



Task engagement and the relationships between the error-related negativity, agreeableness, behavioral shame proneness and cortisol

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Summary Previous results suggest that both cortisol mobilization and the error-related negativity (ERN/Ne) reflect goal engagement, i.e. the mobilization and allocation of attentional and physiological resources. Personality measures of negative affectivity have been associated both to high cortisol levels and large ERN/Ne amplitudes. However, measures of positive social adaptation and agreeableness have also been related to high cortisol levels and large ERN/Ne amplitudes. We hypothesized that, as long as they relate to concerns over social evaluation and mistakes, both personality measures reflecting positive affectivity (e.g. agreeableness) and those reflecting negative affectivity (e.g. behavioral shame proneness) would be associated with an increased likelihood of high task engagement, and hence to increased cortisol mobilization and ERN/Ne amplitudes. We had female subjects perform a flanker task while EEG was recorded. Additionally, the subjects filled out questionnaires measuring mood and personality, and salivary cortisol immediately before and after task performance was measured. The overall pattern of relationships between our measures supports the hypothesis that cortisol mobilization and ERN/Ne amplitude reflect task engagement, and both relate positively to each other and to the personality traits agreeableness and behavioral shame proneness. We discuss the potential importance of engagement–disengagement and of concerns over social evaluation for research on psychopathology, stress and the ERN/Ne.

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1. Introduction

The hormone cortisol has a wide range of physiological functions, including the mobilization of resources and stress-protective down-regulation of other physiological systems (Sapolsky et al., 2000). Mason (Mason et al., 2001) proposed the concept of an engagement-disengagement axis as the primary underlying dimension of the cortisol system (Ennis et al., 2001; Solberg Nes et al., 2005). In the context of post-traumatic stress disorder, Mason argues that the low cortisol levels reflect disengagement coping strategies, which represent secondary compensatory adaptations to counteract primary arousal symptoms, especially those related to an intractable shame-laden depression. The general pattern is below-normal cortisol levels when conditions involve little acutely superimposed psychosocial stress and a supportive setting in which disengagement coping mechanisms can be readily used. On the other hand, above-normal cortisol levels are observed when greater psychosocial stress is superimposed and situations make it more difficult to effectively use disengagement defences (Mason et al., 2001). This explains both the hypocortisolism in syndromes characterized by disengagement (e.g. depersonalization) responses, and the occasional findings of high cortisol responses in the same syndromes (Mason et al., 2001; Tops et al., 2006).

The catalyst for shame seems to be the way one's characteristics divide oneself from others (Ayers, 2003). Hence, negative social evaluation is a strong elicitor of shame and this emotion is thought to be designed to prevent rejection or separation (Ayers, 2003; Trumbull, 2003). Behavioral shame proneness predicts depressive symptoms (Andrews et al., 2002). Recent research has revealed that the strongest and most consistent cortisol responses in humans are evoked by shame, fear of negative social evaluation and threat of loss of control (Dickerson and Kemeny, 2004; Dickerson et al., 2004; Gruenewald et al., 2004). However, for individuals high in shame proneness, disengagement coping strategies may serve to protect against unmanageable shame-related emotional arousal (Dickerson et al., 2004a; Gruenewald et al., 2004; Mason et al., 2001). Dickerson et al. (2004a,b) propose that shame is part of an integrated psychobiological response that may be adaptive in uncontrollable situations when goal disengagement/withdrawal is the most functional response. This predicts that shame proneness relates to either increased or decreased cortisol levels in shame-inducing

settings, depending on the possibility of utilizing disengagement coping.

Evaluation of current performance has a role of central importance in the regulation of cognitive processes. The discovery of the neural correlates of performance evaluation has inspired an abundance of research in recent years. In particular, event-related potential (ERP) studies have revealed a neural response to errors that has been termed the error-related negativity (ERN) or error negativity (Ne), which is typically followed by the error positivity (Pe) (Falkenstein et al., 1990; Gehring et al., 1990). The ERN is a negative event-related potential (ERP) with a fronto-central scalp distribution, peaking 60-110 ms after an error response and is thought to be generated by the anterior cingulate cortex (ACC) (Dehaene et al., 1994; Wijers and Boksem, 2005). The rostral and dorsal ACC are implicated in tasks that require increased response control due to emotional and cognitive interference, respectively (Critchley et al., 2005). However, both rostral and dorsal ACC are activated by conditions that induce changes in visceral arousal, suggesting that ACC supports a generation of integrated bodily responses (Critchley et al., 2005). A large meta-analysis of PET studies (Paus et al., 1998) showed that the common denominator of ACC activation across many task conditions is the level of task engagement, i.e. the amount of effort, which has to be engaged in a task.

Compared to the ERN, the functional significance of the Pe is markedly less substantiated. This ERP component typically follows the ERN and consists of a slow positive going deflection that reaches its maximum between 200 and 400 after subjects make an error. Its distribution is quite diffuse, but appears slightly more posterior compared to the ERN (Falkenstein, Hoormann and Christ, 2000).

Similar to studies of ACC function, recent studies of the ERN have increasingly focused on the motivational, emotional and/or reward-related processes that are often part of the optimal performance of cognitive tasks, and on the control of the autonomic responses that accompany cognitive effort in humans (see e.g. Hajcak, McDonald and Simons, 2003). The ERN has been observed following error responses and also when outcomes are 'worse than expected', suggesting that the ERN reflects not only the detection of errors but also error salience. Luu et al. (2000) found that high-negative affectivity subjects, who were dissatisfied with their performance, showed a characteristic pattern of overengaging and then disengaging from the task, as reflected in the amplitude of the ERN during prolonged task performance. Another finding

is that when subjects were told that their performance was being evaluated on-line by a research assistant, and that the research assistant would compare the subject's performance to other subjects who had performed the task, ERN amplitudes were larger compared to a control condition (Hajcak et al., 2005). This not only implies that the more certain the individual is in having erred, the larger the ERN amplitude, but also the more engaged in the task the individual is, the larger the ERN (Santesso et al., 2005). Hyperactivity of the ACC and a pronounced ERN may reflect task engagement and/or (e.g. socially motivated) concern over the outcome of an event.

In one of our previous studies, the personality factor agreeableness, which measures positive psychological adaptation and low irritability, correlated positively with morning cortisol level (Tops et al., 2006). A positive association between agreeableness and cortisol levels had been reported before in male Navy recruits (Vickers et al., 1995). Indeed, negative relationships have been found between agreeableness scores and depersonalization (Foss, 2002), dissociative experiences including depersonalization (Goldberg, 1999), behavioral disengagement coping (Hettler, 2001), self-reported stress (Hao and Long, 2003), and a positive relationship with the use of active coping strategies (Hettler, 2001; Medvedova, 1998). Agreeableness relates to higher positive affectivity (e.g. DeNeve and Cooper, 1998). A recent study of 10-year olds found that a measure of social sensitivity, positive adaptation and sensitivity to social expectations similar to agreeableness (Aluja et al., 2004; Stöber, 2001) related to a larger ERN (but not Pe), lending support to similar findings in adults (Santesso et al., 2005). This suggests a higher concern over mistakes (or, alternatively, enjoyment of performing well and fulfilling expectations) and engagement in task performance in individuals scoring high on agreeableness (Santesso et al., 2005).

Following from the above considerations, we expect cortisol mobilization and the amplitude of the ERN to reflect task engagement. Hence, we expect both to relate positively to each other and to personality traits that should increase the likelihood of high task engagement: behavioral shame (fear of negative social evaluation and mistakes) and agreeableness (concern over social evaluation and mistakes). Alternatively, behavioral shame may not display the hypothesized relationships, since it is also associated with disengagement coping strategies, which may serve to protect against unmanageable shame-related emotional arousal. In the present study, we had female subjects aged 18-26 years perform a flanker task

while electroencephalographic activity was recorded. Additionally, the subjects filled out relevant questionnaires measuring mood and personality, and salivary cortisol immediately before and after task performance was measured.

2. Methods

2.1. Subjects

Twenty-four healthy participants (females), between 18 and 26 ($M=20$, $SD=3.4$) years of age, were recruited from the university population. They were paid for their participation and had normal or corrected-to-normal vision. None of the subjects worked night shifts or used prescription medication. Written informed consent was obtained prior to the study. Three participants described themselves as being left handed. As removal of these subjects from the analyses did not change the pattern of results substantially, these subjects were included in all analyses. Three subjects had a cortisol value at one point of measurement that was higher than the group average plus three standard deviations. These subjects were excluded from analyses in order to reduce the impact of outliers. From two subjects both the pre-task and post-task cortisol levels were missing due to an insufficient amount of saliva; from one subject only the post-task cortisol level was missing. This leaves a final number of 18 subjects in analyses involving post-task cortisol levels or cortisol decrease during the task, 19 subjects in analyses involving pre-task cortisol levels, and 21 subjects in all other analyses.

2.2. Task

We used a version of the Eriksen Flanker Task (Eriksen and Eriksen, 1974). On each trial, a five-letter string was presented. The central letter was the target, the remaining letters the flankers. The stimuli used for targets and flankers were the letters H and S. During the entire task, a fixation mark was displayed 0.14° above the target letter. On congruent trials the target letter was the same as the flankers (SSSSS or HHHHH); on incongruent trials the target letter differed from the flankers (SSHSS or HSHHH). 40% of the trials consisted of incongruent stimuli and 60% consisted of congruent stimuli. Congruent and incongruent trials were presented in random order.

The stimuli were presented on a 17 inch monitor. The letters were white against a black

background and each letter had a height and width of 0.24° visual angle. Eriksen and Eriksen (1974) showed that reaction times and error rates were highest when letters were presented close together. Therefore, we presented letters 0.05° apart. The complete five-letter string had a width of 1.43° visual angle.

In addition, flankers were presented 100 ms prior to target onset to maximize the expected flanker compatibility effect (Kopp et al., 1996). Target and flankers disappeared simultaneously at the moment a response was made. In case, no response was given; targets and flankers disappeared after 1200 ms. The interstimulus interval was 3 s. Participants received six blocks of 400 trials. Each block had a total duration of 20 min.

After six blocks, participants received additional information by means of a text message on the screen: the reward condition. Participants were informed that they were about to begin the last part of the experiment and that they could earn points by responding correctly. For each correct response, participants would receive 10 points. For every incorrect response, participants would lose 20 points. Responding too slow, or not at all, resulted in no points. Finally, participants were told that their performance would be compared to other participants; the 10 participants with the highest score would receive an extra monetary reward of 20 euros. After this information, a last block consisting of 388 trials was presented. After every 97 trials participants received feedback about the number of points they scored. The duration of the complete task was 2 h and 20 min.

2.3. Questionnaires

2.3.1. Experience of shame scale (ESS)

This 25-item questionnaire was used to measure the disposition to experience shame. The ESS contains three subscales: characterological shame (range: 12-48), behavioral shame (range: 9-36), and bodily shame (range: 4-16) (Andrews et al., 2002).

2.3.2. Five factor personality inventory (FFPI)

We used the 100-item FFPI to assess Extraversion, Agreeableness, Conscientiousness, Neuroticism and Autonomy (Hendriks et al., 1999).

2.3.3. Profile of mood states (POMS)

The 32-item POMS were used to assess mood before and after participants completed the experimental task. The five subscales measure depression, fatigue, vigor, anger and tension (Wald and Mellenberg, 1990).

2.4. Saliva cortisol

Saliva samples were taken with a Salivette (Sarstedt Inc., Rommelsdorf, Germany) immediately before and after task performance. Analyses of saliva cortisol were performed in the biochemical laboratory of the University of Trier. Saliva samples were stored at -20 °C until analysis. Cortisol concentration in saliva was measured using a time-resolved fluorescence immunoassay, as described in detail in Dressendörfer et al. (1992).

2.5. Procedure

Subjects were instructed to abstain from alcohol 24 h before the experiment and from caffeine containing substances 12 h before the experiment. After arrival at the laboratory at 12.00 h, subjects were given written task instructions where after they were trained in performing the task, for 15 min. Following the application of the electrodes, subjects were seated in a dimly lit, sound-attenuated, electrically shielded room at 1.20 m from the screen and they were asked to fill out the POMS and provide the first saliva sample. Their index fingers rested on touch-sensitive response boxes. Subjects were instructed to lift their finger from the response button as quickly as possible when a target was presented, maintaining a high level of accuracy. Immediately following the task, participants were asked to fill out the POMS again and to provide a second saliva sample.

2.6. Electrophysiological recording and data reduction

The electroencephalogram (EEG) was recorded using four Sn Electrodes attached to an electro cap (Electro-Cap International), from positions Fz, FCz, Cz and Pz. All electrodes were referenced to linked earlobes. The electro-oculogram (EOG) was recorded bipolarly from the outer canthi of both eyes and above and below the left eye, using Sn electrodes. Electrode impedance was kept below 5 kΩ. EEG and EOG were amplified with a 10 s time constant and a 200 Hz low pass filter, sampled at 1000 Hz, digitally low pass filtered with a cut-off frequency of 70 Hz, and online reduced to a sample frequency of 250 Hz.

All ERP analyses were performed using the Brain Vision Analyzer software (Brain Products). ERPs were averaged off-line. The data was further filtered with a 0.53 Hz high-pass filter and a slope of 48 dB/oct and a 40 Hz low-pass filter with a slope of 48 dB/oct. Out of range artefacts were rejected

and eye movement artefacts were corrected, using the Gratton, Coles and Donchin method (Gratton et al., 1983). A baseline voltage over the 200 ms interval preceding the response was subtracted from the averages.

2.7. Data analysis

2.7.1. Performance

For the different stimulus conditions mean reaction times (RTs) were calculated. Correct reactions occurring within a 150-1000 ms interval after stimulus presentation were considered as hits. The percentage of false alarms and misses were also determined. Because misses were very rare, we will focus here on hits and false alarms. To investigate strategic performance changes after error detection, we also analyzed RTs on trials following an error or a correct response (i.e. post-error slowing). Additionally, we calculated a measure of speed-accuracy trade-off according to the method used by Nietfeld and Bosma (2003).

2.7.2. ERPs

Mean ERN/Ne, Pe and N2 amplitudes were calculated at Cz, the mean P3 amplitude was calculated at Pz, where visual inspection showed these components were maximal. The averaging epoch for the ERN/Ne and CRN (Correct response-Related Negativity) was between 28 and 100 ms post-response. The averaging epoch for the Pe was from 164 to 360 ms post-response. The N2 was quantified as the average amplitude in the 400-440 ms post-stimulus time interval. The averaging epoch for the P3 was from 400 to 600 ms post-stimulus.

As another measure of the nature of any observed ERN effects, a second common quantification of the ERN was computed: we subtracted the CRN from the ERN (e.g. Luu et al., 2000). This difference ERN, to which we will refer as Δ ERN, essentially reflects the remaining ERN amplitude variation that is specific to the commission of an error.

3. Results

3.1. Performance measures

Reaction times were longer for incongruent stimuli ($M=513$, $SD=62$) compared to congruent stimuli ($M=455$, $SD=88$; $F(1,20)=198.00$, $p<0.001$). Also more errors were committed with incongruent stimuli ($M=0.14$, $SD=0.04$) compared to congruent

stimuli ($M=0.04$, $SD=0.02$; $F(1,20)=50.54$, $p<0.001$). A main effect for post-error slowing was found: reaction times were on average longer on trials following an incorrect response ($M=476$ ms, $SD=14$) compared to reaction times on trials following a correct response ($M=466$ ms, $SD=15$; $F(1,20)=4.08$, $p=0.029$ (one-tailed)).

We performed correlational analyses including the following performance measures: reaction times, percentage of false alarms, post-error slowing, the incongruent–congruent difference in reaction times and percentage of false alarms, and speed-accuracy trade-off (Nietfeld and Bosma, 2003). Personality and cortisol did not relate significantly to performance measures. There were some trends, though. For instance, pre-task cortisol level correlated with post-error slowing in the first block ($r=0.50$, $p=0.030$). Agreeableness generally tended to relate to longer reaction times, less errors, and a speed-accuracy trade-off favoring accuracy ($r=0.36$, $p=0.11$). Behavioral shame proneness did not tend to relate to performance measures.

3.2. Mood, personality and cortisol

The average POMS mood and personality questionnaire scores and cortisol levels of the subjects are displayed in Table 1. The means in the table are

Table 1 Mean score and standard deviations of the subscales of the five-factor personality inventory (FFPI), experience of shame scale (ESS), profile of mood states (POMS), and salivary cortisol levels.

	Mean	SD
<i>FFPI</i>		
Extraversion	0.95	1.11
Agreeableness	2.39	0.97
Conscientiousness	0.63	0.98
Neuroticism	−0.08	1.29
Autonomy	0.58	0.91
<i>ESS</i>		
Behavioral shame	22.62	6.82
Characterological shame	27.43	10.17
Bodily shame	8.33	3.64
<i>POMS (pre-task/post-task)</i>		
Depression	0.79/1.42	1.55/2.71
Fatigue	2.74/9.95	1.94/5.84
Vigor	10.79/3.63	3.72/3.15
Anger	0.74/5.00	1.63/4.57
Tension	1.53/1.26	2.27/2.83
<i>Salivary cortisol (pre-task/post-task)</i>		
Cortisol level (nmol/l)	7.34/5.70	3.42/2.36

close to published norms (Andrews et al., 2002; Hendriks et al., 1999; Wald and Mellenberg, 1990). From pre-task to post-task there were significant increases in fatigue ($t(20) = -5.14$, $p < 0.001$) and anger ($t(20) = -5.06$, $p < 0.001$), while vigor decreased ($t(20) = 10.87$, $p < 0.0001$) and cortisol tended to decrease ($t(17) = 1.83$, $p = 0.085$).

3.3. ERPs, performance

In addition to the hypotheses addressed in this article, the present experiment was also designed to measure the effects of time-on-task and of a reward manipulation on performance and ERPs, to test the dopamine theory of mental fatigue (Tops et al., 2004). The results relating to time-on-task are presented elsewhere (Boksem et al., 2006b). In short, the ERN amplitude decreased, reaction times and error rates increased with time-on-task. After the reward manipulation, ERN amplitude increased and reaction times and error rates decreased (Boksem et al., 2006b). Performance measures did not correlate significantly to ERN amplitude.

3.4. Relations between personality, ERPs and cortisol

In this section, we report on average ERP amplitudes from before the reward manipulation; relations with ERP amplitudes from after the reward manipulation are reported in a separate section. Table 2 shows the correlations between the ERN, cortisol, agreeableness, behavioral shame, and some mood measures. Other correlations that reached or approached significance were between increase in anger and pre-task cortisol ($r = -0.43$, $p < 0.10$) as well as cortisol decrease ($r = -0.48$, $p < 0.05$); between pre-task tension and agreeableness ($r = -0.59$, $p < 0.01$); between pre-task tension and pre-task cortisol ($r = -0.43$, $p < 0.10$); and between increase in tension and agreeableness ($r = 0.44$, $p < 0.10$) as well as behavioral shame ($r = 0.49$, $p < 0.05$).

There were no significant correlations with Pe amplitude.

As can be seen in Table 2, the cortisol decrease during the task showed a large positive correlation with the pre-task cortisol level, but it did not correlate significantly with the post-task cortisol level. The cortisol decrease correlated negatively with ERN amplitude. However, the Δ ERN displayed larger negative correlations to both the pre-task cortisol level and the cortisol decrease.

Agreeableness showed a large positive correlation with pre-task cortisol, and also correlated positively with the cortisol decrease during the task, and with ERN amplitude. Behavioral shame correlated negatively with the ERN, but did not correlate with cortisol measures. When we calculated correlations separately for each of six time intervals, the correlation of agreeableness with ERN amplitude decreased over the intervals. Behavioral shame and the cortisol measures did not show this pattern. Fig. 1 shows scatterplots of the most prominent correlations and Fig. 2 shows the ERP waveforms at Cz.

In order to evaluate the predictive value of personality and cortisol on ERN amplitude, a multiple stepwise regression analysis was performed, including the variables agreeableness, behavioral shame proneness, and cortisol decrease. The results of the regression are summarized in Table 3. The equation explained 46% of the variance of ERN amplitude. Behavioral shame proneness and cortisol decrease contributed significantly to the prediction of ERN amplitude. Agreeableness, which correlated with cortisol decrease and shame proneness, did not explain additional variance (partial $r = -0.33$, $p = 0.157$). When agreeableness was entered first, the effect of shame was no longer significant (partial $r = -0.38$, $p = 0.102$).

A similar stepwise regression analysis was performed, including the same variables, to predict Δ ERN (see Table 3). Here, the only significant predictor of Δ ERN was cortisol decrease, explaining 60% of variance.

Table 2 Pearson correlations between measures.

	Agreeableness	Behavioral shame	Pre-task cortisol	Cortisol decrease
Agreeableness				
Behavioral shame	0.23			
Pre-task cortisol	0.68*	0.21		
Cortisol decrease	0.50**	0.28	0.68*	
ERN	-0.50**	-0.53**	-0.35	-0.54**
Δ ERN	-0.31	-0.09	-0.73***	-0.83***

* $p < 0.01$; ** $p < 0.05$; *** $p < 0.001$. Note: Greater negativity of the ERN indicates greater amplitude.

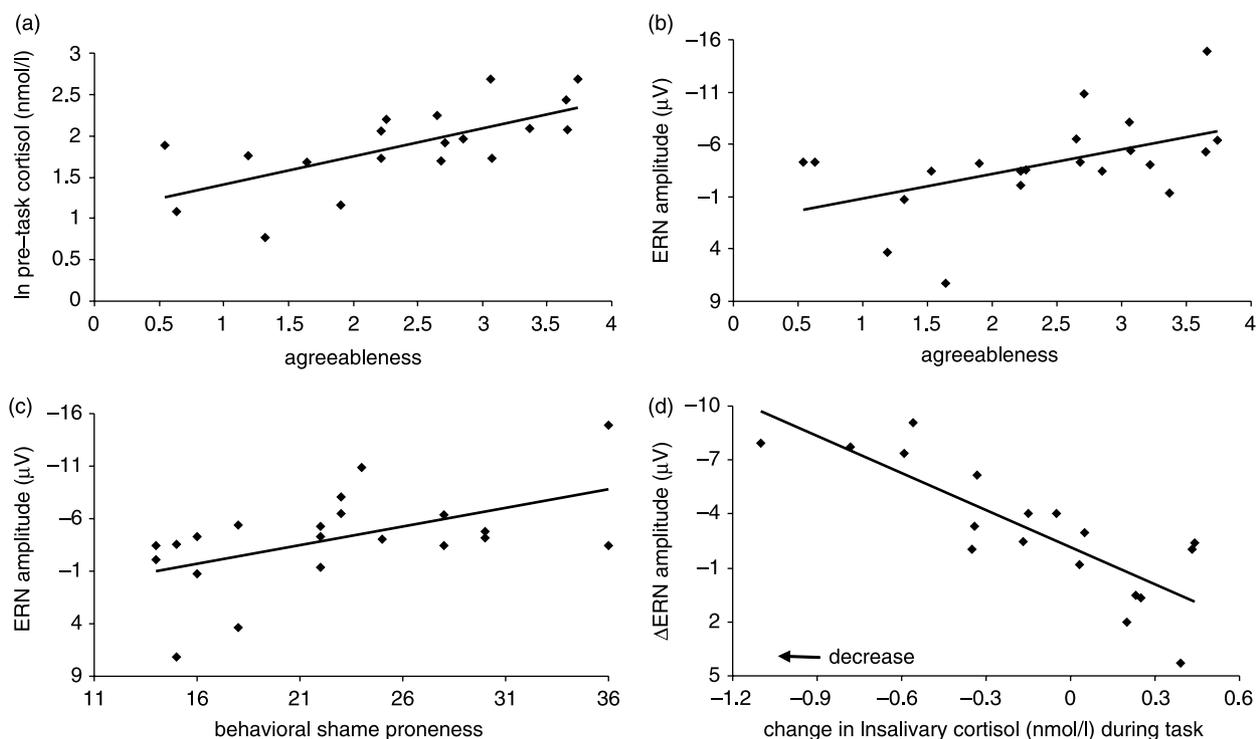


Figure 1 Scatterplot of the relationship between (a) agreeableness and pre-task cortisol levels; (b) agreeableness and ERN amplitude; (c) behavioral shame and ERN amplitude; (d) the change in cortisol and the Δ ERN (ERN-CRN). Note: Greater negativity of the ERN indicates greater amplitude; negative amplitude is displayed in the upward direction.

3.5. The reward manipulation

The ERN and Δ ERN in the interval after the reward manipulation did not show significant correlations with any of the mood, personality or cortisol measures, except for neuroticism. Neuroticism correlated with a larger negative ERN amplitude ($r = -0.68$, $p < 0.001$) and a larger CRN amplitude ($r = -0.46$, $p = 0.044$). Neuroticism also correlated with a larger effect of the reward manipulation, operationalized as the amplitude in the last pre-reward interval subtracted from the post-reward amplitude, for both the ERN ($r = -0.67$, $p = 0.002$) and the Δ ERN ($r = -0.54$, $p = 0.016$). Neuroticism did not correlate with ERN amplitude on any of the intervals before the reward manipulation, but it did correlate with a larger pre-reward CRN amplitude ($r = -0.46$, $p = 0.044$). Partial correlations with neuroticism remained significant after partialling out either scores on agreeableness or behavioral shame proneness.

3.6. Other ERPs

No significant correlations were found between personality or cortisol measures and N2, P3 or Pe amplitudes.

4. Discussion

Previous results suggest that both cortisol mobilization and the ERN reflect goal engagement, i.e. the mobilization and allocation of attentional and physiological resources. Personality measures of negative affectivity have been associated both to high cortisol levels and large ERN amplitudes. However, measures of positive social adaptation and agreeableness have also been related to high cortisol levels and large ERN/Ne amplitudes. We hypothesized that, as long as they relate to concerns over social evaluation and mistakes, both personality measures reflecting positive affectivity (i.e. agreeableness) and those reflecting negative affectivity (i.e. behavioral shame proneness) would be associated with an increased likelihood of high task engagement, and hence to increased cortisol mobilization and ERN amplitudes.

There was a strong relationship between pre-task cortisol levels and the decrease in cortisol during the task: subjects with a higher pre-task cortisol level showed a larger decrease in cortisol during the task. In line with earlier findings (Ennis et al., 2001; Lewis and Ramsay, 2002), we assume that high cortisol levels just before the start of task performance and the associated larger decrease during performance reflect a mobilization of resources for the

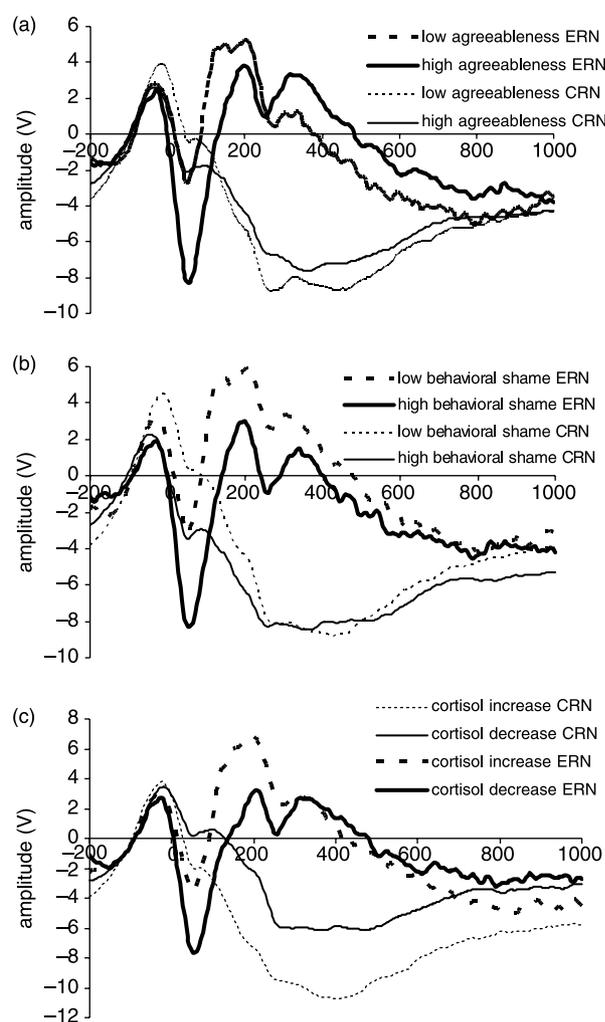


Figure 2 Response-locked ERP waveforms at Cz for (a) incorrect responses by subjects scoring high (strong line) or low (thin line) on agreeableness (b) incorrect responses by subjects scoring high (strong line) or low (thin line) on behavioral shame proneness (c) both correct (thin lines) and incorrect (strong lines) responses for subjects showing a high decrease (solid lines) or no decrease/small increase (dashed lines) in salivary cortisol levels during the task. Groups were formed by median split, for illustrative purposes.

performance of what the subjects knew was going to be a long and demanding task; hence they should relate positively to task engagement. Agreeableness correlated positively to both the pre-task cortisol level and the cortisol decrease, while it correlated negatively to pre-task tension but positively to the increase in tension during the task. A negative relationship between agreeableness and measures of anxiety is a usual finding (e.g. [Hao and Long, 2003](#)). Besides agreeableness, also behavioral shame correlated positively with the increase in tension during task performance. This may reflect a concern over task performance that is related to both personality measures; since performance deteriorated with time-on-task ([Boksem et al., 2006b](#)), subjects with greater concerns over their level of performance are more likely to have experienced increases in tension.

Consistent with higher levels of task engagement in subjects who scored high on agreeableness or on behavioral shame, both personality measures related positively to the size of the ERN. The decrease of the relationship between agreeableness and ERN amplitude with time-on-task may reflect the decrease in task engagement with time-on-task ([Boksem et al., 2006b](#); [Luu et al., 2000](#)). Consistent with a positive relationship between cortisol mobilization processes and task engagement, pre-task cortisol levels and cortisol decreases during performance related positively to the size of both the ERN and Δ ERN. Overall, the pattern of relationships between our measures supports the hypothesis that cortisol mobilization and ERN amplitude reflect task engagement, and both relate positively to each other and to the personality traits agreeableness and behavioral shame proneness. Similar to previous studies (e.g. [Hajcak et al., 2004](#); [Santesso et al., 2005](#)), we did not find relevant relationships between personality and performance. We did not find relations between performance and ERN amplitude. We

Table 3 Stepwise regression analyses.

Variables in the equation		Parameters estimates			Model significance and <i>r</i> square		
		Beta	<i>t</i>	Prob.	<i>F</i>	Sig.	<i>r</i> Square
<i>Dependent variable: ERN</i>							
1 Step	Cortisol decrease	0.54	2.80	0.011	7.85	0.011	0.292
2 Step	Behavioral shame	-0.42	-2.35	0.030	7.62	0.004	0.458
<i>Dependent variable: ΔERN</i>							
1 Step	Cortisol decrease	0.78	5.37	<0.001	28.81	<0.001	0.603

also found no relationship between personality or cortisol and the amplitude of the Pe.

However, two aspects of our results need further discussion. Firstly, although cortisol correlated with both Δ ERN and ERN amplitude, agreeableness and behavioral shame correlated with ERN but not with Δ ERN amplitude. This may be explained by other studies that found that measures of trait negative affectivity relate to larger ERN amplitudes, but also tend to relate to larger CRN amplitudes (the 'ERN' on correct trials) (Hajcak et al., 2004). Especially the behavioral shame scores also tended to relate to larger CRN amplitudes in the present study (see Fig. 2b). Since, Δ ERN is the CRN amplitude subtracted from the ERN amplitude, a same-sign correlation between both ERN and CRN amplitude and the personality trait would decrease or abolish the correlation between Δ ERN and the personality trait. Hajcak et al. (2004) suggested that the positive relationship between CRN amplitude and trait negative affectivity reflects a higher concern over performance also on correct trials. The absence of a CRN amplitude increase in response to an explicit on-line performance evaluation condition as reported by Hajcak et al. (2005) seems inconsistent with this interpretation. However, it remains possible that increased CRN amplitude in conditions of social evaluative concerns relates to individual differences measures like behavioral shame proneness and negative affectivity, and to neuroticism when the significance of performance is increased by a reward manipulation. On the other hand, cortisol may relate differently to ERN compared to CRN amplitudes. For instance, the mobilization of resources as indicated by cortisol, may increase the efficiency of performance monitoring processes, and this may increase the amplitude of the ERN relative to the CRN, and hence increase Δ ERN.

The second aspect of our results that needs discussion is the lack of a correlation between behavioral shame proneness and the cortisol measures. This lack of a correlation is not unexpected. As explained in Section 1, shame proneness should relate to concern over negative social evaluation, and hence probably to task engagement in some situations, but also to disengagement coping in other situations. In a previous study we found that, whereas agreeableness consistently related positively to early morning cortisol mobilization, fear of negative social evaluation related to cortisol mobilization in a direction that depended on the application of either engagement or disengagement coping responses (Tops et al., 2006). Also, it has been suggested that for shame proneness to relate to higher cortisol responses, a shame provocation manipulation and a social-evaluative setting are

necessary (Dickerson et al., 2004b). However, the association of behavioral shame with both larger ERN amplitude and with increases in tension during performance suggest that behavioral shame did in fact relate to higher engagement during task performance. Still, more of the high behavioral shame subjects may have used disengagement coping strategies in anticipation of task performance, displaying less cortisol mobilization. While it may have been easier to use disengagement defences before task performance, the actual on-line social evaluation during performance by the experimenter, combined with limited stress levels may have decreased the likelihood of disengagement coping during task performance (Mason et al., 2001). This would explain the presence of a correlation between behavioral shame proneness and ERN amplitude (engagement during performance) and the absence of a correlation between behavioral shame proneness and cortisol (mobilization before task performance). Future experiments may try to use convergent measures of engagement at different time-points during the experiment, to check the correctness of our interpretation.

The relationship between high neuroticism and larger increase in ERN/CRN amplitudes after a reward manipulation is a replication of a similar finding by Pailing and Segalowitz (2004). Those authors found that as the incentives for accuracy increased, subjects scoring high on neuroticism increased task engagement ('invested more attentional resources') as measured by ERN amplitude.

A large metaanalysis of PET studies (Paus et al., 1998) showed that the common denominator of ACC activation across many task conditions is the level of task engagement, i.e. the amount of effort, which has to be engaged in a task. A recent prominent theory on the ERN suggests that a mesencephalic dopaminergic projection to the ACC is involved in the generation of the ERN (Holroyd and Coles, 2002). It has been proposed that dopaminergic activity at the level of the ACC is essential in the willingness to exert effort and to overcome response costs¹ (Walton et al., 2005). Similarly, Larsen et al. (2003); also Folkman and

¹ Although Walton et al. (2005) recently found that the mesocortical dopaminergic projection to the ACC is not directly involved in effort-related decisions, indirect projections to the ACC may be involved. For instance, one of the areas projecting to the ACC, the insula, receives mesolimbic dopaminergic input and its activity relates to subjective perceptions of effort sense and exertion (de Graaf et al., 2004; Williamson et al., 1999). Like the ACC, the insula seems to have a necessary role in the normal occurrence of the ERN (Ullsperger et al., 2002; Ullsperger and Cramon, in press).

Moskowitz, (2000) suggest that stressors should co-activate positive affect (dopaminergic) approach/appetition systems to overcome simultaneous activation of negative affect (cholinergic) avoidance/aversion systems to enable active, problem-focused coping. The level of activation of this dopaminergic mechanism of effort-allocation and engagement may be reflected in the amplitude of the ERN (Boksem et al., 2006a,b; Lorist et al., 2005). This is supported by a study in which amphetamine administration increased ERN amplitudes, feeling of alertness and subjective level of performance, without affecting actual performance (De Bruijn et al., 2004), and another study in which administration of the dopamine antagonist haloperidol reduced ERN amplitudes (Zirnheld et al., 2004).

The positive association between the size of the ERN and behavioral shame proneness as well as neuroticism in the present study replicates similar findings regarding relationships of trait negative affectivity and neuroticism with ERN amplitude (Hajcak et al., 2005; Pailing and Segalowitz, 2004). However, the similar association between agreeableness and ERN amplitude suggests that it is not negative affectivity per se that is associated with ERN amplitude. Agreeableness relates to positive psychological adaptation, active coping, high positive affect and low negative affect (see the Introduction). Alternatively, it has been suggested that the ERN reflects subjective reactions to errors: Subjectively, errors induce strong emotions of frustration and irritation (Yeung, 2004). However, frustration is the negative pole of agreeableness, and we did not find a correlation with increase in anger, arguing against a direct relation between error emotions and ERN amplitude. However, as suggested in the introduction, agreeableness and behavioral shame proneness have in common a concern over social evaluation. Concern over social evaluation may increase task engagement, and this increase in engagement may be reflected in the ERN amplitude (Boksem et al., 2006a,b; Santesso et al., 2005; Luu et al., 2000). Since, measures of fear of negative social evaluation correlate positively with measures of negative affectivity and neuroticism (e.g. Tops et al., 2006), increased task engagement may be a confounder in previously reported associations between negative affectivity and ERN amplitude (Hajcak et al., 2005; Luu et al., 2000).

Cortisol levels were assessed during a single session. Individual differences in cortisol measures are better assessed by aggregating over multiple sessions (Pruessner et al., 1997). Hence, if

compatible with the study design, future studies should preferably employ average levels over multiple sessions.

The possible important role of engagement-disengagement in psychophysiological research may also be relevant to research on psychopathology (Mason et al., 2001; Tops et al., 2006). For instance, atypical depression is characterized by hypocortisolism, rejection sensitivity/fear of negative social evaluation and disengagement responses (Gold and Crousos, 1998; Tops et al., 2006). In contrast, typical, melancholic depression is characterized by an inability to disengage from painfully charged memories and hypercortisolism (Gold and Crousos). Tucker et al. (2003) found that the ERN was increased or decreased in depressed subjects, depending on the severity of depression; Tucker et al. proposed that this reflected disengagement from the task by the more severely depressed subjects. Tucker et al. suggested that altered ERN amplitude and ACC and insula activity in depression parallels the role of a network including ACC and insula in both physical pain and social separation/rejection pain (e.g. shame, see also Eisenberger et al., 2003; Najib et al., 2004; Panksepp, 2005). Physiologically, error detection is accompanied by skin conductance responses and changes in heart rate (Hajcak et al., 2003, 2004), and both ACC and (especially) the insula are implicated in such responses (Kuniecki et al., 2003), as well as in cortisol and energy (glucose) regulation (Allport et al., 2004; Christensen et al., 2004; Ottowitz et al., 2004) and error-related processes (Menon et al., 2001). Additionally, both ACC and insula have a necessary role in the normal occurrence of the ERN (Ullsperger et al., 2002; Ullsperger and Cramon, in press) and are implicated by neuroimaging studies in depersonalization (Lanius et al., 2005; Phillips et al., 2001) and in risk-avoidance and punishment in relation to neuroticism (Paulus et al., 2003). Interestingly, administration of the anxiolytic benzodiazepine lorazepam has been related to decreased cortisol mobilization (Collomp et al., 1994; Hellhammer et al., 1988), decreased ERN amplitude (De Bruijn et al., 2004) and decreased insula activity (Paulus et al., 2005).

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References

- Allport, L.E., Butcher, K.S., Baird, T.A., MacGregor, L., Desmond, P.M., Tress, B.M., Colman, P., Davis, S.M., 2004. Insular cortical ischemia is independently associated with acute stress hyperglycemia. *Stroke* 35, 1886-1891.
- Aluja, A., Garcia, O., Garcia, L.F., 2004. Replicability of the three, four and five Zuckerman's personality super-factors: exploratory and confirmatory factor analysis of the EPQ-RS, ZKPQ and NEO-PI-R. *Pers. Individ. Dif.* 36, 1093-1108.
- Andrews, B., Qian, M., Valentine, J.D., 2002. Predicting depressive symptoms with a new measure of shame: the experience of shame scale. *Br. J. Clin. Psychol.* 41, 29-42.
- Ayers, M., 2003. *Mother-infant Attachment and Psychoanalysis: The Eyes of Shame*. Brunner-Routledge, New York.
- Boksem, M.A.S., Meijman, T.F., Lorist, M.M., 2006a. Mental fatigue, motivation and action monitoring. *Biol. Psychol.* 72, 123-132.
- Boksem, M.A.S., Tops, M., Wester, A.E., Meijman, T.F., Lorist, M.M., 2006. Anatomizing the ERN. Manuscript submitted for publication.
- Christensen, H., Boysen, G., Johannesen, H.H., 2004. Serum-cortisol reflects severity and mortality in acute stroke. *J. Neurol. Sci.* 217 (2), 175-180.
- Collomp, K., Fortier, M., Cooper, S., Long, A., Ahmaidi, S., Prefaut, C., Wright, F., Picot, M., Cote, M.G., 1994. Performance and metabolic effects of benzodiazepine during suboptimal exercise. *J. Appl. Physiol.* 77 (2), 828-833.
- Critchley, H.D., Tang, J., Glaser, D., Butterworth, B., Dolan, R.J., 2005. Anterior cingulate activity during error and autonomic response. *NeuroImage* 27, 885-895.
- De Bruijn, E.R.A., Hulstijn, W., Verkes, R.J., Ruigt, G.S.F., Sabbe, B.G.C., 2004. Drug-induced stimulation and suppression of action monitoring in healthy volunteers. *Psychopharmacology* 177, 151-160.
- de Graaf, J.B., Gallea, C., Pailhous, J., Anton, J.-L., Roth, M., Bonnard, M., 2004. Awareness of muscular force during movement production: an fMRI study. *Neuroimage* 21, 1357-1367.
- Dehaene, S., Posner, M.I., Tucker, D.M., 1994. Localization of a neural system for error detection and compensation. *Psychol. Sci.* 5, 303-305.
- DeNeve, K.M., Cooper, H., 1998. The happy personality: a meta-analysis of 137 personality traits and subjective well-being. *Psychol. Bull.* 124 (2), 197-229.
- Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. *Psychol. Bull.* 130, 355-391.
- Dickerson, S.S., Gruenewald, T.L., Kemeny, M.E., 2004a. When the social self is threatened: shame, physiology, and health. *J. Pers.* 72 (6), 1191-1216.
- Dickerson, S.S., Kemeny, M.E., Aziz, N., Kim, K.H., Fahey, J.L., 2004b. Immunological effects of induced shame and guilt. *Psychosom. Med.* 66, 124-131.
- Dressendorfer, R.A., Kirschbaum, C., Rohde, W., Stahl, F., Strasburger, C.J., 1992. Synthesis of a cortisol-biotin conjugate and evaluation as a tracer in an immunoassay for salivary cortisol measurement. *J. Steroid Biochem. Mol. Biol.* 43 (7), 683-692.
- Eisenberger, N.I., Lieberman, M.D., Williams, K.D., 2003. Does rejection hurt? An fMRI study of social exclusion. *Science* 302, 290-292.
- Ennis, M., Kelly, K.S., Lambert, P.L., 2001. Sex differences in cortisol excretion during anticipation of a psychological stressor: possible support for the tend-and-befriend hypothesis. *Stress Health* 17, 253-261.
- Eriksen, B.A., Eriksen, C.W., 1974. Effects of noise letters upon the identification of target letters in visual search. *Percept. Psychophys.* 16, 142-149.
- Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1990. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, C.H.M., Gaillard, A.W.K. (Eds.), *Psychophysiological Brain Research*. Tilburg University Press, Tilburg, pp. 192-195.
- Falkenstein, M., Hoormann, J.B., Christ, S., 2000. ERP components on reaction errors and their functional significance: a tutorial. *Biol. Psychol.* 51, 87-107.
- Folkman, S., Moskowitz, J.T., 2000. Stress, positive emotion, and coping. *Cur. Dir. Psychol. Sci.* 9, 115-118.
- Foss, R.W., 2002. Burnout among clergy and helping professionals: situational and personality correlates. *Diss. Abstr. Intern. B: Sci. Engineer.* 63 (3-B), 1596.
- Gehring, W.J., Coles, M.G.H., Meyer, D.E., Donchin, E., 1990. The error-related negativity: an event-related brain potential accompanying errors. *Psychophysiology* 27, S34.
- Gold, P.W., Crousos, G.P., 1998. The endocrinology of melancholic and atypical depression: relation to neurocircuitry and somatic consequences. *Proc. Assoc. Am. Physicians* 111 (1), 22-34.
- Goldberg, L.R., 1999. The curious experiences survey, a revised version of the dissociative experiences scale: factor structure, reliability, and relations to demographic and personality variables. *Psychol. Assess.* 11 (2), 134-145.
- Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468-484.
- Gruenewald, T.L., Kemeny, M.E., Aziz, N., Fahey, J.L., 2004. Acute threat to the self: shame, social self-esteem, and cortisol activity. *Psychosom. Med.* 66, 915-924.
- Hajcak, G., McDonald, N., Simons, R.F., 2003. Anxiety and error-related brain activity. *Biol. Psychol.* 64, 77-90.
- Hajcak, G., McDonald, N., Simons, R.F., 2004. Error-related psychophysiology and negative affect. *Brain Cogn.* 56, 189-197.
- Hajcak, G., Moser, J.S., Yeung, N., Simons, R.F., 2005. On the ERN and the significance of errors. *Psychophysiology* 42, 151-160.
- Hao, L., Long, C., 2003. A study on correlation of personality traits to employees' stress evaluation [in Chinese]. *Chin. J. Clin. Psychol.* 11 (4), 270-272.
- Hellhammer, D.H., Gutberlet, I., Konermann, J., Muller, U., Rolf, L., 1988. Effects of benzodiazepam on salivary cortisol under experimental stress. In: Hellhammer, D.H., Florin, I. (Eds.), *Neurobiological Approaches to Human Disease*. Hans Huber Publishers, Kirkland, WA, US.
- Hendriks, A.A.J., Hofstee, W.K.B., De Raad, B., 1999. Handleiding bij de Five-Factor Personality Inventory (FFPI). [Manual of the FFPI]. Swets Test Publishers, Lisse, The Netherlands.
- Hettler, T.R., 2001. Agreeableness and affective reactions to daily interpersonal stressors: role of appraisals and specific coping strategies. *Diss. Abstr. Int. B: Sci. Engineer.* 61 (8), 4407.
- Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol. Rev.* 109 (4), 679-709.
- Kopp, B., Rist, F., Mattler, U., 1996. N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology* 33, 282-294.
- Kuniecki, M., Urbanik, A., Sobiecka, B., Kozub, J., Binder, M., 2003. Central control of heart rate changes during visual affective processing as revealed by fMRI. *Acta Neurobiol. Exp.* 63, 39-48.
- Lanius, R.A., Williamson, P.C., Bluhm, R.L., Densmore, M., Boksman, K., Neufeld, R.W.J., Gati, J.S., Menon, R.S., 2005. Functional connectivity of dissociative responses in posttraumatic stress disorder: a functional magnetic resonance imaging investigation. *Biol. Psych.* 57, 873-884.

- Larsen, J.T., Hemenover, S.H., Norris, C.J., Cacioppo, J.T., 2003. Turning adversity to advantage: On the virtues of the coactivation of positive and negative emotions. In: Aspinwall, L.G., Staudinger, U.M. (Eds.), *A Psychology of Human Strengths*. APA, Washington, pp. 211-225.
- Lewis, M., Ramsay, D., 2002. Cortisol response to embarrassment and shame. *Child Dev.* 73 (4), 1034-1045.
- Lorist, M.M., Boksem, M.A.S., Ridderinkhof, K.R., 2005. Impaired control and reduced cingulate activity during mental fatigue. *Cogn. Brain Res.* 24, 199-205.
- Luu, P., Collins, P., Tucker, D.M., 2000. Mood, personality, and self-monitoring: negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. *J. Exp. Psychol. Gen.* 129, 43-60.
- Mason, J.W., Wang, S., Yehuda, R., Riney, S., Charney, D.S., Southwick, S.M., 2001. Psychogenic lowering of urinary cortisol levels linked to increased emotional numbing and a shame-depressive syndrome in combat-related posttraumatic stress disorder. *Psychosom. Med.* 63 (3), 387-401.
- Medvedova, L., 1998. Personality dimensions—'Little Five'—and their relationships with coping strategies in early adolescence. *Studia Psychol.* 40 (4), 261-265.
- Menon, V., Adelman, N.E., White, C.D., Glover, G.H., Reiss, A.L., 2001. Error-related brain activation during a Go/NoGo response inhibition task. *Hum. Brain Mapp.* 12 (3), 131-143.
- Najib, A., Lorberbaum, J.P., Kose, S., Bohning, D.E., George, M.S., 2004. Regional brain activity in women grieving a romantic relationship breakup. *Am. J. Psych.* 161 (12), 2245-2256.
- Nietfeld, J., Bosma, A., 2003. Examining the self-regulation of impulsive and reflective response styles on academic tasks. *J. Res. Pers.* 32, 118-140.
- Ottowitz, W.E., Dougherty, D.D., Sirota, A., Niaura, R., Rauch, S.L., Brown, W.A., 2004. Neural and endocrine correlates of sadness in women: implications for neural network regulation of HPA activity. *J. Neuropsych. Clin. Neurosci.* 16 (4), 446-455.
- Pailing, P.E., Segalowitz, S.J., 2004. The error-related negativity as a state and trait measure: motivation, personality, and ERPs in response to errors. *Psychophysiology* 41, 84-95.
- Panksepp, J., 2005. Why does separation distress hurt? Comment on MacDonald and Leary. *Psychol. Bull.* 131 (2), 224-230.
- Paulus, M.P., Rogalsky, C., Simmons, A.N., Feinstein, J.S., Stein, M.B., 2003. Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *NeuroImage* 19, 1439-1448.
- Paulus, M.P., Feinstein, J.S., Castillo, G., Simmons, A.N., Stein, M.B., 2005. Dose-dependent decrease of activation in bilateral amygdala and insula by lorazepam during emotion processing. *Arch. Gen. Psych.* 62 (3), 282-288.
- Paus, T., Koski, L., Caramanos, Z., Westbury, C., 1998. Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: a review of 107 PET activation studies. *NeuroReport* 9, R37-R47.
- Phillips, M.L., Medford, N., Senior, C., Bullmore, E.T., Suckling, J., Brammer, M.J., Andrews, C., Sierra, M., Williams, S.C.R., David, A.S., 2001. Depersonalization disorder: thinking without feeling. *Psych. Res. Neuroimaging Sec.* 108, 145-160.
- Pruessner, J.C., Gaab, J., Hellhammer, D.H., Lintz, D., Schommer, N., Kirschbaum, C., 1997. Increasing correlations between personality traits and cortisol stress responses obtained by data aggregation. *Psychoneuroendocrinology* 22 (8), 615-625.
- Santesso, D.L., Segalowitz, S.J., Schmidt, L.A., 2005. ERP correlates of error monitoring in 10-year olds are related to socialization. *Biol. Psychol.* 70, 79-87.
- Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* 21 (1), 55-89.
- Solberg Nes, L., Segerstrom, S.C., Sephton, S.E., 2005. Engagement and arousal: optimism's effects during a brief stressor. *Pers. Soc. Psychol. Bull.* 31 (1), 111-120.
- Stöber, J., 2001. The social desirability scale-17 (SDS-17). *Eur. J. Psychol. Assess.* 17 (3), 222-232.
- Tops, M., Lorist, M.M., Wijers, A.A., Meijman, T.F., 2004. Stressen of relaxen: neurochemische aspecten van bedrijvigheid en rust. [To stress or relax: neurochemical aspects of activity and rest]. *Gedrag Org.* 17 (1), 32-42.
- Tops, M., Riese, H., Oldehinkel, A.J., Rijdsdijk, F.V., Ormel, J., 2006. The interplay of emotional arousability and protective inhibition may determine depression, fatigue, psychosomatic disease, and cortisol levels in young women. Manuscript submitted for publication.
- Trumbull, D., 2003. Shame: an acute stress response to interpersonal traumatization. *Psychology* 66 (1), 53-64.
- Tucker, D.M., Luu, P., Frishkoff, G., Quiring, J., Poulsen, C., 2003. Frontolimbic response to negative feedback in clinical depression. *J. Ab. Psychol.* 112 (4), 667-678.
- Ullsperger, M., von Cramon, D.Y., Müller, N.G., 2002. Interactions of focal cortical lesions with error processing: evidence from event-related brain potentials. *Neuropsychology* 16 (4), 548-561.
- Ullsperger, M., von Cramon, D.Y., in press. The role of intact frontostriatal circuits in error processing. *J. Cogn. Neurosci.*
- Vickers, R.R., Jr., Hervig, L.K., Poth, M., Hackney, A.C., 1995. Cortisol secretion under stress: test of a stress reactivity model in young adult males. *US Naval Health Res. Center Report, Rpt No 95-17*, 1-34.
- Wald, F.D.M., Mellenberg, G.J., 1990. De verkorte versie van de Nederlandse vertaling van de Profile of Mood States (POMS). *Nederl. Tijdschrift Psychol.* 45, 86-99.
- Walton, M.E., Croxson, P.L., Rushworth, M.F.S., Bannerman, D.M., 2005. The mesolimbic dopamine projection to anterior cingulate cortex plays no role in guiding effort-related decisions. *Behav. Neurosci.* 119 (1), 323-328.
- Wijers, A.A., Boksem, M.A.S., 2005. Selective attention and error processing in an illusory conjunction task: an event-related brain potential study. *J. Psychophysiol.* 19 (3), 216-231.
- Williamson, J.W., McColl, R., Mathews, D., Ginsburg, M., Mitchell, J.H., 1999. Activation of the insular cortex is affected by the intensity of exercise. *J. Appl. Physiol.* 87 (3), 1213-1219.
- Yeung, N., 2004. Relating cognitive and affective theories of the error-related negativity. In: Ullsperger, M., Falkenstein, M., (Eds.), *Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring*. Max-Planck Institute fuer Kognitionen und Neurowissenschaften, Leipzig, 63-70. (MPI special issue in human cognitive and brain sciences; 1).
- Zirnheld, P.J., Carroll, C.A., Kieffaber, P.D., O'Donnell, B.F., Shekhar, A., Hetrick, W.P., 2004. Haloperidol impairs learning and error-related negativity in humans. *J. Cogn. Neurosci.* 16 (6), 1098-1112.