence associated with primary goal conflict. Though not modulated by BIS level, digit sequence OOOE was linked to 2 interactions involving the 'waveband' and 'stimulus' factors; these were a two-way interaction which solely involved these two factors and a three way interaction which also included the 'regions' factor (see Table 4, Stage 1). Both justified investigation at each level of the 'waveband' factor. For theta, this revealed a 'region' × 'stimulus' interaction for low theta coherence and a 'stimulus' main effect for high theta (shown in Table 4, Stage 2).

The low theta coherence 'region' × 'stimulus' interaction justified investigation of the 'stimulus' factor at each level of the 'region' factor. This revealed a 'stimulus' effect at the following pairs of ROIs (the 66 levels in the 'region' factor were comprised of pairs of ROIs): MF-MFC, LF-RF, RF-RFC, LFC-MFC, RFC-MFC, MPO-LPO, MPO-RPO, MPO-MFC, LPO-RPO, LPO-MFC (see Table 4, Stage 3). Next, pairwise analyses were performed on all levels of the 'stimulus' factor at these pairs of

Table 4
Stages in the hierarchy of EEG coherence ANOVAs. Stage 1 shows results of the initial digit sequence specific omnibus ANOVAs (see Section 2.5.2 for details). Stages 2 and 3 are follow-up analyses investigating significant interactions uncovered at Stage 1 in terms of 'waveband' and 'region' respectively. The outcomes of analyses following up 'stimulus' main effects uncovered at Stage 2 are shown in Fig. 3 whilst the outcomes of analyses following up the regions specific 'stimulus' main effects (Stage 3) are shown in Fig. 2. Significant main effects and interactions marked with an asterisk indicated modulation within a waveband other than theta and hence were not followed up in analyses reported here.

Stage 1 (omnibus analysis for each digit sequence)	Stage 2 (waveband)	Stage 3 (region)
EEEE Waveband×stimulus×BIS ($F(20, 620)=1.86$, $p=0.054$, EPS: 0.468)		
OOOE Waveband×stimulus×regions ($F(1300, 41600)=1.61$, $p<0.050$, EPS: 0.020). Waveband×stimulus ($F(20, 640)=3.66$, $p<0.001$, EPS: 0.512)	*Low theta* Region×stimulus ($F(260, 8580)=3.15$, $p<0.001$, EPS: 0.081) *High theta* Stimulus ($F(4, 132)=4.02$, $p<0.05$, EPS: 0.845) *High alpha* * Stimulus ($F(4, 132)=4.77$, $p<0.05$, EPS: 0.814)	MF-MFC Stimulus ($F(4, 132)=8.71$, $p<0.05$, EPS: 0.822) LF-RF Stimulus ($F(4, 132)=7.53$, $p<0.05$, EPS: 0.939) RF-RFC Stimulus ($F(4, 132)=7.42$, $p<0.05$, EPS: 0.906) LFC-MFC Stimulus ($F(4, 132)=11.09$, $p<0.05$, EPS: 0.777) RFC-MFC Stimulus ($F(4, 132)=11.62$, $p<0.05$, EPS: 0.826) MPO-LPO Stimulus ($F(4, 132)=9.15$, $p<0.01$, EPS: 0.801) MPO-RPO Stimulus ($F(4, 132)=7.70$, $p<0.05$, EPS: 0.896) MPO-MFC Stimulus ($F(4, 132)=10.62$, $p<0.05$, EPS: 0.786) LPO-RPO Stimulus ($F(4, 132)=9.95$, $p<0.05$, EPS: 0.767) LPO-MFC Stimulus ($F(4, 132)=11.07$, $p<0.05$, EPS: 0.707)
OOOO Waveband×stimulus ($F(20, 640)=3.49$, $p<0.001$, EPS: 0.328)	*Low theta* Stimulus ($F(4, 132)=3.93$, $p<0.05$, EPS: 0.802) *High alpha* * Stimulus ($F(4, 132)=4.05$, $p<0.05$, EPS: 0.954) *Low beta** Stimulus ($F(4, 132)=5.94$, $p<0.001$, EPS: 0.885)	

regions. Fig. 2 shows where low theta coherence differed significantly from the baseline level. Significant effects were *always* associated with the final digit in this digit sequence, the stage of *primary goal conflict*.

The high theta 'stimulus' main effect for digit sequence OOOE was not modulated by the 'region' factor. Therefore, follow up analyses focused on mean (scalp wide) high theta coherence for each level of the 'stimulus' factor. This also revealed a significant increase in high theta coherence for the *primary goal conflict* stage — this is shown in Fig. 3 (left panel).

3.3.1.2. Mean low theta coherence increased during response execution. When digit sequence OOOO was considered, only the interactions which solely involved the 'waveband' and 'stimulus' factors reached significance (see Table 4, Stage 1) in the initial omnibus factorial ANOVA. This interaction justified investigation of the 'stimulus' factor at each level of the 'waveband' factor. Since the interaction was not modulated by the 'region' factor, follow up analyses considered mean coherence values. Concerning theta, these analyses revealed a 'stimulus' main effect for EEG coherence data associated with low theta only. This was further investigated using pairwise comparisons.

These analyses revealed that mean coherence associated with the final digit within the digit sequence, the stage of *response execution*, was significantly higher than mean coherence associated with the baseline — this is shown in Fig. 3 (right panel).

3.3.2. Power

3.3.2.1. Low theta power was related to response execution. As mentioned previously (Section 3.2.1), the omnibus ANOVA analysis focusing on EEG power data revealed a 'waveband'×'digit sequence'×'stimulus' interaction. The interaction justified follow up analyses at each level of the 'waveband' factor in terms of 'digit sequence'×'stimulus'. As the factor 'region' was not part of the interaction, these analyses were conducted on mean (scalp-wide) EEG power. Regarding theta, these analyses revealed a 'digit sequence'×'stimulus' interaction for low theta only ($F(16, 512)=4.46$, $p<0.001$, EPS: 0.506). Follow up analyses of this effect investigated the 'stimulus' factor in each of the digit sequences. Mean power associated with the individual digits within the digit sequence was investigated separately for the low theta waveband revealing a 'stimulus' main effect of digit sequence OOOO only ($F(4, 132)=18.81$, $p<0.001$, EPS: 0.872).

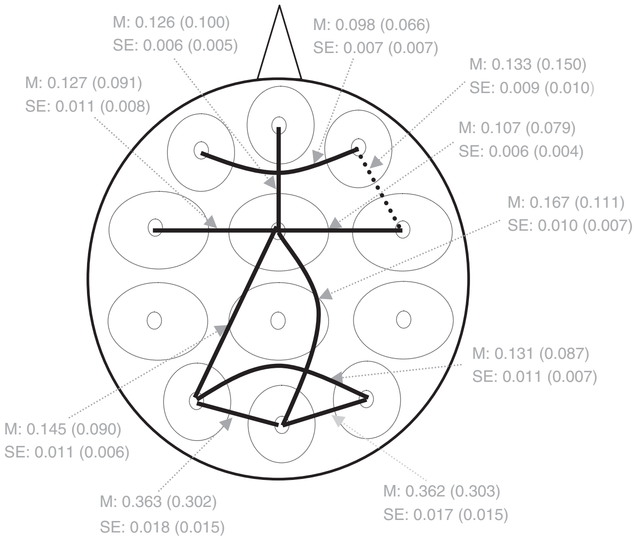

Fig. 2. Low theta coherence increases/decreases with respect to low theta baseline coherence during *primary goal conflict*. The Figure shows ROI pair specific low theta coherence changes with respect to 4–6 Hz coherence baseline at the same pair of ROIs. Solid lines between pairs of ROIs indicates coherence increase and dotted lines indicate coherence decrease. Mean and standard error coherence values are shown for coherence between pairs of ROIs where there was a significant difference from baseline; the baseline mean and standard error coherence values are also shown in parenthesis ($N=34$).

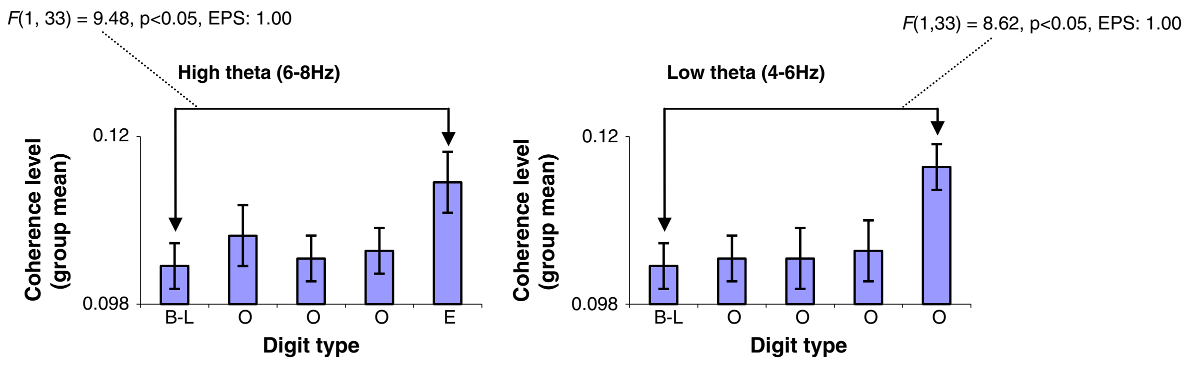

Fig. 3. Theta coherence during primary goal conflict and response execution. Mean theta coherence (4–6 Hz and 6–8 Hz) (±standard errors) associated with digit sequences OOOE and OOOO where there were significant differences evident between digits within either digit sequence. The final digit in each digit sequence is linked to *primary goal conflict* and *response execution* respectively. The arrows show significant differences between digits within each digit sequence ($N = 34$).

Next, this 'stimulus' main effect was investigated by pairwise comparison of each pair of stimuli within the digit sequence. The outcome of these analyses is represented in Fig. 4 and described below. Contrary to prediction, theta power did not increase during *primary goal conflict*. However, Fig. 4 does indicate a non-significant trend towards increased theta at the goal conflict stage in digit sequences OOOE, OEEE, OOEE.

However, the data do indicate that low theta power increased significantly during *response execution*; during this task stage, theta power was significantly increased with respect to all of the other digits in digit sequence OOOO — this is also shown in Fig. 4.

4. Discussion

4.1. Differentiation of EEG response based on participant BIS sensitivity

There were no significant differences in the behavioural responses of the two groups (low and high BIS). This finding indicates that the two groups engaged with the experimental task to the same degree, discounting the possibility that observed EEG differences were due to extraneous motivational effect. The SDA suggested that there were 6 variables that contributed to a model which maximally discriminated between the low/high BIS groups indicating that, in contrast, the task provoked differentiation of response between the 2 groups on a physiological level.

Of the 6 variables contributing to the model, 5 of them were associated with EEG theta (these will all be discussed in Section 4.2). The jack-knife test confirmed the validity of the model represented by the discriminant equation. This level of discrimination between the two groups shows that there are differences in respective EEG responses and that these are heavily represented in the theta waveband — this is consistent with our prediction that differentiation was expected in the theta waveband.

The idea that EEG data associated with the theta waveband (low and high theta) discriminates between low/high BIS participants supports Gray and McNaughton's (2000) view that SHS activity is largely mediated via theta oscillations (region specific effects in the discriminant analysis are discussed further in Section 4.2). However, this finding contrasts with early studies reported by Knyazev (Knyazev and Slobodskaya, 2003; Knyazev et al., 2003, 2002) where higher frequencies (such as alpha) dominate in participants with higher scores on BIS questionnaire measures and lower frequencies (theta and below) dominate in participants with a higher scores on BAS questionnaire measures.

The contrast could be due to different approaches taken by the two laboratories. In Knyazev's studies, resting EEG measures were often related to participant BIS/BAS sensitivity whilst in our laboratory, phasic EEG response is measured while participants engage in tasks which should, in theory, activate BIS circuitry. The use of resting EEG is likely to produce EEG profiles reflecting the expression of a variety of psychological processes linked to BIS and BAS sensitivity in participants, rather than specific phasic activation of BIS circuitry.

However, though differentiation between low/high BIS participants was found in the SDA, this was not the case in the main ANOVA analysis. This null result is consistent with other studies that were also not successful in finding differentiation in terms of EEG variables in low/high BIS groups using a standard ANOVA approach (e.g. Andersen et al., 2009).

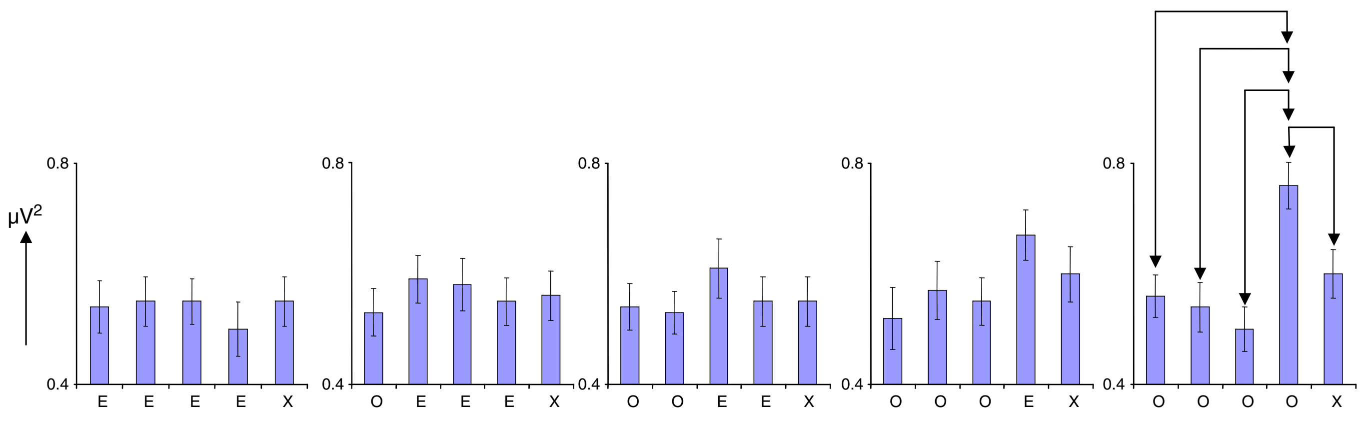

Fig. 4. Mean (scalp-wide) power response in low theta (4–6 Hz) linked to response execution. The arrows indicate where significant differences *($p < 0.05$)* were uncovered between individual digits within the digit sequences. Data associated with other digit sequences are included to show the non-significant trend during goal conflict (i.e. as the first even digit within the digit sequences was presented) — specifically, OEEE, OOEE, OOOE. $N = 34$.

The discrepancy between our ANOVA analysis and SDA is likely to be a by-product of the two approaches. The ANOVA approach was extremely conservative (Bonferroni correction was applied at each stage of the ANOVA hierarchy), hence, a small effect will be difficult to detect unless the power of the study is particularly high (Cohen, 1988, reports that detection of a small effect of, say, 0.2 ($\eta^2 = 0.010$), in a study with a power of 0.75 requires 250 participants if that study had 5 conditions[3] and that even a medium effect of 0.5 ($\eta^2 = 0.059$) requires 40 participants per condition).

In contrast, in the SDA, the number of variables to be entered into the SDA was reduced using *t*-tests and PCA. This data filtering phase hugely reduces sources of error and would result in making effects in data far more salient; this is even true of effects which, in ANOVA parlance, would be characterised by a very small effect size. It is likely that this is why the SDA approach was more fruitful than the ANOVA approach in the current study.

Additionally, the ANOVA approach may have been more likely to bear fruit regarding differences between the two groups if a processing strategy had been adopted that enabled a description of frequency dynamics at a sub-second level, such as a time/frequency (using wavelets). This is in contrast to the FFT approach taken here, where much of the temporal information is lost when calculating the power spectra of a portion of EEG data. Had the alternative strategy been adopted, discrete changes in waveband specific activity at any point during the period in which participants were reacting to individual stimuli (stimuli were presented for 1 second each) would potentially have been more salient. Such activity could then have been analysed in isolation rather than collapsed into a 1 second average where it could possibly become diluted to point where it was invisible to statistical analyses.

To enable comparison, the approach we have taken in this study reflects previous work which has been carried out in our laboratory. However, based on the fact that the data in the current study have shown effects which are consistent with our previous research, we will seek to extend this in follow-up studies where we will employ an EEG processing strategy that enables a finer grained analysis of the sub-second changes in EEG frequency dynamics that appear to be provoked during this experimental task.

Therefore, though EEG variables differentiating the two groups *have* been identified, it is important to take the following into account: that this is only possible using an approach which greatly filters sources of error in the data (i.e. SDA); and that in future investigations, differences between the two groups *may* become more salient in an ANOVA approach, if frequency dynamics of the task related EEG are considered on a sub-second basis.

4.2. EEG theta — a physiological index of goal conflict?

Gray and McNaughton (2000) take the view that the key function of the septo-hippocampal system (SHS) (the heart of the BIS) is to resolve situations in which two goals are concurrently active (i.e. goal conflicts). 'Goals' are the net result of stimuli, memories, responses and plans. They proposed that when a goal conflict is detected, recursive networks linking the SHS and various cortical regions are activated whilst the goal conflict is being experienced. They also proposed that the recursive networks are supported by theta oscillations.

We noted in Section 1 that, consistent with BIS theory, theta coherence and theta power have been shown to increase when goal conflicts are experienced (Moore et al., 2006; Neo et al., 2011; Savostyanov et al., 2009) and also during anxious rumination (Andersen et al., 2009). In the current study, it was predicted that theta coherence and power would increase as participants experienced goal conflicts. Here, goal conflict related increases in theta power were absent (though there was a non-significant trend of this — Fig. 4). However, theta coherence increase was evident during the *primary goal conflict* (Fig. 2). Therefore, the current data provide support to the prediction for theta coherence and are generally consistent with previous results published by our laboratory (Andersen et al., 2009; Moore et al., 2006); they are also generally supportive of the special role of theta oscillation in the activation of BIS circuitry during goal conflict (Gray and McNaughton, 2000).

McNaughton (2006) reported that different types of goal conflicts are resolved by different parts of the SHS. For instance, stimulus-stimulus conflicts, response–response conflicts and stimulus–response conflicts are all dealt with via feedback from the entorhinal cortex (EC), the subiculum and regions CA3 in the hippocampus, respectively. The region specific theta coherence results[4] (see Fig. 2) could be viewed as (speculative) support for this view. For instance, short-range coherence increases between parietal and occipital regions could relate to stimulus-stimulus conflict resolution. The parietal cortex has connections to various brain regions including those linked to sensory processing (Mesulam, 1990) and the occipital cortex is a region with a special role in visual processing (Banich, 1997); each adds weight to this suggestion. Additionally, coherence increases which dominate centro-frontal regions and frontal regions (both within and across regions) could relate to detection and resolution of a response–response conflict. This seems feasible as participants would need either to deploy or inhibit pre-potent response at the task stage where this effect is salient. The location of these effects maps onto the known anterior location of motor control regions (i.e. primary motor cortex, premotor cortex, prefrontal cortex, etc.). The long-range coherence increases from the parieto-occipital regions to the mid centro-frontal regions could relate to the final form of conflict resolution — stimulus–response. Any form of conflict resolution compounding stimuli and responses is likely to synchronise parietal regions associated with sensory processing (Mesulam, 1990), frontal regions associated with motor activity (i.e. the supplementary motor area, primary motor cortex) (Banich, 1997) and also possibly the anterior cingulate which also has a role in planning of motor activity (Vogt et al., 1992).

Also, EEG variables discriminated between low/high BIS participants during *primary goal conflict*. Low BIS participants typically had higher levels of long range theta coupling (mid frontal to left parietal-occipital) than high BIS participants. In contrast, high BIS participants showed higher levels of posterior short range (left centro-parietal to left parieto-occipital) coupling than low BIS participants. Additionally, theta power was higher at one posterior region (mid centro-parietal) for high BIS participants. Speculatively, these data may indicate that high and low BIS participants experience conflict in a different manner. The long range coupling which is more pronounced in the low BIS participants may indicate stimulus–response conflict whilst the enhanced posterior EEG trends in high BIS participants may relate to stimulus-stimulus conflict.

One other interesting effect which was linked to this stage of *primary goal conflict* and which was associated with the theta waveband,

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[3] All follow-up ANOVA which were subordinate to the Omnibus ANOVA varied in the number of conditions being analysed depending on the nature of the follow up. However, for illustration purposes, I have chosen 5 conditions as there were five levels associated with each of the digit sequences so it was rare for any follow up ANOVA to have less than 5 conditions.

[4] It is worth noting that EEG signals recorded from different sources on the surface of the scalp may contain erroneous contributions attributable to volume conduction (or "electrical spread" as suggested by Holsheimer and Feenstra, 1977, p. 52). In practice, activity linked to volume conductance results from electrical activity produced in tissue surrounding the site of active excitation. Signals linked to volume conductance typically have zero phase delay and can distort the appearance of genuine cortical synchrony between cortical regions. In the current study, though we have calculated EEG coherence values between regions of interest based on EEG signals derived according to an average reference (which Nunez et al., 1997, suggest can reduce the contribution of zero spatial frequency to coherency estimates), there is still the possibility that these data could include some spatial distortion through volume conduction. With this in mind, whilst it is very common for EEG coherence studies to tolerate an element of error due to volume conduction, the region specific results reported here (or in any EEG study where error due to volume conduction *may* be present) should be viewed as speculative and in need of further empirical support.

occurred right frontally. In terms of location and EEG waveband, this is consistent with data reported by Neo et al. (2011) (see Introduction for details). Specifically, there was a right-sided, anterior theta coherence reduction. According to Gray and McNaughton (2000), motor inhibition is a process which occurs when a goal conflict is experienced. Additionally, it is fairly well established that the right inferior frontal cortex is involved in response inhibition (e.g. Aron and Poldrack, 2005; Rubia et al., 2003). However, the fact that there is a *reduction* in theta coherence is interesting. Theta's influence in this short range network could be to inhibit the region (i.e. inhibition of the region which plays a role in inhibiting motor activity). The reduction in theta coherence may reflect a reduction of theta's influence in inhibition of the function of the right anterior brain region until its specific role is needed. Citing Heimer (1995) and Kandal, Schwarz & Jessell (1991), Sainsbury (1998) commented that the motor system in mammals works by the selective release of inhibition rather than by selective activation. In this case, theta could be having such an inhibitory role and the theta coherence reductions represent a reduction in the theta's suppressive influence over this brain region.

Allied to this possibility, the SDA showed that high beta coherence discriminated between low/high BIS participants in a proximal mid frontal to right frontal short range network; coherence was typically higher in low BIS participants. Whilst, the right sided theta coherence driven network could be suppressing a brain region linked to inhibiting motor activity, the beta network may emerge and act to play a role in task specific response inhibition once theta's suppressive influence over the right inferior frontal cortex had diminished. If reduced beta oscillation is taken as an index of increased cortical activation, higher beta coherence level (characteristic of low BIS participants in this network), may indicate that task specific inhibition is much stronger in high BIS participants than low BIS participants in this case.

4.3. Attentional control during deployment of pre-potent response — EEG theta

The task stage linked to *response execution* was free of goal conflict. In the discriminant analysis, the low/high BIS groups were discriminated in terms of right fronto-central theta coherence at this task stage. This is not something which would have been expected as there is no explicit reason within the RST framework to suspect that low/high BIS sensitivity would be differentiated for execution of motor activity. High BIS participants typically had higher levels of coupling between the right fronto-central region and the right parieto-occipital region. Conversely, low BIS participants typically had higher levels of coupling from the same right fronto-central location to the mid centro-parietal region. These different patterns of coupling could indicate differences in processing which is taking place in the two groups during *response execution* that is not specifically linked to goal conflict processing.

For instance, describing their theory of attentional control, Eysenck et al. (2007) suggest that anxiety levels play a role in determining which of two attentional systems become dominant during attentional processing. They suggest that increased anxiety decreases the influence of a goal-directed attentional network in favour of a stimulus-driven attentional system. They draw on Posner and Petersen's (1990) description of attentional networks and suggest that the former resembles Posner and Petersen's (1990) anterior attentional system (which is mainly focused around the anterior cingulate) whilst the latter resembles the posterior attentional system (incorporating tempo-parietal and ventral frontal cortex). For the high BIS participants, the long range frontal to posterior coupling could possibly reflect use of the stimulus driven attentional network. Also, when the pattern of coupling which is associated with the low BIS participants is considered, there are also grounds to speculate that this may indicate the anterior network, specifically because the right frontal region shows greater synchrony with the mid centro-parietal region of interest which is located nearer to the anterior cingulate cortex. This effect is not something which would have been predicted within the RST framework, but it is interesting to speculate that there may be differences in attentional control which relate to BIS level, nonetheless.

Lastly, in the ANOVA analysis, both theta power and coherence increased significantly during response execution; this is consistent with Moore et al. (2006). This effect has previously been linked to the known association between movement and increased theta (e.g. Morris and Hagen, 1983; Vanderwolf, 1969). Since full coverage of that effect has been discussed in Moore et al. (2006) it will not be revisited here but it is important to point out that this effect has been successfully replicated.

4.4. Conclusion

The primary aim of this study was to determine whether EEG responses of extreme groups of low/high BIS participants are differentiated during goal conflict, and whether this differentiation is in conformity with the Gray and McNaughton (2000) theory of anxiety. Whilst EEG responses were not differentiated in the main ANOVA analysis, a discriminant analysis function was found that maximally differentiated the groups on 6 EEG variables, 5 of which were in the theoretically-relevant theta EEG range. Additionally, a right frontal theta coherence effect linked to theta during *primary goal conflict* has been reported. The neural regions at which differentiating EEG variables were prevalent were consistent with the induction of goal conflict by the task. We conclude that our data support Gray and McNaughton's (2000) view that EEG theta oscillations reflect BIS activation and activity.

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