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Neural mechanisms of reward processing associated with depression-related personality traits

Akina Umemoto *, Clay B. Holroyd

University of Victoria, P.O. Box 1700 STN CSC, Victoria, British Columbia V8W 2Y2, Canada

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HIGHLIGHTS

- We examined individual differences in depression, reward sensitivity, and motivation.
- Elevated depression scores were associated with poor learning of improbable rewards.
- Event-related potentials revealed reduced anticipation for and processing of rewards.

ABSTRACT

Objective: Although impaired reward processing in depression has been well-documented, the exact nature of that deficit remains poorly understood. To investigate the link between depression and the neural mechanisms of reward processing, we examined individual differences in personality.

Methods: We recorded the electroencephalogram from healthy college students engaged in a probabilistic reinforcement learning task. Participants also completed several personality questionnaires that assessed traits related to reward sensitivity, motivation, and depression. We examined whether behavioral measures of reward learning and event-related potential components related to outcome processing and reward anticipation—namely, the cue and feedback-related reward positivity (RewP) and the stimulus preceding negativity (SPN)—would link these personality traits to depression.

Results: Participants who scored high in reward sensitivity produced a relatively larger feedback-RewP. By contrast, participants who scored high in depression learned the contingencies for infrequently rewarded cue-response combinations relatively poorly, exhibited a larger SPN, and produced a smaller feedback-RewP, especially to outcomes following cue-response combinations that were frequently rewarded.

Conclusion: These results point to a primary deficit in reward valuation in individuals who score high in depression, with secondary consequences that impact reward learning and anticipation.

Significance: Despite recent evidence arguing for an anticipatory deficit in depression, impaired reward valuation as a primary deficit should be further examined in clinical samples.

1. Introduction

Reward processing impairments are commonly observed in depression (see Der-Avakian and Markou, 2012; Pizzagalli, 2011, for review), but the exact nature of these deficits is still not fully understood. Inconsistent experimental results reported throughout the literature (e.g., Knutson and Heinz, 2015) may stem from the fact that reward processing is not actually a unitary construct but is rather characterized by distinct but interrelated processes with specific temporal dynamics. In particular, reward processing can be subdivided into separate functions related to *outcome processing* (evaluating the reward value of feedback), *reward learning* (adapting stimulus-response contingencies based on principles of reinforcement learning), and *reward anticipation* (evaluating the reward value of cues that predict or anticipate reward acquisition; Berridge and Kringelbach, 2015; Berridge and Robinson, 1998, 2003; Berridge et al., 2009). All of these processes have been reported to be deficient in depression, as described below. Our goal in this study was to investigate the neurocognitive processes that link these distinct reward processes with individual differences in depression-related personality traits.

* Corresponding author at: University of Toyama, Faculty of Humanities, Department of Psychology, Toyama-city, Toyama 930-8555, Japan.
E-mail address: akumemoto@gmail.com (A. Umemoto).

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Depression has been associated with impaired reward learning (Kunisato et al., 2012; but see also Chase et al., 2010), particularly when rewards are intermittent (Kumar et al., 2008; Pizzagalli et al., 2005, 2008). Likewise, the neuroimaging literature has implicated both abnormal reward anticipation and outcome processing in depression (Knutson et al., 2008; Santesso et al., 2012; Smoski et al., 2009). Relative to that of control groups, striatal regions are hypoactive during reward anticipation (Pizzagalli et al., 2009; Smoski et al., 2009; Stoy et al., 2012; but see Gorka et al., 2014 and Knutson et al., 2008) and reward acquisition (Forbes et al., 2009; Pizzagalli et al., 2009; Smoski et al., 2009) in depressed individuals. Moreover, the activity of anterior cingulate cortex (ACC) is typically (Mies et al., 2013; Steele et al., 2007; see also Harvey et al., 2010) – but not uniformly (Smoski et al., 2009) – reduced during outcome processing. Further, when clinically depressed individuals anticipate monetary rewards or pleasant images, ACC activity is sometimes enhanced (Knutson et al., 2008; Gorka et al., 2014; see also Dichter et al., 2012), sometimes reduced (Smoski et al., 2009, 2011), and sometimes unchanged (Pizzagalli et al., 2009) relative to that of control subjects, discrepancies that may stem from differences in task design and participant demographics.

In contrast to these inconsistent results in the hemodynamic neuroimaging literature, a growing body of electrophysiological studies in humans has consistently indicated that reward processing is impaired in depression. These studies have focussed on the reward positivity (RewP), a component of the human event-related potential (ERP) elicited in response to unexpected reward delivery that is proposed to index the impact of fast, phasic midbrain dopamine reward prediction error (RPE) signals carried to ACC (Holroyd and Coles, 2002). RewP appears to be generated in ACC (Becker et al., 2014; Miltner et al., 1997; but see also Proudfit, 2015) and a wealth of evidence indicates that it indexes an RPE, being larger for unexpected than for expected rewards (Sambrook and Goslin, 2015; Walsh and Anderson, 2012). Further, RewP amplitude is reduced in individuals diagnosed with depression, as well as in healthy individuals with depressive symptoms (Proudfit, 2015 for review; see also Holroyd and Umemoto, 2016).

RewP amplitude is correlated across individuals with self-reports of reward sensitivity (Bress and Hajcak, 2013; see also Cooper et al., 2014; Liu et al., 2014; Parvaz et al., 2016) and has been proposed as a potential neural marker for depression (Proudfit, 2015). However, these findings are complicated by the fact that other reward processes can also affect RewP amplitude. For instance, impaired reward learning would be expected to disrupt reward anticipation, thereby disrupting RPE signals to the outcome and altering the amplitude of the RewP. Conversely, impaired reward learning associated with depression, as noted above, could stem from an impairment of outcome processing, as suggested by the smaller RewP in depression. Given that RewP amplitude is inversely correlated with reward expectancy (see below, Holroyd and Krigolson, 2007; Holroyd et al., 2003, 2009; Sambrook and Goslin, 2015), a blunted RewP could also result from elevated reward anticipation of the forthcoming reward.

To investigate the link between impaired reward processing and depression, we adopted an approach recently promoted by the United States National Institute of Mental Health called the Research Domain Criteria (RDoC) framework (National Institute of Mental Health). To better characterize the etiology of mental disorders, the RDoC approach encourages the study of basic functional processes (such as reward responsiveness) mediated by specific neural substrates (such as midbrain dopamine neurons). According to this view, these functional processes vary dimensionally across the population (e.g., from low to high reward sensitivity), and only manifest in the symptoms of mental disorders when their extreme expression is maladaptive (Insel et al., 2010). Inspired by this approach, we examined in a normal population the relationships between personality traits related to reward sensitivity and motivation (e.g., reward responsiveness, anhedonia and persistence) and several neural measures of reward processing in order to assess the contributions of these processes to depression.

Toward this end we recorded the electroencephalogram from healthy college students engaged in a reinforcement learning task. In order to parse apart different reward-related processes, we utilized the high temporal resolution afforded by the ERP technique (Novak and Foti, 2015; Novak et al., 2016; Pornpattananangkul and Nusslock, 2015). State depression levels were assessed using a self-report questionnaire (Foti and Hajcak, 2009; Foti et al., 2015; Liu et al., 2014) (see Section 2.3. Questionnaires). In addition, because depression is not a unitary construct, participants also completed several personality questionnaires that assessed personality traits related to depression,[1] enabling us to parse which aspects of depression are most related to the reward processes of interest. In order to characterize the dynamic evolution of these different reward processes across each trial, we then examined how the following three ERP components related to these personality traits.

First, we examined the feedback-related RewP to assess individual differences in sensitivity to reward feedback. In line with previous reports, we predicted that participants who self-report high reward sensitivity would exhibit a relatively large feedback-related RewP (Bress and Hajcak, 2013; Cooper et al., 2014; Liu et al., 2014; Parvaz et al., 2016), whereas those high in depression-related personality traits would exhibit a small feedback-related RewP (Proudfit, 2015).

Second, in order to assess reward anticipation, we examined the stimulus preceding negativity (SPN), a slow negative-going ERP component that predicts forthcoming feedback stimuli (Brunia, 1988; Brunia and Damen, 1988; Brunia et al., 2011, for review). SPN is sensitive to motivationally relevant outcomes, increasing in amplitude (i.e., becoming more negative) when participants anticipate forthcoming monetary rewards (Fuentemilla et al., 2013; Kotani et al., 2003; Ohgami et al., 2006) or positively-valenced stimuli (Böcker et al., 1994, 2001). We predicted that traits related to anticipation of future outcomes would be associated with increased and decreased SPN, respectively, according to the degree to which participants anticipated or desired the forthcoming rewards. Importantly, as depression has been associated with impaired reward anticipation, participants high on depression-related traits were expected to produce an abnormal SPN, although the direction of this effect (reduced or enhanced) was difficult to predict.

Third, because the feedback-related RewP has been shown to propagate with learning from outcomes to events that predict the outcomes (e.g., Holroyd et al., 2011), we examined the RewP to the cue (“cue-RewP”) in order to assess the response to external stimuli that predict reward. Because both the cue-RewP and the SPN reflect processes related to reward anticipation, personality traits associated with outcome anticipation were expected to affect both ERP components similarly.

Finally, as depression has been associated with impaired reward learning, participants high on depression-related traits were expected to perform the task poorly relative to the other participants.

[1] Because our study examined individual differences in personality across the normal population (as opposed to in a clinical sample with depression), we refer to the differences as personality “traits” (e.g., traits associated with reward sensitivity, depression-related traits). Further, we use the term “score” to refer to the specific traits as revealed by each questionnaire (e.g., “participants who scored high in reward responsiveness”). By contrast, we refer to “depression” or “depression symptoms” when referring to the clinical definition of depression.

2. Materials and methods

2.1. Participants

Sixty-eight undergraduate students were recruited from the University of Victoria Department of Psychology subject pool to fulfill a course requirement or earn bonus credits. All subjects (7 males, 9 left-handed, age range = 17–26 years, mean age = 20 ± 1.9 years) had normal or corrected-to-normal vision. Each also received a monetary bonus in addition to the credits, the amount of which depended on their task performance (see Section 2.4. Procedure). All subjects provided informed consent as approved by the local research ethics committee. The experiment was conducted in accordance with the ethical standards prescribed in the 1964 Declaration of Helsinki.

2.2. Task design

Participants performed a probabilistic reinforcement learning task (Fig. 1) in which one of five possible cues (3.3° by 3.3° square visual angle), selected at random, was presented for 800 ms on each trial. These five cues were randomly selected from a set of ten different images from different object categories (Fig. 1, bottom). Immediately following cue offset a small white cross (.5° by .5° square visual angle) appeared at the center of the screen, to which participants were instructed to make a response. Participants were told to respond by freely choosing either the "Z" key or the "/" key within a 500 ms response limit, after which the image of the small white central cross was replaced with a blank screen for 1000 ms, followed by the appearance of a feedback stimulus. If the participant responded within the 500 ms deadline, the 1000 ms delay was extended by the time remaining between their response and the 500 ms deadline (e.g., if the response time was 200 ms, then the remaining 300 ms was added to the 1000 ms delay, resulting in a total delay of 1300 ms on that trial). If participants failed to respond within 500 ms, then the message "Respond quickly!" was presented immediately following the deadline and the same trial was repeated. Otherwise, after the delay period, a feedback stimulus (3.3° by 3.3° square visual angle) was presented for 800 ms, consisting of either a gray circle or a diamond representing reward and no-reward, the mappings of which were counterbalanced across participants. Finally, the next trial started after an inter-trial interval of 600 ms during which a small black fixation dot was presented at the center of the screen.

Unbeknownst to the participants, each of the five cues was uniquely associated with a reward probability of either 100%, 75%, 50%, 25%, or 0% for one of the two possible responses (hereafter called the "correct response"), whereas the other response to each cue (hereafter called the "incorrect response") always resulted in no-reward feedback. One of the two response keys was selected at random to serve as the correct response for two of the four cues associated with the 100%, 75%, 50%, or 25% reward probabilities, while the other response key served as the correct response for the remaining two cues. For the 0% reward probability cue, the "correct" response was selected at random between the two response keys, but both correct and incorrect responses for this cue always resulted in no-reward. Halfway through the experiment the five cues were replaced with the remaining 5 cues from the set of ten cues (Fig. 1, bottom), requiring participants to learn the appropriate stimulus-response mappings anew.

2.3. Questionnaires

Participants completed a total of six personality questionnaires related to motivation, reward sensitivity, and other depression-related traits, described below, administered through LimeSurvey (https://www.limesurvey.org/) on the same computer where the task was performed. These included (1) The 20-item Persistence Scale (PS: Cloninger et al., 1993; Gusnard et al., 2003), which assesses the tendency to overcome daily challenges on a scale of 1 (definitely false) to 5 (definitely true). (2) The 8-item Reward Responsiveness (RR) Scale (Van den Berg et al., 2010), which is a self-report measure of reward-related behavior on a scale of 1 (strong disagreement) to 4 (strong agreement). The RR scale was derived in part from the Behavioral Inhibition/Activation Scale (Carver and White, 1994) in order to provide a purer measure of reward responsiveness. (3) The 18-item Temporal Experience of Pleasure Scale (TEPS), which assess two components of hedonic capacity, namely consummatory pleasure (TEPS-C: i.e., "liking" or in-the-moment experience of pleasure) and anticipatory pleasure (TEPS-A: i.e., "wanting"), on a scale of 1 ("very false for me") to 6 ("very true for me") (Gard et al., 2006). (4) The 12 item, short-form of the Intolerance of Uncertainty Scale (IU), which measures sensitivity to and avoidance of uncertain and ambiguous situations (Carleton et al., 2007; Freeston et al., 1994) on a scale of 1 (not at

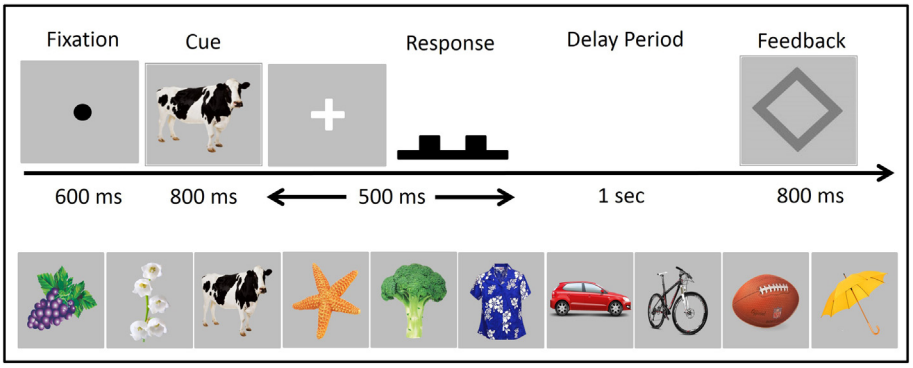

Fig. 1. Sequence of events for an example trial (top) and the set of ten cue images (bottom). Five cues were randomly selected for the first phase (i.e., block 1 through 8, see Section 2.2. Task Design), and the remaining five cues were used for the second phase (i.e., block 9 through 16). Top: Each trial began with presentation of a fixation dot for 600 ms (the 1st panel from left) followed by one of the cues for 800 ms (the 2nd panel from left). At the offset of the cue a small white cross appeared (the 3rd panel from left); participants were required to learn by trial-and-error which of the two response keys to press for a potential reward (the "X" or the "/" key, illustrated by the two black boxes on a thick black line) within a 500 ms response deadline. After a 1 s delay period (in addition to the remaining time within the 500 ms response deadline; see Section 2.2. Task Design) a feedback stimulus was presented for 800 ms (the last panel). The gray diamond image (as shown in the figure) indicated a 2 cents reward and a gray circle image (not shown here) indicated a no-reward for half of the participants, and the feedback-reward mappings were reversed for the other half of the participants (counterbalanced across subjects). Presentation of the fixation dot indicated the start of the next trial. Note that the stimulus images are enlarged in the figure for the purpose of illustration.

all characteristic of me) to 5 (entirely characteristic of me). IU was included because it has been considered a transdiagnostic construct across depression and anxiety, and impacts reward anticipation in depression (Nelson et al., 2014). (5) The 21 item short-form of the Depression Anxiety Stress Scale (DASS-21) (Lovibond and Lovibond, 1995), which measures severity of depression, anxiety, and stress on a scale from 0 ("did not apply to me at all") to 3 ("applied to me very much, or most of the time"). Participants also completed the 22-item Ruminative Responses Scale (RRS: Treynor et al., 2003), which measures the propensity to ruminate in response to depressed mood on a scale of 1 (almost never) to 4 (almost always). However, the rumination scale and the stress subscale of the DASS-21 were not included in the analyses as they tended to strongly correlate with other variables (for example, with anxiety and depression scores), and because they were not the primary focus of the study. Summed total scores were used for each of the questionnaires such that high scores indicated, respectively, high persistence, high reward responsiveness, high hedonic capacity (or reduced anhedonia), high intolerance of uncertainty, and high levels of depression and anxiety. In order to minimize the duration of the experiment, the non-negatively framed questionnaires (PS, RR, and TEPS) were administered halfway through the task (i.e., at the end of 8th block) and the questionnaires related to other depression-related traits (RRS, IU, and DASS-21) were administered at the completion of the experiment.

2.4. Procedure

Participants were seated comfortably in front of a computer monitor (1024 by 1280 pixels) at a distance of about 60 cm in an electromagnetically shielded dimly lit room. The task was programmed in Matlab (MathWorks, Natick, MA, USA) using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). Subjects rested the fingertips of their index fingers comfortably on two response keys (see Section 2.2. Task Design) of the computer keyboard. Participants were provided with both written and verbal instructions that explained the procedure, and were told to maintain correct posture and to minimize head movements and eye blinks during the experiment. They were instructed that they would be presented with one of five cue images on each trial and to respond to each cue by pressing either of two specified response keys after the cue disappeared and was replaced with a small central white cross, after which they would see a feedback stimulus (Fig. 1). Half of the participants were told that an image of a gray circle indicated that they earned a 2 cents reward and an image of a gray diamond indicated that they did not earn any reward; the feedback-reward mappings were reversed for the other half of the participants. Participants were informed that they should perform the task as best as they could in order to maximize their reward earnings, and that all of the money that they earned would be theirs to take home at the end of the experiment. In addition, participants were told that some cues were associated with a higher reward probability than the other cues, and that they should respond as quickly as possible.

Participants first performed a practice block consisting of 30 trials. The practice block utilized two cue images randomly selected from a set of 5 images (i.e., a chair, a house, a shoe, a soccer ball, and a frying pan) that were not used in the actual experimental blocks. In the practice block the correct response differed for the two cues (i.e., left response for one cue and right response for the other cue), but was associated with an 80% reward probability for both cues, thus exposing the participants to the probabilistic nature of the task. Participants earned between 10 and 25 cents from the practice block. The practice trials were followed by the task proper, which consisted of 16 blocks of 60 trials each. Each cue appeared 12 times in each block. The experiment consisted of 2 phases, each consisting of 8 blocks. When the 8th block was completed (Phase 1), participants were given a small break during which they answered several demographic questions (related to age, gender, history of concussion, medication status, and so on) and three personality questionnaires (see Section 2.3. Questionnaires) on the computer screen. The second half of the experiment (Phase 2) resumed afterwards; participants were told that they would continue performing the same task with five new cues. When the experiment was completed, participants answered the three remaining personality questionnaires (see Section 2.3. Questionnaires) and were paid their reward earnings, which varied approximately from CAN $5 to $10.

2.5. ERP data acquisition and pre-processing

The electroencephalogram (EEG) was recorded using a montage of 41 electrode sites in accordance to the extended international 10–20 system (Jasper, 1958). Signals were acquired using Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response high cut-off at 50 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain Vision Recorder software (Brain Products GmbH, Munich, Germany). Interelectrode impedances were maintained below 20 kΩ. Two electrodes were also placed on the left and right mastoids. The EEG was recorded using the average reference. The electrooculogram (EOG) was recorded for the purpose of artifact correction; horizontal EOG was recorded from the external canthi of both eyes, and vertical EOG was recorded from the suborbit of the right eye and electrode channel Fp2.

2.6. Data analysis

Post-processing and data visualization were performed using Brain Vision Analyzer software (Brain Products GmbH). The digitized signals were filtered using a fourth-order digital Butterworth filter with a passband of 0.10–20 Hz. Segmentation of epochs of data differed depending on the type of stimuli analyzed. For the cue and reward feedback, the data were segmented for an 800 ms epoch extending from 200 ms prior to 600 ms following presentation of each stimulus (i.e., cue or feedback). For the SPN, the data were segmented for a 3300 ms epoch extending from 200 ms prior to 3100 ms following presentation of each cue stimulus. As an exploratory analysis, we also examined the readiness potential component, which is reported in Supplementary Material. Ocular artifacts were corrected using an eye movement correction algorithm (Gratton et al., 1983). The EEG data were re-referenced to linked mastoids electrodes. Data were baseline corrected by subtracting from each sample for each channel the mean voltage associated with that electrode during the 200 ms interval preceding stimulus onset for all the ERP components (except for the readiness potential, see Supplementary Material). Trials with muscular and other artifacts were excluded according to a 150 μV Max–Min voltage difference, a ±150 μV level threshold, a ±35 μV step threshold, and a 0.1 μV lowest-allowed activity level as rejection criteria. ERPs were then created for each electrode and participant by averaging the single-trial EEG according to the reward and no-reward conditions for the feedback stimuli, and for each probability condition, separately for the cue, response, and delay periods.

Following convention the feedback-related RewP (feedback-RewP) was measured at channel FCz, where it reaches maximum amplitude (see Section 3.3. ERPs), utilizing a difference wave approach that isolated the RewP from overlapping ERP compo-

nents such as the P300 (Holroyd and Krigolson, 2007; Sambrook and Goslin, 2015). Furthermore, feedback-RewP amplitude was evaluated post-learning. For each reward probability cue, participants were considered to have learned the cue-response association when three consecutive correct responses were made (see alsoFuentemilla et al., 2013; Morris et al., 2008). Feedback-RewP was analyzed in the blocks after this criterion was reached for each reward probability condition and for each participant. ERPs were then averaged across reward probability as follows (cf. Holroyd and Krigolson, 2007; Holroyd et al., 2009): for each participant the ERP to reward feedback stimuli in the 100% reward probability condition (100% predicted reward) was subtracted from the ERP to no-reward feedback stimuli in the 0% reward probability condition (100% predicted no-reward) to generate a "predicted" difference wave (predicted feedback-RewP). Likewise, the ERP to reward feedback stimuli in the 75% reward probability condition (expected reward) was subtracted from the ERP to no-reward feedback stimuli in the 25% reward probability condition (expected no-reward) to generate an "expected" difference wave (expected feedback-RewP). The ERP to reward feedback stimuli in the 25% reward probability condition (unexpected reward) was subtracted from the ERP to no-reward feedback stimuli in the 75% reward probability condition (unexpected no-reward) to generate an "unexpected" difference wave (unexpected feedback-RewP). Finally, the ERP to reward feedback stimuli in the 50% reward probability condition (50% reward) was subtracted from the ERP to no-reward feedback stimuli in the 50% reward probability condition (50% no-reward) to generate a "50%" difference wave (50% feedback-RewP). Feedback-RewP amplitude was then determined by finding the maximum negative deflection in the difference wave from 200 to 320 ms (determined based on visual inspection of the overall feedback-RewP for each participant and condition) following feedback onset, separately for the predicted, expected, unexpected, and 50% feedback-RewP; this difference-wave approach isolates the interaction of expectancy with valence by removing the main effect of probability (Holroyd and Krigolson, 2007; Sambrook and Goslin, 2015). Consistent with previous studies, we expected feedback-RewP amplitude to scale with the expectation of reward probability, in keeping with an RPE signal, being largest when rewards are least expected (unexpected feedback-RewP), intermediate when rewards are random (50% feedback-RewP), smaller when rewards are expected (expected feedback-RewP), and smallest when rewards are completely predicted (predicted feedback-RewP) (Holroyd and Krigolson, 2007; Holroyd et al., 2003, 2009; Sambrook and Goslin, 2015).

We analyzed the other ERP components at channel FCz, where they reached maximum amplitude collapsed across conditions (but see Section 3.3. ERPs), but only for the last four blocks of both task phases (i.e., blocks 5 to 8 and blocks 13–16),[2] as we assumed that participants acquired the cue-response mappings in the latter half of each phase. First, the "cue-RewP" was measured within a time-window of 200–320 ms post-cue onset (determined based on the same criterion as for the feedback-RewP) and analyzed with the difference wave approach (see below). Second, the SPN was measured as mean ERP amplitude from 600 ms before until the onset of feedback delivery,[3] time-locked to cue onset. In contrast to how we assessed the feedback RewP, which was averaged separately according to feedback valence (reward, no reward) and then assessed as a difference wave, cue-RewP and SPN amplitude were each averaged across feedback valence (reward, no reward), separately for each of the five reward probability conditions (hereafter, these ERPs will be called "raw" ERPs for each reward probability condition to distinguish them from the ERPs assessed as difference waves, below). In addition, to conduct multiple regression analyses on the personality trait scores, we utilized a difference wave approach on cue-RewP and SPN amplitude in order to equate the expectedness of rewards with "predicted" and "expected" difference waves as per above. Specifically, the ERP in the 100% reward probability condition was subtracted from the ERP in the 0% reward probability condition to generate a "predicted" cue-RewP. The ERP in the 75% reward probability condition was subtracted from the ERP in the 25% reward probability condition to generate an "expected" cue-RewP. Further, as a control comparison, the ERP to the 50% reward probability condition was analyzed by subtracting the ERP preceding positive feedback from the ERP preceding negative feedback, yielding a "50%" cue-RewP. The same procedure was applied to generate a "predicted" SPN, an "expected" SPN, and a "50%" SPN. Finally, each ERP component was also averaged across trials irrespective of the outcome probabilities, yielding an "overall feedback-RewP" (i.e., across the four feedback-RewP difference waves), an "overall cue-RewP" (i.e., across the three cue-RewP difference waves), and "an overall SPN" (i.e., across the five SPN waveforms).

All of the analyses were conducted using SPSS (IBM SPSS 23). A within-subject ANOVA with repeated measures was conducted on the amplitude of each of the ERP components, followed as appropriate by a post-hoc contrast that assessed linearity as a function of reward probability. Means and standard deviations (SD) are provided for these analyses. Greenhouse-Geisser correction was applied when the sphericity assumption was violated. In addition, a multiple linear regression analysis was conducted separately on the amplitude of each ERP component with the personality traits as predictors, using the backward method in which all of the predictors were entered into the model first and then non-contributing predictors were step-wise eliminated (with the SPSS default minimum p-value of 0.1 for retaining each predictor in the model. E.g., Kudlicka et al., 2014; Umemoto and Holroyd, 2016; see also Brunborg et al., 2010; Mackie et al., 2013). The backward method was used in order to explore the joint effect of related-personality traits (e.g., reward sensitivity traits) on performance.

Crucially, we entered this experiment with several specific predictions that were mainly related to the multiple regression analysis conducted on the overall ERP components (i.e., that were independent of reward probability). To reiterate, we predicted that the overall feedback-RewP would be associated with reward sensitivity traits, being larger (more negative) in participants who score high in reward responsiveness and low in anhedonia and depression, and smaller in participants who score high in anhedonia and depression. In line with the previous reports (Bress and Hajcak, 2013; Liu et al., 2014; Proudfit, 2015), we also expected to observe this pattern of results particularly for the 50%-feedback RewP condition. Likewise, we predicted that both the overall cue-RewP and overall SPN would be associated with traits related to anticipation of future outcomes, being larger (more negative) in participants who score high in TEPS-A and smaller in participants who score high in IU; although we predicted that the overall SPN would also be modulated by participants' level of depression, the direction of this modulation was not specified. Note that although both the cue-RewP and SPN reflect reward anticipatory processes, the former is produced by a relatively transient neural response to reward-predictive stimuli, whereas the latter is produced by a more sustained neural response that anticipates the forthcoming outcome. In addition, for completeness we conducted multiple regression analyses on each ERP component

[2] This criterion was used for all the ERP components except for the feedback-RewP. The feedback-RewP analysis utilized a different learning criterion (see Section 2.6. Data Analysis) in order to increase the number of trials for the unexpected RewP, which were relatively few (but always more than 5).

[3] SPN amplitude generally reaches maximum immediately before reward delivery; nevertheless, we took a broader time-window to capture the sustained nature of SPN (see also Fuentemilla et al., 2013). Increasing the window size by 200 ms did not materially change the results.

separately for each probability condition (i.e., predicted, expected, unexpected, and 50%); a multiple regression analysis that tested a specific a priori prediction about the feedback-RewP is presented in the main text, and the remaining multiple regression analyses on the other ERP components, which were exploratory, are reported in Supplementary Material.

To account for the potential influence of outliers, we adopted the following jackknife approach. For each dependent variable, the same multiple regression analysis was performed multiple times by a method of leave-one-out (i.e., by excluding the data for a different participant at each iteration) (Hewig et al., 2011; Umemoto and Holroyd, 2016). Based on the result of each iteration, if any single participant was found to contribute uniquely to the final regression model—in that removing their data resulted in an inclusion or exclusion of one or more personality predictors from the model, and the same result was not obtained by the other iterations within the same analysis – then the data of this participant were excluded from the given analysis. This procedure was applied to each multiple regression analysis. This method provides an objective means for the systematic removal of outliers that is free of experimenter bias, ensuring that the results are robust against the contribution of any single participant. Across all of the tests reported below, this method excluded the data of between zero and two participants, with an average of 0.9 participants excluded per test. The degrees of freedom indicate the number of participants included in each analysis.

3. Results

The data of two participants who reported taking more than one psychotropic medication (including an anti-depressant and either an anti-psychotic or an anti-epileptic) were excluded from the analysis. In total the data of 66 participants were analyzed.[4]

3.1. Questionnaires

Table 1 provides a summary of the questionnaire scores, and Table 2 provides the zero-order correlations between questionnaire scores.

3.2. Behavior

Accuracy and reaction times (RTs) for each condition are shown in Fig. 2. Note that the dip in accuracy at block 9 corresponds to the new set of stimulus cues introduced at the start of Phase 2. Moreover, because the cue stimulus was presented for 800 ms before participants were allowed to make a response, relatively fast RTs across blocks likely indicate that participants prepared for the response early while the cue was still on the screen. A repeated-measures ANOVA on accuracy with reward probability as the within-subject factor revealed a significant effect of probability, $F(3.4,222) = 180$, $p < 0.01$, $\eta_p^2 = 0.74$. Polynomial contrasts indicated a significant linear trend, $F(1,65) = 470.6$, $p < 0.01$, $\eta_p^2 = 0.88$, a quadratic trend, $F(1,65) = 94.4$, $p < 0.01$, $\eta_p^2 = 0.59$, and a cubic trend, $F(1,65) = 17.7$, $p < 0.01$, $\eta_p^2 = 0.21$. The same analysis on RT also revealed a significant effect of probability, $F(3.4,219) = 16.8$, $p < 0.01$, $\eta_p^2 = 0.21$. Polynomial contrasts indicated a significant linear trend, $F(1,65) = 47.5$, $p < 0.01$, $\eta_p^2 = 0.40$, and a quadratic trend, $F(1,65) = 7.3$, $p < 0.01$, $\eta_p^2 = 0.10$. These results indicate that performance improved (i.e., higher accuracy and faster RT) as a function of increased reward probability. Zero order correlations revealed that persistence scores were correlated positively with overall accuracy (N = 66, r = 0.25, p = 0.04), which was the case in the 75%, 50%, and 25% reward probability conditions (all $p < 0.05$). Depression scores on the other hand were correlated negatively with accuracy in the 25% reward probability condition (N = 66, r = −0.24, p = 0.05) (Fig. 3).

Table 1
Participant questionnaire scores. RR = reward responsiveness scale. TEPS-C = temporal experience of pleasure scale, consummatory pleasure subscale. TEPS-A = temporal experience of pleasure scale, anticipatory pleasure subscale. PS = persistence scale. DASS-D = depression subscale of the depression, anxiety, stress scale (DASS-21). DASS-A = anxiety subscale of DASS-21. IU = intolerance of uncertainty scale.

	Mean	SD	Range
RR	26.4	2.7	20–32
TEPS-C	38.8	4.8	24–48
TEPS-A	45.9	5.6	26–60
PS	69.4	10.4	36–90
DASS-D	3.9	4.1	0–19
DASS-A	5	4.6	0–21
IU	29.5	9.4	16–59

3.3. ERPs

3.3.1. Cue RewP

Fig. 4. presents the 3 s time-course of ERPs time-locked to the onset of the predictive cues. Because the amplitude of the cue-RewP was numerically larger at channel Cz but not statistically different from channel FCz (p = 0.4), we conducted the analyses on ERP data recorded at channel FCz. A repeated-measures ANOVA on cue-RewP amplitude with reward probability as a within-subject factor (i.e., predicted, expected, and 50% cue-RewP) revealed a significant effect of probability, $F(2,130) = 9.7$, $p < 0.01$, $\eta_p 2 = 0.13$ (Fig. 5a). The polynomial contrast indicated a linear trend, $F(1,65) = 16.1$, $p < 0.01$, $\eta_p 2 = 0.20$, such that the predicted cue-RewP (−3.7 μV ± 3.8 μV) was the largest (most negative), the expected cue-RewP (−2.1 μV ± 3 μV) was the second largest, and the 50% cue-RewP (−1.3 μV ± 2.5 μV) was the smallest (most positive), in line with the theory that the RPE signals propagate back in time with learning from feedback stimuli to events that predict the feedback (Baker and Holroyd, 2009; Holroyd et al., 2011; see also Holroyd and Coles, 2002).[5] Table 3 summarizes the results of multiple linear regressions on the overall ERP amplitudes across probabilities with the personality trait scores as predictors. This analysis on the overall cue-RewP amplitude (averaged across the three difference waves) did not reveal a significant model. The results of separate multiple linear regressions for each probability condition with the same predictors are reported in Supplementary Material (Supplementary Table S2a).

3.3.2. SPN

SPN was examined immediately preceding the receipt of the reward feedback (Fig. 4). A repeated ANOVA on the raw SPN amplitude with reward probability as the within-subjects factor revealed a significant effect of probability, $F(2.5,160) = 3$, p = 0.04, $\eta_p 2 = 0.05$ (Fig. 5b). Polynomial contrasts indicated a significant linear trend, $F(1,65) = 5.7$, p = 0.02, $\eta_p 2 = 0.08$, and a cubic trend, $F(1,65) = 4.7$, p = 0.03, $\eta_p 2 = 0.07$ (0%: 2.3 μV ± 4.4 μV; 25%: 2.8 μV ± 3.3 μV; 50%: 3.2 μV ± 2.7 μV; 75%: 2.7 μV ± 3 μV; 100%: 3.7 μV ± 2.9 μV), revealing that raw SPN amplitude became more negative as the

[4] The data of two participants who were taking a single anti-depressant (Cipralex) were included in the analyses. Excluding these data did not change the obtained results.

[5] The peak detection algorithm can overestimate effect sizes (Luck, 2014, online Chapter 9), as suggested by the non-zero cue-RewP in Fig. 5. Whereas relative comparisons of cue-RewP amplitude using the peak detection approach appear reliable, absolute measures of RewP amplitude should be interpreted with caution due to potential overestimation of effect sizes. See Supplementary Material ("Related to footnote #5").

Table 2
Zero-order correlations between questionnaire scores. Abbreviations are given in Table 1.

	RR	TEPS-C	TEPS-A	PS	DASS-D	DASS-A
RR						
TEPS-C	0.25*					
TEPS-A	0.43*	0.24				
PS	0.41**	0.08	0.12			
DASS-D	0.05	0.16	0.24	−0.00		
DASS-A	0.15	0.14	0.27*	0.14	0.65**	
IU	−0.11	−0.03	−0.16	0.05	0.44**	0.38**

* $p < 0.05$.
** $p < 0.01$.

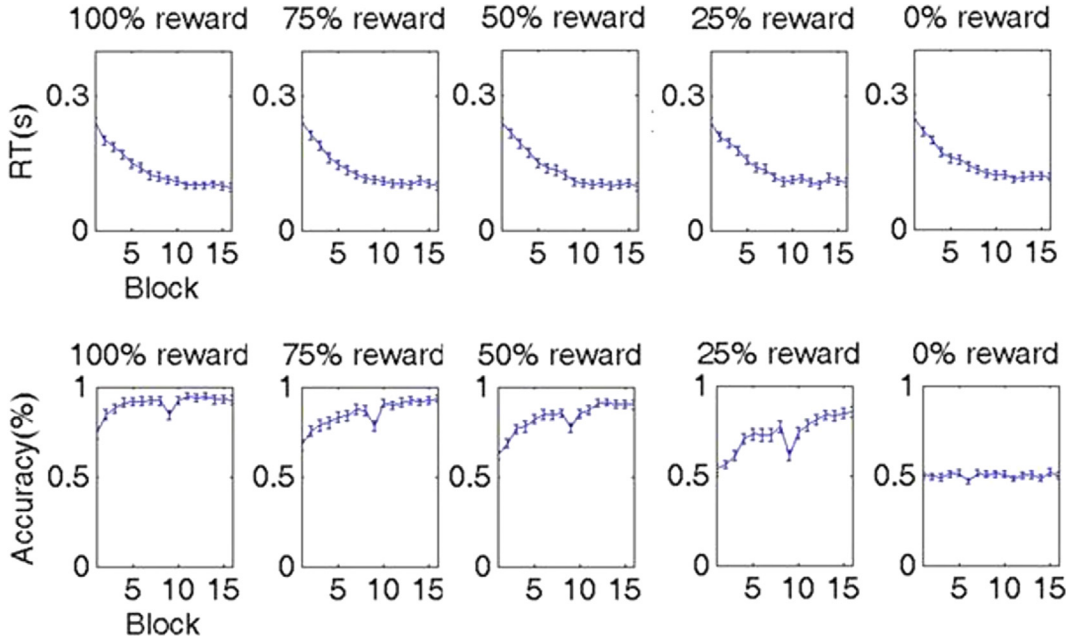

Fig. 2. Block by block performance in reaction times (RT) (top) and accuracy (bottom) across different probabilities (from the 100% reward probability condition on the left to the 0% reward probability condition on the right). The x-axis indicates each block from block 1 to block 16 (new cues were introduced at the beginning of block 9). Error bars indicate standard errors of the mean.

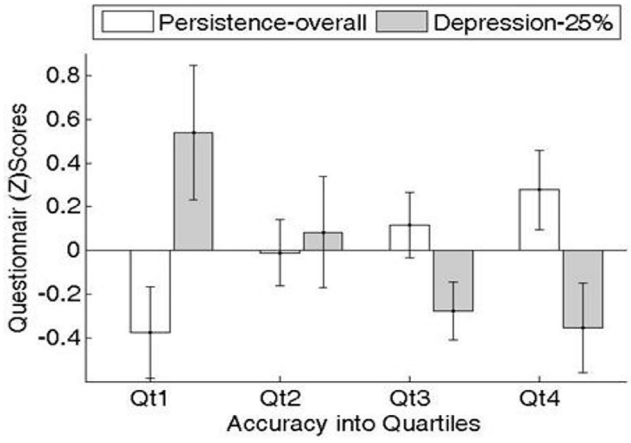

Fig. 3. Performance accuracy averaged into quartiles in relation to persistence and depression scores. The x-axis shows accuracy for each quartile (Qt), with Qt1 associated with lowest accuracy and Qt4 associated with highest accuracy. For the persistence scores (white bars), the accuracy for each quartile was averaged across the probability conditions (100%, 75%, 50%, and 25%). For the depression scores (gray bars), the accuracy for each quartile is presented for the 25% reward probability condition only. The y-axis indicates standardized questionnaire scores for the persistence and depression scales. Error bars indicate standard errors of the mean.

rewards became less probable.[6] Simple contrasts comparing the raw SPN amplitude for each probability condition to the raw SPN amplitude for the 100% probability condition, which served as a reference, indicated that the raw SPN was significantly more negative in the 0%, 25%, 75% probability conditions (all p = 0.01), but not in the 50% probability condition (p = 0.09). A multiple linear regression analysis on the overall SPN amplitude (averaged across the five probability conditions) indicated that participants high in depression and low in IU scores produced larger (more negative) SPNs overall, $F(2,61) = 3.5$, p = 0.04, explaining 10% of the variance (Table 3a). See Supplementary Material for the results of exploratory multiple linear regression analyses conducted separately for each probability condition (Supplementary Table S2b).

3.3.3. Feedback-RewP

A repeated ANOVA on feedback-RewP amplitude with reward probability as a within-subject factor (i.e., predicted, expected, unexpected, and 50% feedback-RewP) revealed a significant effect of probability condition, $F(2.6,167) = 22.4$, $p < 0.01$, $\eta_p 2 = 0.26$ (Fig. 6). Polynomial contrasts indicated a significant linear trend, $F(1,65) = 37.1$, $p < 0.01$, $\eta_p 2 = 0.36$, and quadratic trend, $F(1,65) = 12.7$, $p < 0.01$, $\eta_p 2 = 0.16$. Further analysis revealed that predicted

[6] Time-locking the ERPs to response onset yielded comparable results.

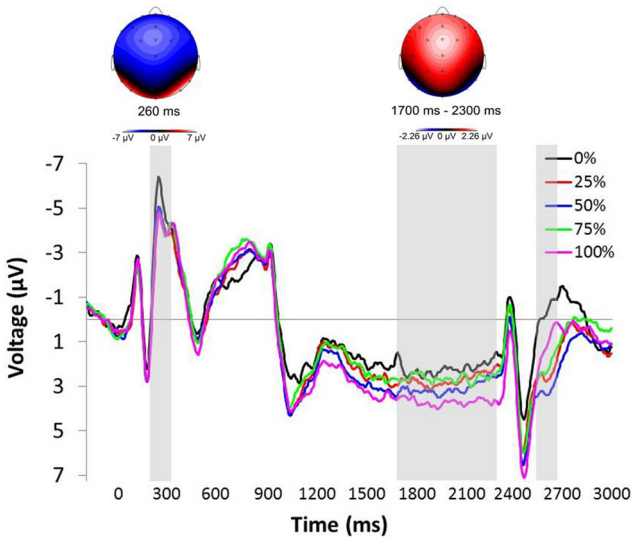

Fig. 4. Event-related brain potentials (ERPs) and associated scalp voltage maps time-locked to the onset of predictive cues (0 ms) and measured at channel FCz. The five reward probability conditions are shown in different colors: 0% reward probability = black, 25% reward probability = red, 50% reward probability = blue, 75% reward probability = green, 100% reward probability = pink. Time periods of evaluation are shown for each ERP component in the grey shaded areas. The cue-RewP is evaluated between 200 and 320 ms, SPN is evaluated during the 600 ms interval preceding the onset of feedback stimulus between 1700 and 2300 ms, and the feedback RewP is evaluated around 2700 ms; note that because the feedback-RewP was time-locked to the onset of feedback stimuli, the indicated time-interval is only approximate. The scalp voltage maps for the cue-RewP (left) and SPN (right) are illustrated over their associated period of evaluation. Negative is plotted up by convention. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

feedback-RewP (−3 µV ± 3.6 µV) was numerically, but not significantly, smaller than the expected feedback-RewP (−3.3 µV ± 3.5 µV) (p = 0.4), which was numerically, but not significantly, smaller than the 50% feedback-RewP (−4.1 µV ± 3.4 µV), $F(1,65) = 3.7$, p = 0.06, which in turn was significantly smaller than the unexpected feedback-RewP (−6.4 µV ± 3.5 µV), $F(1,65) = 26.5$, $p < 0.01$, $\eta_p 2 = 0.28$. Broadly consistent with previous observations, the feedback-RewP amplitude displayed an interaction of valence with expectancy (Holroyd and Krigolson, 2007; Sambrook and Goslin, 2015).

A multiple regression analysis on the overall feedback-RewP (averaged across the four difference waves) indicated a trend that participants high in reward responsiveness produced a larger (more negative) overall feedback-RewP, $F(1,63) = 2.8$, p = 0.1, explaining 4% of the variance in feedback-RewP amplitude (Table 3b). We predicted that participants high in reward sensitivity would exhibit a larger feedback-RewP particularly to the 50% reward condition (Bress and Hajcak, 2013; Liu et al., 2014), whereas those high in depression scores would exhibit a smaller feedback-RewP to this condition (Proudfit, 2015). The multiple linear regression analyses on feedback-RewP conducted separately for each probability condition (Table 4) indicates that participants high in reward sensitivity (i.e., reward responsiveness and consummatory pleasure) and low in depression scores produced a large feedback-RewP, particularly when rewards were highly expected. In contrast to our prediction, feedback-RewP amplitude for the 50% condition was not modulated by traits related to depression or to reward sensitivity.

3.4. Correlations between behavior and ERPs

Zero-order correlations were examined for overall accuracy, RTs, and the three overall ERP components (averaged across reward probabilities). There was a marginally significant positive correlation across individuals between the overall accuracy and overall feedback-RewP (Pearson r = 0.23, p = 0.06), indicating that the feedback-RewP was smaller for people who performed the task better (likely due to decreased prediction errors to the feedback stimuli once the stimulus-response mappings were learned). Also, there was a trend for a positive correlation across individuals between the amplitudes of the overall cue-RewP and the overall SPN (Pearson r = 0.21, p = 0.09), indicating that reduced reward anticipation in response to reward predictive cues was associated with reduced reward anticipation of forthcoming feedback stimuli.

4. Discussion

Recent investigations on the neurobiological mechanisms of reward processing in depression have centered on understanding its relation to anhedonia (Der-Avakian and Markou, 2012; Pizzagalli, 2011). Although anhedonia is classically defined as the inability to experience pleasure, more recent considerations have associated it with deficits in motivation and reward anticipation rather than with the inability to experience pleasure per se (Treadway and Zald, 2011 for review). The evidence to date is therefore inconclusive as to which reward processes are dysfunctional in individuals with elevated levels of depression.

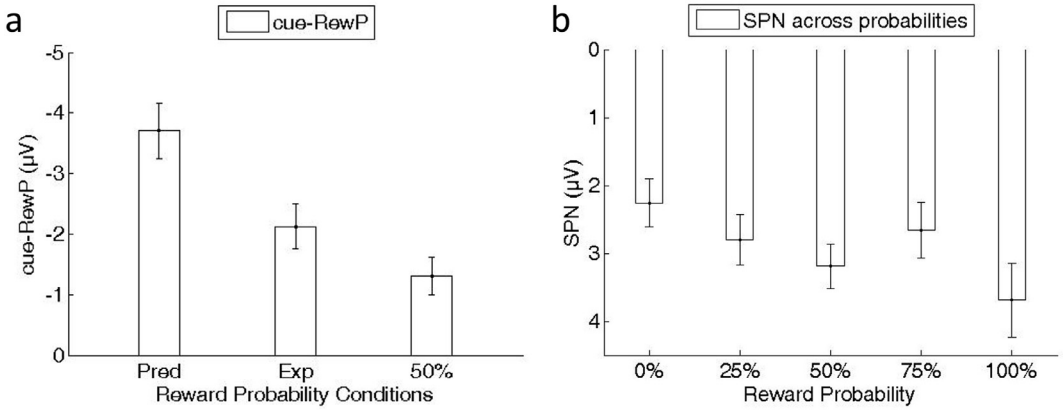

Fig. 5. ERP component amplitudes across conditions. (a) cue-RewP amplitudes for the predicted cue-RewP (Pred), the expected cue-RewP (Exp), and the 50% cue-RewP (50%). (b) Stimulus Preceding Negativity (SPN) amplitude for each of the reward probabilities (x-axis). Negative is plotted up for consistency with the ERP figures. Error bars indicate standard errors of the means.

Table 3
A summary of multiple regression analyses on the overall amplitude across probabilities for the ERP components with personality traits as predictors. Only the significant results are reported. (a) Overall stimulus preceding negativity (SPN) amplitude. (b) Overall feedback-related reward positivity (Feedback-RewP) amplitude.

Multiple linear regression on the overall ERP components						
	Predictors	Beta	t	p	Final model	R^2
(a) SPN overall						
SPN	Depression	−0.35	−2.5	0.01	$F(2,61) = 3.5$, $p = 0.04$	0.1
	IU	0.24	1.8	0.08		
(b) Feedback-RewP overall						
Feedback-RewP	RR	−0.21	−1.7	0.1	$F(1,63) = 2.8$, $p = 0.1$	0.04

Note: There was no significant result on the overall cue-RewP.

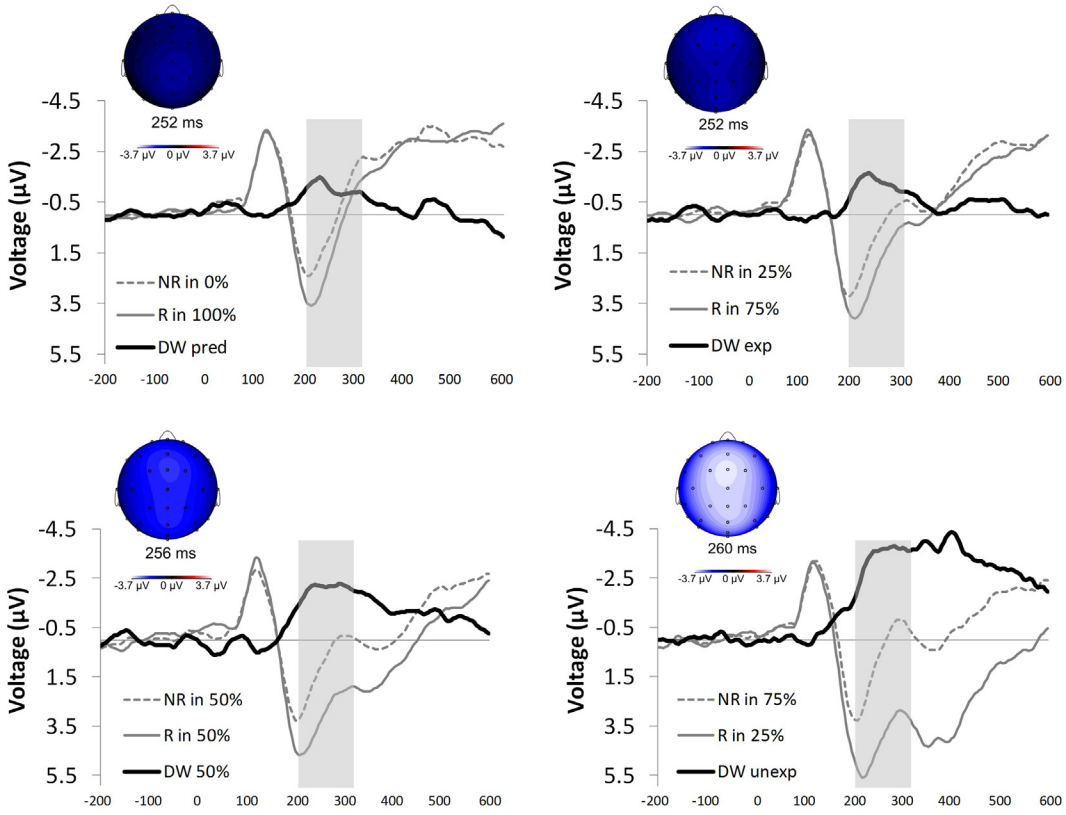

Fig. 6. Event-related brain potentials (ERPs) elicited by reward (R) and no-reward (NR) feedback, the feedback reward positivity difference waves (feedback-RewP DW), and associated scalp voltage maps. ERPs are measured at channel FCz and stimulus onset occurs at 0 ms; negative is plotted up by convention. Top left: Feedback-RewP for the predicted condition elicited by the ERP to the no-reward feedback in the 0% reward probability condition (gray, dotted line) and to the reward feedback in the 100% reward probability condition (gray line). Top right: Feedback-RewP for the expected condition elicited by the ERP to the no-reward feedback in the 25% reward probability condition (gray, dotted line) and to the reward feedback in the 75% reward probability condition (gray line). Bottom left: Feedback-RewP for the 50% condition elicited by the ERP to the no-reward feedback in the 50% reward probability condition (gray, dotted line) and to the reward feedback in the 50% reward probability condition (gray line). Bottom right: Feedback-RewP for the unexpected condition elicited by the ERP to the no-reward feedback in the 75% reward probability condition (gray, dotted line) and to the reward feedback in the 25% reward probability condition (gray line).

Table 4
A summary of multiple regression analyses on feedback-related reward positivity (Feedback-RewP) amplitude separately for each probability condition with personality traits as predictors. Only the significant results are reported.

Multiple linear regression on feedback-RewP conducted separately for each probability condition						
	Predictors	Beta	t	p	Final model	R^2
Predicted FB-RewP	RR	−0.27	−2.2	0.03	$F(2,62) = 3.8$, $p = 0.03$	0.11
	Depression	0.21	1.8	0.08		
Expected FB-RewP	TEPS-C	−0.29	−2.4	0.02	$F(2,63) = 4.4$, $p = 0.02$	0.12
	Depression	0.26	2.1	0.04		

To investigate this issue, in the current study we recorded the EEG from healthy college students engaged in a probabilistic reinforcement learning task and examined whether separate ERP components associated with reward learning, anticipation, and outcome processing would link individual differences in reward sensitivity and motivation to personality traits related to depression.

In terms of their behaviour, the participants' task performance (as indicated by accuracy and RT) differed according to the reward probabilities for each stimulus condition, confirming that they learned the stimulus-response mappings more easily for higher reward probabilities compared to lower reward probabilities. Moreover, the participants who scored high in the trait persistence performed the task more accurately overall, whereas the participants who scored high in depression performed the task worse, but only when the rewards were unlikely (i.e., following cues that predicted reward with 25% probability). This observation is consistent with previous findings that indicated that clinically depressed individuals or those with elevated depressive symptoms fail to exhibit a response bias towards rewarding stimuli, especially when these are delivered with intermittent reward schedules (Kunisato et al., 2012; Pizzagalli et al., 2005, 2008), which has been said to reflect a difficulty in integrating reward history across trials (Pizzagalli et al., 2008). Conversely, given the putative association of persistence with the cognitive control process mediated by ACC (Gusnard et al., 2003; Kurniawan et al., 2010; see also Parvizi et al., 2013), the high accuracy by persistent individuals might reflect a better ability to integrate rewards across many trials.

RPE signals carried by dopamine neurons are known to "travel back in time" with learning to the earliest indication of forthcoming reward (Schultz et al., 1997). A wealth of RewP studies has revealed a comparable process in humans (Walsh and Anderson, 2012). Accordingly, we found that the amplitude of the cue-RewP increased (i.e., became more negative) as the predictability of reward outcomes increased. There was no relation between the overall cue-RewP amplitude and individual differences in personality.

Reward anticipation was examined with the SPN, which is characterized by a sustained negative potential over frontal-central areas of the scalp during the delay period prior to the delivery of reward feedback stimuli. Raw SPN amplitude increased (became more negative) as reward probability decreased, being largest in the 0% reward probability condition and smallest (most positive) in the 100% reward probability condition, indicating that raw SPN increases for improbable positive outcomes, or alternatively, for probable negative outcomes (Fuentemilla et al., 2013). Modulation of SPN amplitude by feedback stimuli inducing negative affect has also been observed previously; for example, anticipation of an aversive noise compared to a neutral tone elicited a larger SPN (Kotani et al., 2001), which aligns with the interpretation that inevitable negative outcomes elicit larger SPNs while expected positive outcomes elicit smaller (more positive) SPNs (see also Morís et al., 2013).

In the present study participants who scored high in depression and low in IU produced a larger (more negative) overall SPN. With respect to depression, larger (more negative) overall SPN may indicate a pessimistic assessment of forthcoming outcomes by these participants. By contrast, smaller (more positive) overall SPN amplitude in participants high in IU – who are characterized by excessive worry over unknown future events – may indicate a relatively more optimistic view of forthcoming rewards. Yet contrary to this interpretation an exploratory analysis suggests that participants high in IU are relatively insensitive to highly probable forthcoming negative outcomes, presumably because of constant worry about future unknowns (see Supplementary Material and Supplementary Figure S3). Taken together, these results suggest that SPN amplitude is inversely correlated with reward probability, and that the relatively large (more negative) SPN observed in participants with elevated depression scores reflects biased attention towards negatively-valenced stimuli, consistent with past findings (Beck, 1976; De Raedt and Koster, 2010; Matt et al., 1992).

We also examined the amplitude of the feedback-RewP as an indicator of reward sensitivity. As expected, feedback-RewP amplitude increased (i.e., became more negative) as the reward outcomes became more unexpected. This result is the opposite of the effect of expectedness on cue-RewP amplitude, consistent with the theory that the reward signals propagate with learning to the reward predictive cues (see above). Participants high in reward responsiveness produced a relatively larger (more negative) overall feedback-RewP; although this result only exhibited a statistical trend, it is in line with observations from several previous studies (Bress and Hajcak, 2013; see also Cooper et al., 2014; Liu et al., 2014; Parvaz et al., 2016). Moreover, participants who scored high in reward sensitivity (as indicated by reward responsiveness and consummatory pleasure) and low in depression produced a larger feedback-RewP for the rewards that were especially probable.

Although the relatively large feedback-RewP to highly probable rewards could indicate that the reward signals failed to propagate back with learning to their associated reward-predictive cues for these individuals, a few considerations argue against this possibility: First, these traits were unrelated to the size of cue-RewP, which would have been smaller for those participants who produced a larger feedback-RewP. Second, the result is also inconsistent with the finding that people who scored high in depression learned more slowly from improbable rewards, and that they exhibited a relatively pessimistic view of forthcoming rewards as suggested by a relatively large (more negative) overall SPN – which together would have caused reward delivery to be relatively more unexpected, producing a larger feedback-RewP. These findings therefore suggest that individual differences in feedback-RewP amplitude directly reflect differences in outcome processing, rather than indirectly reflect other aspects of the task performance such as differences in reward learning or reward anticipation.

Together these results point to impaired reward valuation in individuals high in depression-related traits rather than to impaired reward anticipation per se (or to impaired reward learning). In other words, these individuals appear not to experience rewards as rewarding as other individuals do. By contrast, RewP amplitude is normal in people with schizophrenia, suggesting that these individuals value rewards normally but that the rewards fail to motivate behaviours (e.g., Kring and Barch, 2014 for review; Morris et al., 2011). Note that although the RewP is said to index the impact of RPE signals carried by midbrain dopamine neurons on ACC (Holroyd and Coles, 2002; see also Walsh and Anderson, 2012), the origin of impaired reward valuation in depression may arise outside of ACC and the dopamine system. In particular, the RPE signals themselves are produced in dopamine-innervated reward regions including the nucleus accumbens and orbitofrontal cortex. Impaired reward valuation by these regions, which are often seen to be hypoactive in depression, would therefore result in the dopamine system carrying abnormal RPE signals to the ACC (Holroyd and Umemoto, 2016)—as appears to be the case in clinically depressed individuals (Gradin et al., 2011; Kumar et al., 2008).

Taken together, these results can be summarized as follows. First, persistent individuals exhibited a superior ability to integrate rewards across many trials, as revealed by better learning of stimulus-response associations. Second, IU was associated with reduced reward anticipation, as revealed by a smaller SPN. Third, participants who score high in depression exhibited greater difficulty in learning stimulus-response associations with infrequent rewards. Although the depression and IU scores were strongly correlated (see also, Nelson et al., 2014), only the depression scores and not the IU scores were associated with a more pessimistic assessment of reward delivery (as revealed by a larger overall SPN) and blunted reward sensitivity (as revealed by a smaller

feedback-RewP), particularly when rewards were highly expected. As discussed above, the high expectation for negative outcomes and reduced reward learning in the low reward probability condition, coupled with a smaller feedback-RewP, is indicative of a primary deficit in reward valuation, as opposed to deficit in reward anticipation per se, which likely slowed learning to infrequent rewards.

Further, as observed in several previous studies (Proudfit, 2015), participants high in reward responsiveness produced relatively larger (more negative) feedback-RewP amplitudes, particularly when rewards were predicted; and the consummatory pleasure subscale of the anhedonia scale (i.e., TEPS) was correlated with larger feedback-RewP amplitude when rewards were expected, in line with a previous finding of a study with healthy individuals (Liu et al., 2014; but see also Cooper et al., 2014). Although a predicted association between reward responsiveness and larger RewP amplitude exhibited only a statistical trend,[7] the weakness of this effect may be task-dependent.[8]

A limitation of the current study is that the experiment involved only healthy college students, so the results might not generalize to clinically depressed individuals. Yet, it is promising that the amplitude of the feedback-RewP has been consistently associated with reward sensitivity both in sub-clinical and clinically depressed individuals (Foti and Hajcak, 2009; Liu et al., 2014; see also Parvaz et al., 2016). Moreover, reduced reward valuation as indicated by blunted feedback-RewP is already seen in pre-pubertal children and adolescents (Proudfit, 2015). Nevertheless, blunted reward valuation as a biomarker for depression requires further investigation, as one recent study observed a normal feedback-RewP in depressed individuals who reported intact positive mood reactivity (Foti et al., 2014).

Examination of reward anticipation indicated a link between depression and reward anticipation prior to feedback delivery (i.e., SPN). This suggests that participants who scored high in depression were more pessimistic about the probability of reward delivery, as revealed by an increased overall SPN. A link between SPN and ACC activation has been reported in a recent combined EEG and fMRI study (Kotani et al., 2015; but see also Böcker et al., 1994; Masaki et al., 2010), suggesting that past studies reporting increased ACC activity during reward anticipation (Knutson et al., 2008; Gorka et al., 2014; see also Dichter et al., 2012) may in part reflect increased pessimism about the outcomes. In particular, these studies utilized tasks in which rewards were probabilistically delivered on about 50 or 66 % of the trials, so the more depressed participants may have expected negative outcomes more than positive outcomes, inducing larger ACC activity. Furthermore, observations of a reduced fMRI BOLD response in ACC in depression may be due to evaluating data pooled across different reward probability conditions (Smoski et al., 2009). These observations also highlight the importance of incorporating learning into tasks in order to examine reward processing (see Adams et al., 2016), as it has been widely acknowledged that the midbrain dopamine system is heavily involved in a variety of reward-related processes including reward learning (Berridge et al., 2009; Schultz, 2007).

Finally, it is worth noting that the severity or the clinical profile of depression may differentially impact reward anticipation, as previous studies have observed impaired reward anticipation only in individuals with early depression onset prior to adulthood (Nelson et al., 2014; Shankman et al., 2007, 2013). Therefore, future investigations examining SPN amplitude in individuals who exhibit such a clinical profile would be beneficial.

In conclusion, our study highlights how individual differences in personality contribute to the dynamics of reward processing. Consistent with past studies we found that individuals who scored high in depression exhibited difficulty in learning stimulus-response contingencies for improbable rewards, a more pessimistic view of reward acquisition, and blunted sensitivity to reward value; crucially, although the behavioural and SPN results would predict a larger feedback-related RewP due to the rewards being more unexpected, the reduced feedback-RewP confirms a primary deficit in reward valuation in individuals who score high in depression. Future studies should expand on these results by further examining individual differences in personality in clinically depressed patients.

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Conflict of interest: None.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.clinph.2017.03.049.

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[7] Note also that the analysis for feedback-RewP only included post-learning trials (defined as following three consecutive correct responses for each probability condition), and feedback-RewP for predictable outcomes generally becomes smaller with learning (see also the observed negative correlation between accuracy and feedback-RewP in this study).

[8] In addition, the task design regarding the 50% reward probability condition is characterized by a critical difference from previous studies. In most previous task designs, reward feedback was delivered with 50% probability irrespective of which response is chosen by the subject (e.g., Holroyd and Coles, 2002). For this reason the condition can control for individual differences in learning and performance on feedback-RewP amplitude; because the reward and no-reward outcomes are entirely unpredictable on such trials, they generate a feedback-RewP that is unconfounded by other task variables (e.g., Morris et al., 2011). However, in the present study on such trials the rewards were delivered with 50% probability following only one of the 2 responses, and were never delivered following the other response (Holroyd et al., 2009). Hence participants still had to learn the correct responses in this condition, and the no-reward outcomes occurred more frequently overall than the reward outcomes did. This nuance in the task design may explain why no association was found between the reward sensitivity scores (i.e., reward responsiveness, TEPS-C, and depression) and the 50% feedback-RewP as reported in previous studies, as well as for the remaining ERP components in this condition. Future investigations should take into account such differences in task design.

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