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Error-related oscillatory activity is modulated by novelty seeking in the reward condition

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ABSTRACT

Behavioural research has revealed the influence of motivation conditions on cognitive task performance and demonstrated that these influences are modulated by temperament factors. Modern neuroimaging methods enable analysis of neuropsychological mechanisms through which individual differences in reinforcement sensitivity may influence cognitive functioning. In the study, fifty-six participants were scored on the Cloninger's Temperament and Character Inventory to assess punishment and reward sensitivity. Then, subjects participated in an EEG experiment using the numerical Stroop task under different motivational conditions. In one condition, they were punished for erroneous responses; in the other, they were rewarded for correct performance. We analysed event related changes in EEG spectral power to investigate the influence of temperamentally driven differences on error-related oscillatory brain activity. In agreement with previous findings, after incorrect responses an increase in frontocentral theta (3–7 Hz) and a decrease in occipital alpha (10–11 Hz) power were observed. Moreover, a multivariate regression analysis showed that these spectral markers were modulated by temperamental trait Novelty Seeking in the reward condition. To our knowledge, we are the first to demonstrate such a relationship between individual differences and error-related oscillatory activity. This neuronal pattern may explain why participants that score high on Novelty Seeking trait are highly motivated and strongly engaged in a task when a reward might be earned. Thus, in conclusion we emphasise that to understand an individual's response to errors, it is necessary to account simultaneously for motivational conditions as well as temperament traits.

1. Introduction

In psychology, there are several biologically based models built on the assumption that human personality is generated by neurobiological processes (Eysenck, 1970; Gray, 1987; Tellegen, 1985; Watson and Clark, 1993). Despite conceptual differences, these approaches appear to have common higher order dimensions reflecting main temperamental characteristics that are emotion-based, heritable, present in early childhood, and relatively stable through life. Elliot and Thrash (2002) structural dimensions of personality called *avoidance* and *approach temperaments*. The former refers to a general neurobiological sensitivity to negative/undesirable stimuli (i.e., punishment), while the latter responds to a general neurobiological sensitivity to positive/desirable (i.e. reward) stimuli.

One of the most widely known theories is The Reinforcement Sensitivity Theory authored by Jeffrey Gray (Gray, 1987), which reflects this approach and defines fundamental personality traits in terms of individual differences in the sensitivity to reinforcing stimuli. This theory proposed two basic systems: the behavioural activation system (BAS) and the behavioural inhibition system (BIS) and outlined their potential to influence behaviour. More precisely, the BAS facilitates the processing of reward stimuli and antagonizes the processing of punishment stimuli, whereas BIS has the opposite pattern.

Inspired by Gray's theory, Robert Cloninger (1994) created a model defining the neurobiological basis of sensitivity to reward and punishment. The author refers to temperament as an automatic emotional arousal in response to events that is defined in terms of individual differences in learning by reward and punishment (Cloninger, 2002). The author proposed genetically independent dimensions, related to heritable variations in patterns of response to specific stimuli. Novelty Seeking is the tendency to respond actively to novel stimuli, leading to the pursuit of rewards and escape from punishment. Harm Avoidance is

Abbreviations: BAS, behavioural activation system; BIS, behavioural inhibition system; ERN, error-related negativity; TCI, temperament and character inventory; ERSP, event-related spectral perturbations; RT, reaction times

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the tendency to inhibit responses to signals of aversive stimuli that lead to avoidance of punishment and non-reward. Reward Dependence is a tendency for a positive response to conditioned signals of reward that maintain behaviour, while Persistence is the ability to generate and maintain arousal and motivation internally in the absence of immediate external reward. The Novelty Seeking influences approach and initial acquisition of rewarded behaviour, whereas Reward Dependence influences the rate of extinction of previously rewarded behaviour (Stallings et al., 1996). Based on Cloninger's model, Novelty Seeking and Harm Avoidance explicitly refer to BAS and BIS in their theoretical foundations and are the two major temperamental dimensions responsible for activation and inhibition of behaviours, respectively (Cloninger, 1987; Cloninger et al., 1993).

Both theoretical assumptions and empirical research revealed a number of relationships between *avoidant/approach* personality traits and responsiveness to punishment/reward respectively (Corr, 2004; Corr et al., 1995). The behavioural results showed the influence of reinforcement conditions on cognitive task performance as well as its modulation by temperament factors (Corr, 2004). Rapid development of modern neuroimaging techniques enables further analysis of neuropsychological mechanisms through which individual differences in reinforcement sensitivity may influence cognitive functioning such as error-related processing in different motivation conditions. Research on neuronal markers of error monitoring is dominated by examination of error-sensitive components of brain potentials known as error-related negativity (ERN) (Falkenstein et al., 1990; Gehring et al., 1993). Extensive scientific research resulted in description of wide array of factors modulating the ERN amplitude including motivational context (Hajcak et al., 2005; Potts, 2011), personality traits (Boksem et al., 2006; Olvet and Hajcak, 2008) and interaction of motivational variables and individual differences (Boksem et al., 2008; Cavanagh and Allen, 2008).

However, the analysis of event-related changes in the EEG spectral power may also convey additional relevant information about cognitive processing. Using variety of experimental tasks, it has been shown that with increasing cognitive task demands the frontal midline theta (4–7 Hz) band increases whereas posterior alpha (8–13 Hz) band decreases (Klimesch, 1999; Meltzer et al., 2007). Theta oscillations, with a source in medial frontal cortex, were linked to the recruitment of cognitive control in the information-processing stream (Nigbur et al., 2011) during several cognitive processes including memory, attention, conflict resolution and learning (Cavanagh et al., 2009; Coles et al., 2001; Luu and Pederson, 2004; Trujillo and Allen, 2007). On the other hand, alpha suppression reflects an attentional process of routing information to task-relevant regions by inhibiting task-irrelevant regions (Jensen and Mazaheri, 2010). Interestingly, this oscillatory pattern is enhanced after error commission. That is, when compared to correct responses, errors elicit substantially greater frontal theta synchronization and posterior alpha desynchronization (Mazaheri et al., 2009; Novikov et al., 2015; van Driel et al., 2012). The former can be linked with a goal-directed evaluation of response outcome, whereas the latter represents reducing the perception state of the brain in subsequent trials. Thus, these oscillatory markers provide a great opportunity for investigating two separate cognitive processes. To our knowledge, little is known about how these electrophysiological markers are modulated by individual and motivational factors.

Taking into account theoretical assumptions of neurobiological basis of sensitivity to reward and punishment (Cloninger, 1994a, 1994b) and previous empirical findings of ERN sensitivity to individual factors (Boksem et al., 2008), we hypothesize that both ERN amplitude and oscillatory markers of error commission are influenced by interaction of temperamental traits and motivational conditions. In this study, we used event related changes in EEG spectral power to obtain alpha and theta power dynamics. Considering the analogy between Gray's and Cloninger's dimensions and their role as factors predisposing to higher responsiveness to positive and negative reinforcement, we hypothesize that error-related brain markers are modulated by Novelty Seeking in the reward condition, whereas Harm Avoidance modulates these measures in the punishment condition. In other words, we hypothesize that individuals high on Novelty Seeking experience errors as more aversive when they were in the position to acquire rewards but failed to do so. Similarly, subjects high on punishment sensitivity (Harm Avoidance) experience mistakes as more aversive when they are punished for committing errors.

2. Material and methods

2.1. Participants

Sixty-two subjects participated in this experiment, but six were excluded from the analysis due to too few (below 4%) errors. The remaining fifty-six subjects (29 females) had a mean age of 22.9 ± 2.3 years. Participants met the experiment requirements: right-handedness, normal or corrected-to-normal vision, no physical and psychiatric disorders and drug-free. Participants were informed about the procedure and goals of the study and gave their written consent. The study was approved by the Bioethics Commission at Jagiellonian University.

2.2. Temperament assessment

A valid Polish translation (Zakrzewska et al., 2001) of the Temperament and Character Inventory (TCI) (Cloninger, 1994a, 1994b) was used for measuring the temperament of each subject. The original method measures four temperament dimensions (Novelty Seeking, Harm Avoidance, Reward Dependence, Persistence) and three character dimensions (Self-directedness, Cooperativeness and Self-transcendence). The self-report questionnaire consists of 240 items (107 items related to temperament traits) worded as statements that are rated on a "true or false" scale. The reliability of each main scale of the Polish version of TCI was previously confirmed (Zakrzewska et al., 2001) and can be used for the assessment of personality dimensions both in experimental and clinical studies (Mikołajczyk et al., 2008; Rybakowski et al., 2004). In this study, we have focused only on temperament dimensions of the TCI.

2.3. Stimuli and task

To evoke errors we used the numerical Stroop task as a conflict paradigm test, prepared and generated using E-Prime 2.0 (©Psychology Software Tools) and presented on a 17-in. screen located approximately 80 cm from the eyes of participants. In the task, stimuli were two one-digit numbers that appeared simultaneously in a black font on a light grey background. The stimulus was presented for 350 ms; however, the response was registered for 550 ms. Next, a blank screen appeared (varying duration between 800 and 1200 ms), followed by feedback (900 ms duration). Between the trials, a fixation point (i.e. a hash symbol, #) was shown for 1100, 1600 or 2100 ms (equal rates). The fixation point disappeared for 300 ms before the next stimuli appeared. Together, on average there was 4150 ms between the two trials, ranging from 3450 to 4850 ms. The scheme of the task is presented in Fig. 1.

The stimuli were a pair of Arabic digits (from 1 to 9) of varying size in Arial font. In the numerical task, subjects were instructed to press the left/right button with the index/middle finger if the digit on the left/right side had higher magnitude. In the physical task, they were instructed to indicate the digit with greater font size. There were three congruence conditions (congruent, neutral and incongruent trials) at equal rates. One block comprised 160 trials: half of them within the numerical task and half within the physical task. The correct responses were equally distributed between the left and right side of the screen.

There were four blocks, with different feedback presented after the