

Frontal theta power linked to neuroticism and avoidance

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Abstract Approach–avoidance conflict is thought to generate negative affective bias, mediated by theta rhythms. This process is distinct from, and adds to, the effects of simple aversive input. We assessed this distinction by holding gain constant and increasing loss value so that conflict and simple aversion peaked in the conflict (gain equals loss) and loss (net loss) conditions, respectively. Right frontal areas showed increases in both conflict- and loss-induced theta power. However, loss, but not conflict, power was correlated with avoidance and neuroticism, showing a Gender x Hemisphere interaction. We concluded that multiple aversive processes converge in lateral frontal networks and that individual differences in theta response in these networks may reflect differences in behavioural and emotional reactivity to aversive events.

Keywords Conflict · Theta · Neuroticism · Avoidance · Behavioural inhibition · Frontal cortex

Threat and other aversive stimuli can require either avoidance or cautious approach. Simple avoidance is thought to be controlled by the fight/flight/freeze system (FFFS). Cautious approach, induced by approach–avoidance conflict, is thought to be controlled by a distinct behavioural inhibition system (BIS; Gray, 1982; Gray & McNaughton, 2000; McNaughton & Corr, 2004). Conflict between approach and avoidance tendencies (goal conflict) is thought to initiate a conflict resolution process in the BIS. This resolution process could increase behavioural inhibi-

tion, negative bias, arousal, attention, and risk assessment. Consistent with the distinction between the BIS and FFFS, there is evidence in humans for separate sources of aversion (Perkins, Kemp, & Corr, 2007). However, we do not currently have specific biological markers that can be used to distinguish these sources in humans.

Several different types of experiment have linked the lateral frontal cortex, especially on the right, with avoidance-related processing (Aron, 2009; Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009; Coan & Allen, 2004; Fecteau et al., 2007; Gianotti et al., 2009; Harmon-Jones, Gable, & Peterson, 2010; Robbins, 2007). These are likely to involve somewhat different neural networks, especially with active versus passive avoidance. This suggests that the right frontal region could be a key common node for different avoidance signals before they enter the motor system. In particular, the right frontal regions have been linked both to personality measures of behavioural inhibition (Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009; Wacker, Chavanon, Leue, & Stemmler, 2010) and to the simple inhibition of motor actions (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Sharp et al., 2010). If it is involved in behavioural inhibition, the right frontal region should be sensitive to approach–avoidance conflict, in addition to simple aversive stimuli.

Correct network communication within the BIS depends on intact theta (4- to 7-Hz) rhythms (Gray & McNaughton, 2000). Theta rhythms can be of various sorts, and are particularly known for their involvement in memory and spatial processing (Basar, Schuermann, & Sakowitz, 2001; Kahana, 2006; Klimesch, 1999). They have also been linked with conflict (Cavanagh, Cohen, & Allen, 2009; Moore, Gale, Morris, & Forrester, 2006; Trujillo & Allen, 2007), but this may not be specific to goal conflict in the BIS.

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Our primary hypothesis, driven by the BIS theory, was that conflict should be a source of avoidance, separate from simple aversion. To assess the unique influence of conflict on neural activation and behaviour, we manipulated dollar gains and losses in a simple choice task. We predicted that when the potential amounts of gain and loss for a response were equal (generating approach–avoidance conflict), this should increase right frontal theta spectral power more than either net gain (greater approach tendency) or net loss (greater avoidance tendency). We also tested for increases in right frontal theta power in loss as compared to gain. We predicted that both conflict-specific and loss-related theta power would correlate with avoidance. Our goal was to identify unique components of the neural responses to aversive stimuli and so to enhance our understanding, not only of normal, but also of pathological behaviours. To link our economic manipulations to aversive motivational systems, we also assessed their interaction with established anxiety-related measures of personality.

Method

Participants

A total of 30 participants (15 females, 15 males) responded to an advertisement displayed by University of Otago Student Job Search for a 2-h psychology experiment (Lower South Regional Ethics Committee Approval number: OTA/04/03/019). The participants were right-handed and between 19 and 25 years old. They reported no psychological treatment in the past year. All participants read an information sheet describing the task and the electroencephalography (EEG) procedures, and all signed informed consent forms.

Behavioural test

The participants were motivated to make as much cash as possible. They kept any amount made in excess of their hourly wage rate (NZ \$9.50) but were not penalized for making less. On each trial, they chose between a left or a right mouse click. A left click produced one of two possible payoffs, with 50% probability. A right click produced no monetary consequences and allowed participants to skip the trial and maintain the monetary status quo. The value of gain from a left click was held constant at 10 cents (10c), and the extent of loss was varied over four conditions: (a) continuous gain (+10c or +10c); (b) net gain over trials (GAIN; +10c or –10c); (c) net zero over trials (CONFLICT; +10c or –10c); or (d) net loss over trials (LOSS; +10c or –20c).

A trial (Fig. 1) started with the presentation of a frame that decreased in size in three 1-s steps. A mouse click was

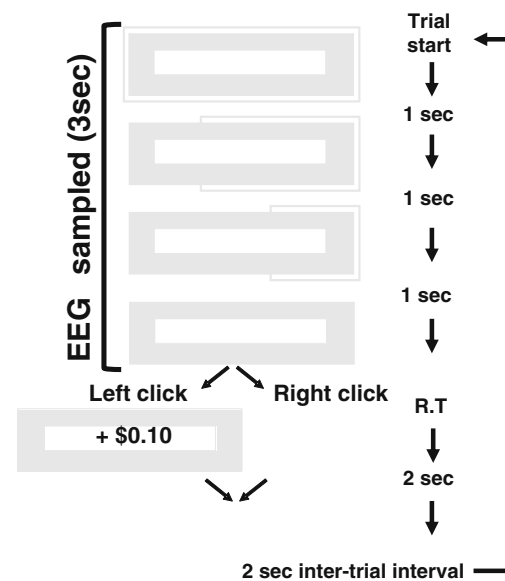


Fig. 1 Sequence of stimuli presented in each trial. RT, reaction time

ineffective in this preresponse period. The end of the period was cued by the disappearance of the frame. A left click would then cause the actual payoff received to appear in the feedback box for 2 s, followed by a 2-s intertrial period (blank screen). A right click initiated a 4-s intertrial period (blank screen), so participants had no time-related incentive to choose either left or right.

Participants first had 10 practice trials. The subsequent actual test included eight 10-trial blocks from each payoff condition, with a rest break between blocks. Payoff conditions across blocks and payoffs for left clicks within each block were counterbalanced. Right clicks did not alter the predetermined consequences of the next left click. Thus, the sequence of left-click payoffs received was the same for all participants, regardless of when right clicks were made. The following instructions were presented at the start of each block (the values are for LOSS in this example; only the values changed between conditions)

For the next 10 turns, you may gain \$0.10 or lose \$0.20 if you click the left button. Click the right button to skip a turn. The outcomes are randomized, and there is no pattern to it.

The payoff conditions were coded by colours (shaded areas in Fig. 1). The participants were not explicitly informed about this colour coding. GAIN was aquamarine (IBM colour &H00808000&), CONFLICT brown (IBM colour &H00404080&), LOSS dark purple (IBM colour &H00400040&), and continuous gain green (IBM colour &H00404000&). Practice trials were coloured grey (IBM colour &H80000004&). The stimuli were presented against a blue background (IBM colour &H00800000&).

Questionnaires

The Eysenck Personality Questionnaire–Revised (EPQ-R; Hodder & Stoughton, U.K.) and the Spielberger State–Trait Anxiety Inventory (STAI; Mind Garden Inc., CA) were also administered. These questionnaires were chosen as being well-established measures with strong links to affective processing and threat-related mental disorders.

EEG

Participants were fitted with an Electro-Cap (Electro-Cap International, Eaton, OH) and seated in a dental chair. Data from Fp1, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, and T6 were recorded, with Gnd as a ground electrode. Clip-on pure tin ear electrodes were linked together as reference via a Mindset Model MS-1000 (Nolan Computer Systems, Yuma, AZ; band pass 1.8–36 Hz, 48 dB/octave roll-off, sample rate 128 Hz).

Ocular artefacts in the EEG were removed automatically by fitting a template to the ballistic components of eye blinks recorded at Fp1 and then removal of the fitted components from each channel via linear regression (Gratton, 1998). Remaining artefacts were removed manually by deletion and were replaced with missing-data markers. Deletions were always made from all channels for the relevant time period.

After artefact removal, each 0.5-s segment of the preresponse period was replaced with a fast Fourier transform (FFT; 1-s overlapping Hanning window centred on the midpoint of the 0.5-s period, with 0.25-s leading and trailing overlaps), log transformed to normalise error variance, and then averaged across trials. If more than 30% of the trials contributing to the averaged power spectrum contained missing data for the same time period, the averaged spectrum for that period was replaced with missing-data markers. This procedure led to excessive missing values in 2 female and 1 male participants, who were excluded from further analysis.

Procedure

Participants filled out the consent forms, EPQ-R, and STAI–Trait scale upon arrival. They were then fitted with Electro-Caps and prepared for EEG recording. Electrode impedances were lowered below 5 k Ω . Participants' voluntary eye blinks and relaxation-induced alpha were inspected to determine whether further adjustments to impedances were required. The participants filled out the STAI–State scale just before the actual test, and then performed the practice trials and experimental blocks. A second STAI–State was administered immediately after testing, and the participants were debriefed and thanked for their participation.

Data analysis

ANOVAs were performed with the PASW Statistics 18 package for SPSS, and orthogonal polynomial contrasts were extracted for the factors of interest (Snedecor & Cochran, 1967). All *p* values reported are uncorrected unless stated otherwise. We focused our analyses on the 3-s preresponse period, which was divided into two half-periods. The first period included the average of FFTs in the first 1.5 s, and the second included the average of FFTs in the remaining 1.5 s.

Changes in average 4- to 7-Hz theta spectral power were assessed separately for the first and second half-periods. The effect of conflict was assessed as an orthogonal quadratic contrast of payoffs, with the experimental conditions GAIN, CONFLICT, and LOSS as successive value levels. Mathematically, this was the difference between CONFLICT and the average of GAIN and LOSS. The effect of loss was assessed as a linear contrast of payoffs across GAIN, CONFLICT, and LOSS. Mathematically, this was the difference of LOSS – GAIN power, ignoring CONFLICT. We excluded from our analyses the fourth condition, which produced continuous gain (+10 or +10). This was included in the experiment to strengthen the association of left clicks with gain and so to increase the effects of left-click avoidance in CONFLICT and LOSS. Changes across frontal recording sites were assessed with linear and quadratic contrasts, with F3, F7, Fz, F4, and F8 as successive levels.

An effect of conflict resolution was predicted in the early trials because active task solving was most likely to occur in this period. Habitual responding was likely towards the end of the experiment, so we did not expect active conflict resolution and its effects to continue then. We had no prior prediction of when the transition from acquisition to habit would occur, so we ran as many trials as we could within 45 min. As can be seen in Fig. 2, the number of left clicks in the LOSS condition tended to stabilize after the third 10-trial block, so we analysed the first 30 trials of each payoff condition for our predicted conflict effects. We also analysed the last 30 trials for a lack of the predicted effects. The trials analysed included both left- and right-click response trials.

Results

Theta power in the first 30 trials

As predicted (see the [Data Analysis](#) section), reliable effects were not detected in the last 30 trials, when responding had stabilised. Thus, here we report the results for the first 30 trials only. In the first half of the preresponse period, theta

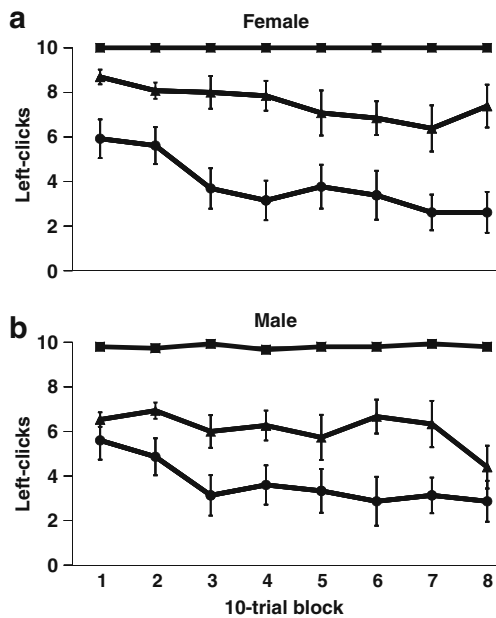


Fig. 2 Average number of left clicks made in each 10-trial block by (a) females and (b) males, in the following payoff conditions: GAIN (squares), CONFLICT (triangles), and LOSS (circles)

power peaked in CONFLICT trials at the right frontal site F8 (Fig. 3a). F3 and F7, on the left, and Fz, at the midline, did not show the same trend [quadratic contrast of Payoff \times linear contrast of Site, $F(1, 26) = 5.182, p < .031$]. In contrast, frontal theta power was reliably higher on LOSS than on GAIN trials across all the frontal sites, with little variation between them [linear contrast of Payoff, $F(1, 26) = 12.101, p < .002$; linear contrast of Payoff \times linear contrast of Site, $F(1, 26) = 2.971, p = .097$; linear contrast of Payoff \times quadratic contrast of Site, $F(1, 26) = 0.944, p = .34$]. The second half of the prereponse period did not show any reliable effects.

Conflict theta: Relation to avoidance, neuroticism, and STAI–trait

A contrast of theta power—that is, CONFLICT minus average of (GAIN + LOSS)—was calculated for each participant at F8, and its value was correlated, separately, with (a) the number of left clicks (average of the initial three 10-trial blocks of each payoff condition) in CONFLICT trials, (b) the number of left clicks for LOSS trials, (c) neuroticism score from EPQ-R, and (d) STAI–Trait score. F8 conflict-specific power was not significantly correlated with any of these variables. To test, post hoc, for the possibility of an effect of early conflict on avoidance in later trials, we also correlated the same theta power values with left clicks averaged across the 4th, 5th, and 6th trial blocks and found no significant correlations.

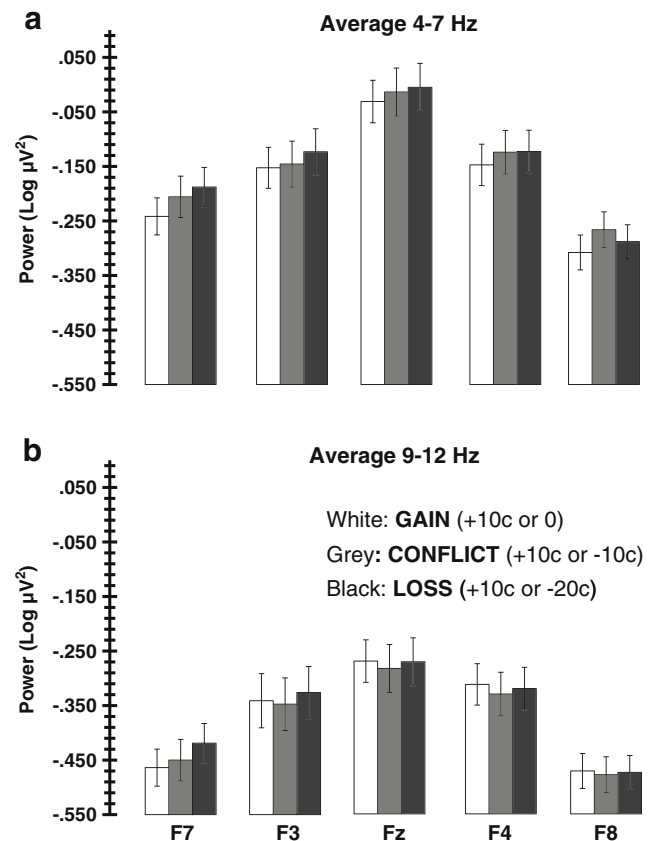


Fig. 3 Frontal power across payoff conditions in the first prereponse period (average of 0.5-s fast Fourier transforms in the first 1.5 s). (a) Average 4- to 7-Hz theta power. (b) Average 9- to 12-Hz alpha power

Loss theta: Relation to avoidance, neuroticism, and STAI–trait

A LOSS minus GAIN contrast of theta power was calculated for each participant for left (average of F7 and F3), central (Fz), and right (average of F4 and F8) recording sites. These were included as predictor variables in each of a set of separate stepwise regressions that predicted the same variables described in the previous section.

STAI–Trait and left clicks in CONFLICT trials did not show reliable effects. Right LOSS–GAIN power emerged as the sole significant predictor of left clicks in LOSS ($r = -0.465, F(1, 25) = 6.9, p < .014$), with greater LOSS–GAIN power difference predicting fewer left clicks (see the next section, Fig. 5c). Central and left power differences had progressively lower, nonsignificant correlations [$r(27) = -.271$ and $-.149, p = .086$ and $.228$, respectively], and when all three were forced into a single regression equation, left and centre had semipartial (part) correlations of $< .1$ ($< 1\%$ of the variance), while the right was only moderately reduced to $-.387$ (15% unique variance, 7% shared). We interpreted this reduction of left clicks as an increase in avoidance. Making a left as opposed to a right

click was the only way of making cash. Virtually all participants made 100% left clicks in GAIN, so the extent to which a participant avoided left clicks in CONFLICT or LOSS trials was indicative of the level of behavioural inhibition, and so of aversion experienced.

In a separate stepwise regression, both left and right power differences were detected as significant predictors of EPQ-R neuroticism [multiple $r = .668$; $F(1, 24) = 11.894$, $p < .002$]. Examination of the simple and part correlations suggest that left ($r = -.338$, part = $-.524$) and right ($r = .414$, part = $.576$) were unique predictors, with any shared variance constituting a suppression effect. More interestingly, these values for left and right loss power showed correlations in opposite directions. These results raised the possibility that F7 + F3 on the left and F4 + F8 on the right were showing significant correlations with independent subgroups in the participant pool.

Female and male differences

Gender differences in emotional brain activation are well documented (Hakamata et al., 2009; Hamann & Canli, 2004) and could account for the results above. To test this hypothesis, we forced left and right loss power into the same equation for predicting neuroticism, but separately for females and males. Both models showed significant effects [females, $r = .76$, $F(2, 10) = 6.887$, $p < .013$; males, $r = .674$, $F(2, 11) = 4.58$, $p < .036$]. However, the zero and part correlations suggest that the significant effects were accounted for, in females, predominantly by the right (F4 + F8, $r = .746$, part = $.744$; F3 + F7, $r = .16$, part = $-.153$), and in males, predominantly by the left (F3 + F7, $r = -.6$, part = $-.67$; F4 + F8, $r = .034$; part = $.307$). These results suggest that females with high F4 + F8 loss power scored high on neuroticism (see Fig. 4a; see Fig. 4b for the matching scatterplot for males), while males with low F3 + F7 loss power scored high on neuroticism (see Fig. 4c; see Fig. 4d for the matching scatterplot for females).

Given the findings above, we repeated our analyses of avoidance by correlating right loss theta and left clicks in LOSS trials for males and females separately. Right power reliably predicted avoidance in females [$r(13) = -.637$, $p < .01$; see Fig. 5a]; there were slight signs of a similar trend in males, but this was not reliable [$r(14) = -.242$, $p = .202$; Fig. 5b]. As a result of the exclusion of males, the variance of avoidance accounted for by right frontal theta increased from about 20% to 40%. There was no reliable relationship between left power and LOSS-trial left clicks in males [$r(15) = -.053$, $p = .429$] or females [$r(13) = -.339$, $p = .128$].

Since right frontal loss power at F4 + F8 showed significant relationships with neuroticism and avoidance, we included female neuroticism and left-click scores into the same equation for predicting right loss power in

order to extract the shared and unique variances. As shown in Fig. 5d, neuroticism predicted about 55% of the variance in loss power. About half of this loss power variance that was shared with neuroticism also predicted avoidance. About 16% of the variance in loss power, which was not shared with neuroticism, also predicted a component of avoidance.

Differences in correlations can result from differences in statistical properties such as the range of parameters. Males and females did not show significant differences in left or right loss power [F4 + F8, $t(25) = -0.981$, $p = .336$; F3 + F7, $t(25) = 0.403$, $p = .687$], and both groups had similar standard errors (F4 + F8: females, 0.017; males, 0.012; F3 + F7: females, 0.013; males, 0.018) and similar ranges (F4 + F8: females, -0.07 to 0.11 ; males, -0.03 to 0.1 ; F3 + F7: females, -0.016 to 0.147 ; males, -0.057 to 0.166). The variances in the behavioural score in LOSS trials were also similar (see Fig. 1). Similarly, with neuroticism, both groups had similar standard deviations (females, 4; males, 5), although males had a somewhat wider range (females, 4–15; males, 0–21). It should be noted that the direction of this range difference cannot account for our finding relationships in females that we did not find in males.

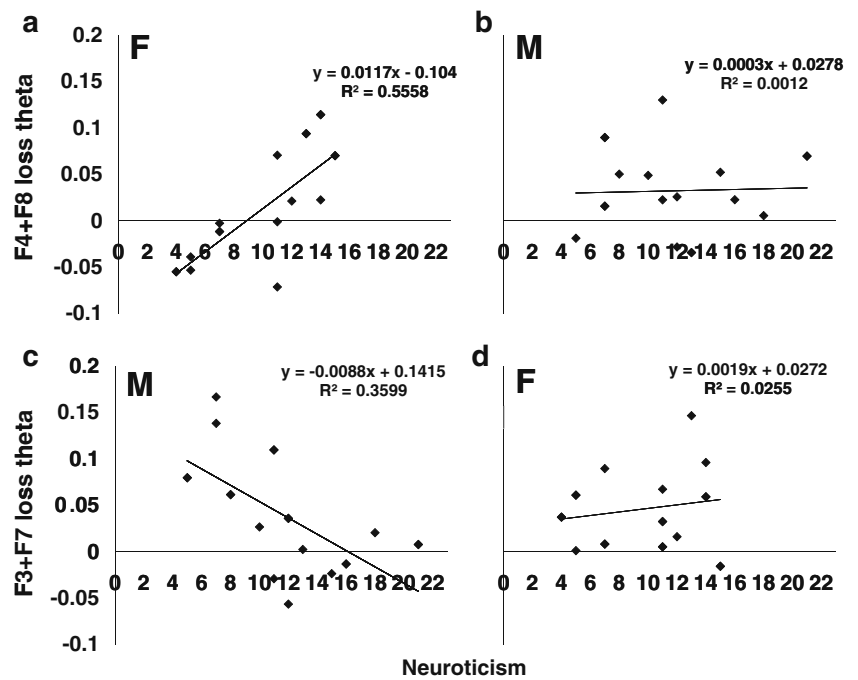
Alpha power

We tested for changes in average 9- to 12-Hz power in the first prereponse period (first 30 trials), where significant conflict and loss theta power were detected. A loss effect was detected at F7 on the left, which was not evident on the right at F8 [linear contrast of Payoff \times linear contrast of Site: $F(1, 26) = 5.429$, $p < .028$; see Fig. 3b]. Reliable relationships with neuroticism, STAI-Trait, and avoidance in LOSS and CONFLICT trials were not detected.

Reaction times

The speed/reaction time (RT) statistics for males and females across the three payoff conditions are shown in Table 1. We transformed the RT values using a reciprocal to normalise the error distributions. The speed values shown in the table are averages taken from ANOVAs of the data. The corresponding RTs shown in the table were calculated as the inverse of these speed values. Males and females did not differ in speed [gender, $F(1, 25) = 1.38$, $p = .252$]. Their speeds across payoff conditions also did not differ significantly [Gender \times linear contrast of Payoff, $F(1, 25) = 1.65$, $p = .2$; Gender \times quadratic contrast of Payoff, $F(1, 25) = 0.48$, $p = .49$]. Speed averaged across genders also did not show variation across payoff conditions [payoff, $F(2, 50) = 1.14$, $p = .328$]. Similarly, we did not detect any speed–theta power relationships (see the correlation coefficients r given for the relevant speed;

Fig. 4 Correlations between loss power and neuroticism. (Top row) Right electrodes (F4 + F8). (Bottom row) Left electrodes (F3 + F7). F, females; M, males



these report the speed–theta power relationships in Table 1).

Discussion

Consistent with our predictions, the right frontal region (F8) showed conflict-specific increases in theta power. Loss-related theta power was also detected (F4 + F8),

and this was linked to increased avoidance and to neuroticism, albeit mostly in females. Although we cannot rule out the possibility that the variance in measured avoidance might be due to a difference in rates of learning, the linkage with neuroticism suggests a specific link with avoidance.

These results, together with the current literature, support a role of right frontal cortex in multiple avoidance-related processes. Shackman et al. (2009)

Fig. 5 (a–c) Correlations between F4 + F8 loss theta power and avoidance. (d) Shared variances between right frontal loss power, neuroticism, and avoidance in females. F, females; M, males

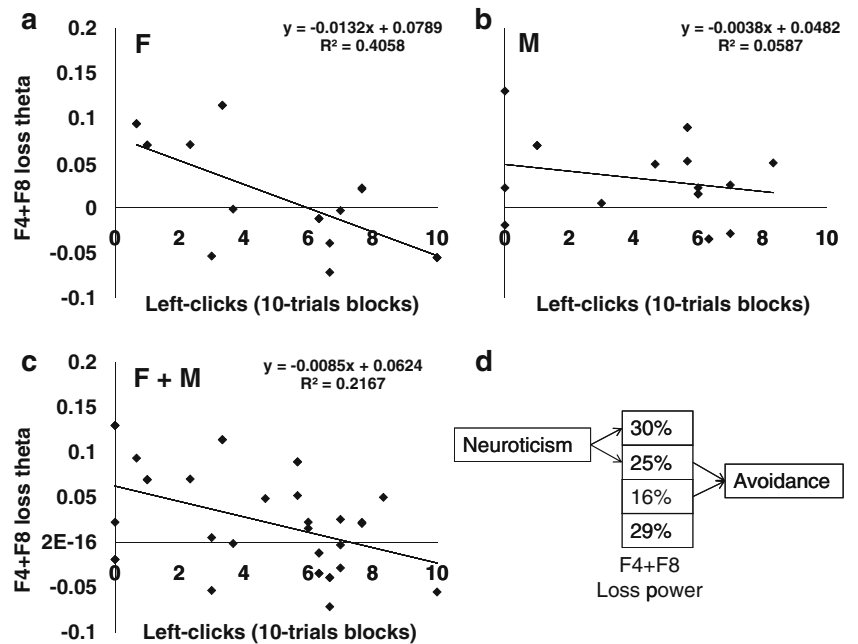


Table 1 Speed/reaction time (RT) statistics for males and females across the three payoff conditions

	Female			Male		
	Gain	Conflict	Loss	Gain	Conflict	Loss
Speed (1/s)	4.38	4.42	3.75	4.54	5.72	5.22
Std. Error	0.85	0.77	0.45	0.82	0.74	0.43
RT (ms)	229	226	266	220	175	192
r:Conflict F8		-.06	-.07		-.14	-.11
r:Loss F4,F8		-.27	-.29		-.44	-.19
r:Loss Fz		-.17	-.23		-.41	.00
r:Loss F3,F7		-.08	-.01		-.32	-.22

identified the right inferior frontal gyrus (IFG) as the link between alpha asymmetry and the personality factor of behavioural inhibition. A recent study (Hirose et al., 2009) demonstrated within-participant activations in different sub-regions of the right IFG to response inhibition and negative feedback, respectively. These subregions were separated by only 8.7 mm. This raises the possibility that the source of the right frontal conflict- and loss-related theta increases observed here could originate from distinct subregions in the IFG. However, given the spatial limitations of the EEG techniques used here, localization even to IFG is speculative and requires further testing.

In contrast to the right frontal loss power, the conflict power at F8 did not show any behavioural or emotional links. This goes against our original predictions; however, we used a simple task and relatively low values of a monetary reinforcer in the present study. On average, participants were still making left clicks more than half of the time in the CONFLICT condition, whereas, if the BIS was strongly involved, this would have been substantially less than half of the time. It is possible that the resultant motivational conflict, although detectable with neural measures, was too low in intensity to produce externally observable behavioural and emotional links.

Frontal midline structures such as the anterior cingulate cortex are known to guide value-based decision-making (Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006; Walton, Crosson, Behrens, Kennerley, & Rushworth, 2007). Our frontal midline result supports this view, in that theta power increased steadily with negative value, but this occurred also on the left- and right-hand sides. The failure of midline loss power to predict avoidance in our study appears less consistent with this perspective (with the slight, nonsignificant trend to an effect being entirely attributable, statistically, to a spread of power from the right).

The frontal midline region has also been strongly associated with response conflict monitoring (Botvinick, 2007; Botvinick, Cohen, & Carter, 2004), and the frontal midline error related negativity (ERN) has been linked to a personality factor of behavioural inhibition (Boksem, Tops, Wester, Meijman, & Lorist, 2006). At first sight, the lack of conflict-specific frontal midline power goes against this view. However, the ERN is observed after the commission of errors. One possibility, therefore, is that the effects of postresponse processing have dissipated before the presentation of the trial-start stimulus that triggered our analysis.

The underlying causes driving the gender differences observed here are unclear but are likely to be linked to variation in the level, or consequences, of threat processing. Such differences have been reported before (Hakamata et al., 2009; Hamann & Canli, 2004; Nolen-Hoeksema, 2001; Thayer, Rossy, Ruiz-Padial, & Johnsen, 2003). Our results, then, may reflect a difference in the emotional styles with which male and female participants approach the simple negative payoffs in our task. On this view, the males, like the females, experienced the emotional effects of the LOSS condition (indicated by the links between left/right frontal loss power and neuroticism), but the males may have controlled their behaviour via more cognitively loaded strategies. This could explain the lack of a behavioural link to the observed “emotional” frontal power in males.

Our data demonstrate that gain and loss do not simply subtract from each other neurally, but instead showed effects of conflict, in addition to loss, in the right frontal cortex. Taken in combination with the right-frontal-loss theta–avoidance/neuroticism link in females, our results are consistent with FFFS and BIS as distinct neural systems that mediate and modulate avoidance (Gray & McNaughton, 2000; McNaughton & Corr, 2004). However, we did not demonstrate a link between conflict theta and avoidance. Further work will be required to determine whether this reflects insufficient behavioural control in the conflict condition or a failure of the BIS theory. The link between left frontal theta power and neuroticism in males also suggests a possible left-hemisphere link to aversive processes. It appears that multiple aversive mechanisms may converge in the lateral frontal regions, and theta responses in these networks could represent different forms of behavioural and emotional sensitivities.

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References

- Aron, A. R. (2009). Introducing a special issue on stopping action and cognition. *Neuroscience and Biobehavioral Reviews*, *33*, 611–612.
- Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, *6*, 115–116.
- Basar, E., Schuermann, M., & Sakowitz, O. (2001). The selectively distributed theta system: Functions. *International Journal of Psychophysiology*, *39*, 197–212.
- Boksem, M. A. S., Tops, M., Wester, A. E., Meijman, T. F., & Lorist, M. M. (2006). Error-related ERP components and individual differences in punishment and reward sensitivity. *Brain Research*, *1101*, 92–101.
- Botvinick, M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective & Behavioral Neuroscience*, *7*, 356–366.
- Botvinick, M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*, 539–546.
- Cavanagh, J. F., Cohen, M. X., & Allen, J. J. B. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *The Journal of Neuroscience*, *29*, 98–105.
- Christopoulos, G. I., Tobler, P. N., Bossaerts, P., Dolan, R. J., & Schultz, W. (2009). Neural correlates of value, risk, and risk aversion contributing to decision making under risk. *The Journal of Neuroscience*, *29*, 12574–12583.
- Coan, J. A., & Allen, J. J. B. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, *67*, 7–49.
- Fecteau, S., Knoch, D., Fregni, F., Sultani, N., Boggio, P., & Pascual-Leone, A. (2007). Diminishing risk-taking behavior by modulating activity in the prefrontal cortex: A direct current stimulation study. *The Journal of Neuroscience*, *27*, 12500–12505.
- Gianotti, L. R., Knoch, D., Faber, P. L., Lehmann, D., Pascual-Marqui, R. D., Diezi, C., et al. (2009). Tonic activity level in the right prefrontal cortex predicts individuals' risk taking. *Psychological Science*, *20*, 33–38.
- Gratton, G. (1998). Dealing with artifacts: The EOG contamination of the event-related potential. *Behavior Research Methods, Instruments, & Computers*, *30*, 44–53.
- Gray, J. A. (1982). *The neuropsychology of anxiety: An inquiry into the functions of the septo-hippocampal systems*. New York: Oxford University Press.
- Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system* (2nd ed.). Oxford: Oxford University Press.
- Hakamata, Y., Iwase, M., Iwata, H., Kobayashi, T., Tamaki, T., Nishio, M., et al. (2009). Gender difference in relationship between anxiety-related personality traits and cerebral brain glucose metabolism. *Psychiatry Research: Neuroimaging*, *173*, 206–211.
- Hamann, S., & Canli, T. (2004). Individual differences in emotion processing. *Current Opinion in Neurobiology*, *14*, 233–238.
- Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology*, *84*, 451–462.
- Hirose, S., Chikazoe, J., Jimura, K., Yamashita, K., Miyashita, Y., & Konishi, S. (2009). Sub-centimeter scale functional organization in human inferior frontal gyrus. *Neuroimage*, *47*, 442–450.
- Kahana, M. J. (2006). The cognitive correlates of human brain oscillations. *The Journal of Neuroscience*, *26*, 1669–1672.
- Kennerley, S. W., Walton, M. E., Behrens, T. E. J., Buckley, M. J., & Rushworth, M. F. S. (2006). Optimal decision making and the anterior cingulate cortex. *Nature Neuroscience*, *9*, 940–947.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*, 169–195.
- McNaughton, N., & Corr, P. J. (2004). A two-dimensional neuropsychology of defense: Fear/anxiety and defensive distance. *Neuroscience and Biobehavioral Reviews*, *28*, 285–305.
- Moore, R. A., Gale, A., Morris, P. H., & Forrester, D. (2006). Theta phase locking across the neocortex reflects cortico-hippocampal recursive communication during goal conflict resolution. *International Journal of Psychophysiology*, *60*, 260–273.
- Nolen-Hoeksema, S. (2001). Gender differences in depression. *Current Directions in Psychological Science*, *10*, 173–176.
- Perkins, A. M., Kemp, S. E., & Corr, P. J. (2007). Fear and anxiety as separable emotions: An investigation of the revised reinforcement sensitivity theory of personality. *Emotion*, *7*, 252–261.
- Robbins, T. W. (2007). Shifting and stopping: Fronto-striatal substrates, neurochemical modulation and clinical implications. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *362*, 917–932.
- Shackman, A. J., McMennamin, B. W., Maxwell, J. S., Greischar, L. L., & Davidson, R. J. (2009). Right dorsolateral prefrontal cortical activity and behavioral inhibition. *Psychological Science*, *20*, 1500–1506.
- Sharp, D. J., Bonnelle, V., De Boissezon, X., Beckmann, C. F., James, S. G., Patel, M. C., et al. (2010). Distinct frontal systems for response inhibition, attentional capture, and error processing. *Proceedings of the National Academy of Sciences*, *107*, 6106–6111.
- Snedecor, G. W., & Cochran, W. G. (1967). *Statistical methods* (6th ed.). Ames: Iowa State University Press.
- Thayer, J. F., Rossy, L. A., Ruiz-Padial, E., & Johnsen, B. H. (2003). Gender differences in the relationship between emotional regulation and depressive symptoms. *Cognitive Therapy and Research*, *27*, 349–364.
- Trujillo, L. T., & Allen, J. J. B. (2007). Theta EEG dynamics of the error-related negativity. *Clinical Neurophysiology*, *118*, 645–668.
- Wacker, J., Chavanon, M. L., Leue, A., & Stemmler, G. (2010). Trait BIS predicts alpha asymmetry and P300 in a go/no-go task. *European Journal of Personality*, *24*, 85–105.
- Walton, M. E., Crosson, P. L., Behrens, T. E. J., Kennerley, S. W., & Rushworth, M. F. S. (2007). Adaptive decision making and value in the anterior cingulate cortex. *Neuroimage*, *36*, T142–T154.