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P300 amplitude variation is related to ventral striatum BOLD response during gain and loss anticipation: An EEG and fMRI experiment

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ABSTRACT

The anticipation of favourable or unfavourable events is a key component in our daily life. However, the temporal dynamics of anticipation processes in relation to brain activation are still not fully understood.
A modified version of the monetary incentive delay task was administered during separate functional magnetic resonance imaging (fMRI) and electroencephalogram (EEG) sessions in the same 25 participants to assess anticipatory processes with a multi-modal neuroimaging set-up.
During fMRI, gain and loss anticipation were both associated with heightened activation in ventral striatum and reward-related areas. EEG revealed most pronounced P300 amplitudes for gain anticipation, whereas CNV amplitudes distinguished neutral from gain and loss anticipation. Importantly, P300, but not CNV amplitudes, were correlated to neural activation in the ventral striatum for both gain and loss anticipation. Larger P300 amplitudes indicated higher ventral striatum blood oxygen level dependent (BOLD) response.
Early stimulus evaluation processes indexed by EEG seem to be positively related to higher activation levels in the ventral striatum, indexed by fMRI, which are usually associated with reward processing. The current results, however, point towards a more general motivational mechanism processing salient stimuli during anticipation.

Introduction

Waiting for a loved-one to return or being afraid of losing his or her affection after a long period of separation — the anticipation of favourable or unfavourable events is a key component of our daily life. Our wellbeing is highly dependent on how we deal with the constant confrontation with positive and negative challenges and their consequences. Thus, understanding the neural basis of the cognitive and affective processes associated with reward and loss anticipation in normally functioning individuals is of particular importance when trying to understand mental conditions in which reward-related processing is disrupted.

Reward processing is mainly characterised by two temporally distinct stages — an appetitive (i.e., preparatory or anticipatory) phase is followed by a consummatory phase (Berridge, 1999). The current study focuses on the appetitive phase where potential rewards and losses are present. The appetitive phase is composed of reward anticipation and related motor-preparation processes. The anticipatory affect model (Knutson and Greer, 2008) suggests that the anticipation of positive stimuli leads to positive arousal which in turn promotes approach behaviour, whereas the anticipation of negative stimuli leads to negative arousal promoting avoidance behaviour. So far, research mainly used functional magnetic resonance imaging (fMRI) to study anticipation-related processes. Only a few studies investigated these processes with electroencephalography (EEG). The combination of both methods, which was applied in the current study, allows for multimodal assessment of anticipation-related processes benefitting from the technical advantages of both methods.

Extensive evidence suggests that brain structures such as the midbrain, the ventral striatum including nucleus accumbens (NAcc), amygdala, and orbital mesial parts of the prefrontal cortex are chiefly involved in reward processing (e.g., Arias-Carrion and Poppel, 2007; Liu et al., 2011; McClure et al., 2004; O'Doherty, 2004; Schultz, 2006; Sescousse et al., 2013). The neurotransmitter dopamine is attributed an important role in reward processing (Schultz, 2006). Note however, that the same brain regions which are associated with reward play also an important role during aversive motivation and learning in animal models (Salamone et al., 1994). Therefore, it is still a matter of debate

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whether these brain networks reflect only reward processing or whether they reflect, in more general terms, a motivational system.

Electroencephalographic components such as the P300 event-related potential (ERP) and the slow wave contingent negative variation (CNV; Walter et al., 1964) have also been implicated in anticipatory reward and motor preparation processes. Both have been previously termed as putative reward-related electrophysiological markers (Goldstein et al., 2006) and have been described to be evoked during the anticipatory phase of an electrophysiological monetary incentive delay (MID) task in which participants can win or lose money after being cued whether monetary gain or loss is possible in the current trial (Broyd et al., 2012; Santesso et al., 2012). The MID task was also used in the current study.

In general, the P300 is a positive-going ERP deflection peaking between 300 and 600 ms after stimulus presentation (Duncan Johnson and Donchin, 1977; Johnson and Donchin, 1980). P300 amplitude variation is related to categorical stimulus probability (Johnson and Donchin, 1980; Kutas et al., 1977), stimulus quality, attention (Polich and Kok, 1995), task relevance (Coles et al., 1995), task complexity (Isreal et al., 1980), and effort spent on a task (Brocke et al., 1997). Moreover, P300 amplitude variation is related to reinforcer magnitude (Goldstein et al., 2006). Thus, whenever task-relevant stimuli are presented during an experiment a positive ERP deflection in the time window around 300 ms post stimulus can be observed, with maxima at midline electrodes. Prominent theoretical accounts relate P300 amplitude variation to context updating in working memory (Bonala and Jansen, 2012; Donchin and Coles, 1988), e.g., updating whether a potential gain or loss is at stake in the MID task.

The CNV is a negative-going potential shift which is primarily associated with anticipatory attention and preparation of effortful processes (Falkenstein et al., 2003; Gómez et al., 2007). The CNV component is assumed to reflect neural activity within the thalamo–cortico–striatal network (Fan et al., 2007; Macar and Vidal, 2003; Pfeuty et al., 2005).

Although these two ERP components are not specific for reward anticipation, they might be indirectly influenced by similar underlying neuronal processes related to dopamine which drive activation patterns during fMRI investigations. Indeed, an association between P300 amplitude variation and central dopamine system has been reported previously (Pogarell et al., 2011; Takeshita and Ogura, 1994). Clinical and genetic studies provide further evidence for a potential contribution of dopaminergic neurotransmitter systems to P300 amplitude variation (Berman et al., 2006; Blackwood, 2000; Houston et al., 2003; Mulert et al., 2006; Oribe et al., 2013). The CNV component has been associated with central dopaminergic activity in a similar vein (Fan et al., 2007; Linssen et al., 2011). Note, however, that these assumptions are based on indirect evidence since actual dopamine transmission is not accessible by neither fMRI nor EEG, as used here.

The current study aimed to further investigate the question whether activation in so-called reward-related brain areas, in particular the ventral striatum, reflects only reward processing or more general motivational processes. To this end, a modified version of the MID task (Knutson et al., 2000), a prototypical cued response task, was administered during separate fMRI and EEG sessions in the same participants. To investigate this question, we performed fMRI and EEG measurements (1) to use fMRI for assessing neural activations in "classical" reward-related brain areas, and (2) to compare these activations to ERP components such as the P300 and CNV. The rationale of this comparison was to investigate whether associations can be found with either an ERP component reflecting aspects of salience and attention during the anticipation process – in particular the P300 component – or with an ERP component reflecting more cognitive effort aspects of the anticipation process – in particular the CNV component. For the imaging data, we expected enhanced neural activation in reward-related brain areas for reward anticipation compared to non-reward and neutral anticipation (Knutson and Greer, 2008; Knutson et al., 2000, 2003). For the electrophysiological data, we expected a differentiation for reward compared to non-reward and neutral anticipation for P300 and CNV amplitudes (Broyd et al., 2012; Gruber and Otten, 2010). To answer our research question, we combined results of both methods via calculating correlations between electrophysiological amplitude variation and hemodynamic activation in the ventral striatum (Goldstein et al., 2006; Pogarell et al., 2011; Takeshita and Ogura, 1994). Finding a significant correlation for both gain and loss cues between ERPs and ventral striatum BOLD responses would support the general motivational mechanism hypothesis by reflecting that similar underlying mechanisms are engaged during gain and loss anticipation. In contrast, a significant correlation between ERPs and BOLD response solely for gain cues would support the reward hypothesis. Moreover, correlations with P300 vs. CNV amplitudes would indicate different processes. While P300 correlations would be related to salience and attention, correlations with CNV amplitudes would indicate the engagement of processes related to cognitive effort.

Material and methods

Participants

Initially, 29 volunteers took part in our experiment. Four participants dropped out during the study due to technical problems with the scanning. The final sample consisted of 25 individuals (13 women) with a mean age of 23.8 years (SD = 3.60). All participants were right-handed as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, and were screened with the Structural Clinical Interview for DSM-IV (SCID; APA, 1994) to exclude individuals with psychiatric disorders. Moreover, participants reported no metal implants, no past or present substance abuse, no psychopharmacological medication within the last three months, and no pregnancy (tested with urine human chorionic gonadotropin pregnancy test). All participants gave written informed consent prior to data acquisition. The study was approved by the Ethics Committee of the Medical University of Vienna and the General Hospital of Vienna. Participants were reimbursed for their study participation. They participated in further paradigms which are outside the scope of the current manuscript (Hahn et al., 2013).

Stimuli and task procedures

Monetary incentive delay (MID) task

Participants were administered comparable versions of the MID task (Knutson et al., 2000) for both fMRI and EEG measurements (see Fig. 1). The MID task is designed in a way that participants can maximise rewards and minimise losses by responding as quickly as possible by button press to a visual target. Prior to target presentation, incentive cues are presented to indicate what is at stake in the current trial, i.e., whether responding relates to an attempt to win money, or to avoid losing money, or that no money is at stake. Each trial started with the presentation of the incentive cue for 1000 ms in black colour on a grey background. A potential monetary gain or win was indicated by a circle surrounding a "+" symbol. A potential loss was indicated by a circle surrounding a "−" symbol. Neutral trials in which neither monetary gains nor losses could be incurred were indicated by empty circles. During the subsequent anticipation phase where participants prepared their motor response, the cue symbols were replaced by a question mark presented for a duration that varied in 100 ms steps between 2000 and 2500 ms (uniformly distributed). A black square on a grey background was used as target stimulus. Initially, the target was presented for 264 ms and the participants were required to respond within this time window for a correct response. Participants responded with their right index finger on an MRI compatible response pad for fMRI measurements (Current Designs Inc., Philadelphia, PA, USA) and on button 1 on a standard PC USB keyboard for EEG measurements. Based on individual reaction times for gain, loss, and neutral cue