

Mood congruent tuning of reward expectation in positive mood: evidence from FRN and theta modulations

Katharina Paul and Gilles Pourtois

Cognitive and Affective Psychophysiology Laboratory, Department of Experimental-Clinical and Health Psychology, Ghent University, Ghent, Belgium

Correspondence should be addressed to Katharina Paul, Cognitive and Affective Psychophysiology Laboratory, Department of Experimental-Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Gent, Belgium. E-mail: katharina.paul@ugent.be

Abstract

Positive mood broadens attention and builds additional mental resources. However, its effect on performance monitoring and reward prediction errors remain unclear. To examine this issue, we used a standard mood induction procedure (based on guided imagery) and asked 45 participants to complete a gambling task suited to study reward prediction errors by means of the feedback-related negativity (FRN) and mid-frontal theta band power. Results showed a larger FRN for negative feedback as well as a lack of reward expectation modulation for positive feedback at the theta level with positive mood, relative to a neutral mood condition. A control analysis showed that this latter result could not be explained by the mere superposition of the event-related brain potential component on the theta oscillations. Moreover, these neurophysiological effects were evidenced in the absence of impairments at the behavioral level or increase in autonomic arousal with positive mood, suggesting that this mood state reliably altered brain mechanisms of reward prediction errors during performance monitoring. We interpret these new results as reflecting a genuine mood congruency effect, whereby reward is anticipated as the default outcome with positive mood and therefore processed as unsurprising (even when it is unlikely), while negative feedback is perceived as unexpected.

Key words: EEG; FRN; mid-frontal theta; positive mood; reward prediction error

Mood-related modulation of reward processing during performance monitoring

Performance monitoring (PM) is responsible for detecting mismatches between actions and goals, and the swift updating of expectations in order to foster goal-adaptive behavior (Botvinick and Braver, 2015). Converging evidence suggests that negative emotion profoundly influences PM brain mechanisms (Weinberg et al., 2012; Koban and Pourtois, 2014) but modulatory effects of positive emotion have not been scrutinized yet. This literature gap is somewhat surprising given that positive psychology has been acknowledged as an important research domain (Csikszentmihalyi, 1999; Sheldon and King, 2001; Seligman et al.,

2005). Moreover, previous research already showed the compelling influence of positive emotions on attention (Vanlessen et al., 2016), cognitive control (Chiew and Braver, 2014; Goschke and Bolte, 2014) and decision making (Isen, 2008; Blanchette and Richards, 2010). Accordingly, in this study, we set out to assess whether positive mood could influence PM brain mechanisms.

Effects of positive mood on cognition have usually been explained using two different theoretical frameworks. Within the ‘mood as distractor’ model, positive mood is viewed as potent distractor, occupying mental resources, like attention (Dreisbach and Goschke, 2004; Olivers and Nieuwenhuis, 2006). This is supported by the adaptive significance of affect, where positive mood signals a benign environment and a creative and heuristic

Received: 27 September 2016; Revised: 15 January 2017; Accepted: 23 January 2017

© The Author (2017). Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work properly cited. For commercial re-use, please contact journals.permissions@oup.com

processing style is promoted, while the use of analytical processing styles is reduced (Schwarz, 1990; Bohnet and Chaiken, 1994; Fredrickson, 2001). By comparison, within the ‘mood as information’ model, positive mood is conceived as an utilizable embodied information in itself, which influences attribution and executive functions differentially (Schwarz and Clore, 2003; Mitchell and Phillips, 2007). A well-established finding of this motivational account is the observation of ‘mood congruency effects’: (external) emotional information congruent with the current mood state draws attention and gets processed preferentially (Mayer et al., 1992; Rusting, 1998), which impacts expectations about future events (Loewenstein and Lerner, 2003). Recently, Eldar et al. (2016) extended this model and conceived mood as a ‘representation of momentum’, where positive mood is thought to arise from the interaction between high reward expectations and experiencing better than expected events. Hence, within the ‘mood as information’ framework, positive mood is a potent motivational drive that can shape reward expectations specifically, as opposed to being associated with unspecific deleterious effects on cognition and attention. Even though previous studies have already shown that happy participants tend to overestimate/underestimate the likelihood of positive/negative events (Mayer et al., 1992; Wright and Bower, 1992; Sharot et al., 2011), research on positive emotions and PM is scant and inconclusive, as the focus was on traits indirectly associated with positive affect, like extraversion (Smillie et al., 2011; Cooper et al., 2014), behavioral approach motivation (Lange et al., 2012; Bress and Hajcak, 2013) or hypomania (Mason et al., 2012; Mason et al., 2012). Noteworthy, no study to date has systematically explored possible changes in reward expectation brain mechanisms as a function of positive mood. The goal of the current study was to fill this gap.

At the electrophysiological level, reward processing can be investigated by means of the feedback-related negativity (FRN), an event-related brain potential (ERP) time locked to the onset of evaluative feedback during PM. The FRN is a negative deflection peaking at around 250–300 ms at fronto-central electrodes with larger amplitudes for negative compared to positive feedback, especially if unexpected, making this ERP component a standard measure of reward prediction errors (RPE) (Holroyd and Coles, 2002; Walsh and Anderson, 2012; Ullsperger et al., 2014; Sambrook and Goslin, 2015). More recently, mid-frontal theta activity (4–8 Hz) has been put forward as a complementary marker of RPE and cognitive control (Cohen et al., 2007; Cavanagh et al., 2010; Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014; Cavanagh and Shackman, 2015; Osinsky et al., 2016). Time-frequency decompositions enable capturing trial by trial fluctuations varying in phase that a standard ERP averaging technique cannot measure, and hence provide additional information regarding PM brain mechanisms (Cohen and Donner, 2013).

In this study, we capitalized on these two well-established electrophysiological markers of RPE (i.e., FRN and mid-frontal theta oscillations) to explore the nature and extent of changes brought about by positive mood during reward processing under conditions varying in reward probability (and hence expectation). To this aim, we directly induced either a positive or neutral mood state by means of guided imagery (Holmes et al., 2006, 2008), a mood induction procedure (MIP) validated in our laboratory before (Vanlessen et al., 2012, 2014, 2015, Bakic et al., 2014, 2015; Paul et al., 2017). Participants performed a previously used gambling task (Hajcak et al., 2005), which allowed us to manipulate reward expectation by controlling its probability independently of performance, while 64-channels EEG was recorded concurrently.

In an auxiliary analysis, we also assessed whether positive mood could influence reward anticipation, besides reward

consumption (at the FRN and theta levels) given that positive mood is best conceived as a tonic mood change. To this aim, we analyzed the contingent negative variation (CNV) time-locked to cue onset, as well as the stimulus preceding negativity (SPN) in anticipation of feedback delivery, as these two ERP components have been related previously to reward anticipation (Chwilla and Brunia, 1991; Broyd et al., 2012; Novak and Foti, 2015; Pornpattananangkul and Nusslock, 2015; Novak et al., 2016).

Based on the two different frameworks outlined here above, different predictions were derived. If positive mood signals a safe environment and enhances distractibility, then it should impair reward processing generically (i.e., regardless of reward probability and expectation), leading in turn to blunted FRN/Theta responses to any feedback. By comparison, if positive mood is accompanied by specific motivational changes and increases reward expectation, we surmised that it could lead to enhanced RPE signals (FRN and theta activity, see Holroyd and Coles, 2002; Cavanagh and Shackman, 2015) for negative feedback and/or decrease RPE signals for positive feedback, compared to a control condition with a neutral mood state.

Methods

Participants

Fifty undergraduate students (right-handed, corrected-to-normal vision, no history of psychiatric disorders), gave written informed consent and were compensated with €30 for participating in this study (approved by the local ethics committee). Participants were randomly assigned to either a positive or neutral mood induction. One participant did not complete the experiment due to sickness and four participants had to be excluded due to technical problems during data acquisition. Hence, 23 participants in the neutral and 22 in the positive mood group were included, matched for gender distribution and age ($M_{\text{Positive}} = 22.3$ years, $s.d. = 2.81$, 15 females; $M_{\text{Neutral}} = 21.2$ years, $s.d. = 1.85$, 18 females). This sample size was similar to previous studies where the same MIP and between-subjects experimental designs were used (Vanlessen et al., 2012, 2014, 2015, Bakic et al., 2014, 2015; Paul et al., 2017).

Mood induction

A validated MIP was used and detailed description can be found elsewhere (Vanlessen et al., 2012, 2014, Bakic et al., 2014, 2015; Paul et al., 2017). In short, either positive or neutral mood was induced by means of an imagery procedure, fostering vivid imagination and re-experiencing of a positive/happy or neutral memory (Holmes et al., 2006, 2008). Current mood state was checked with three visual analog scales anchored with ‘neutral’ and ‘as happy/pleasant/sad as I can imagine’. Subjective arousal was assessed with the Self-Assessment Manikin (Bradley and Lang, 1994).

Task

A previously used gambling task was adapted and administered (Hajcak et al., 2007) (Figure 1). On each and every trial, participants chose one of four doors by pressing with their right index finger the corresponding key on the response box. After a fixation dot (700 ms) this choice was followed by either positive feedback (green ‘+’), indicating a win of 8 cents, or (negative) no-reward feedback (red ‘o’) (1000 ms). At the beginning of each trial participants were informed about their winning chances with a cue (600 ms), followed by a fixation dot (1500 ms). The cue was presented in the form of a small circle. Either one, two

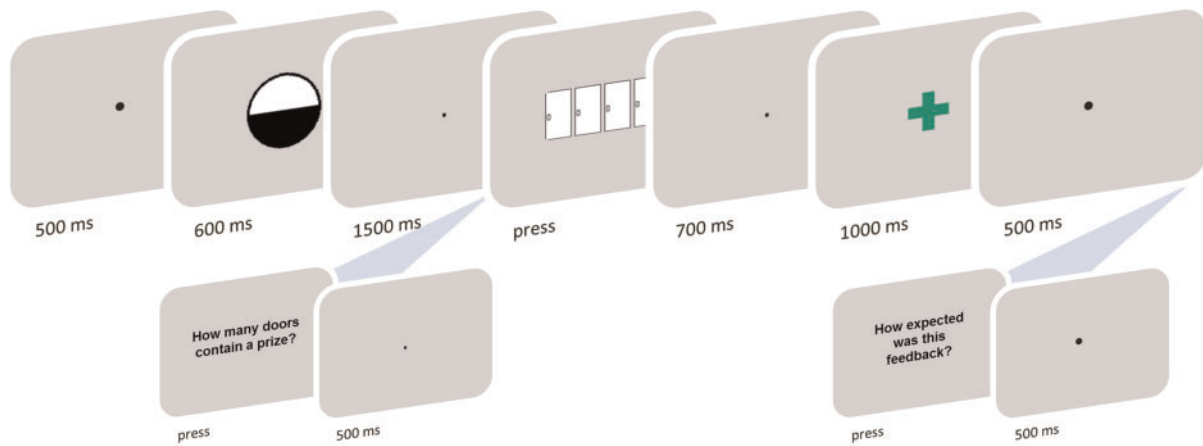


Fig. 1. Overview of the task and trial structure: At the beginning of each trial, participants were informed about their winning chances (black or white part of the circle, 25, 50 or 75%). After they picked one door, they received either positive monetary rewarding or negative (i.e., no reward) feedback. Additionally, in 13% of the trials participants had to rate their winning chances or/and the expectedness of the given feedback by means of extra probes/questions.

or three quarters were filled (black/white) announcing a winning likelihood of 25, 50 or 75%. Feedback was only related to these three objective reward probabilities, ending up with a preset winning of €14.72. To ensure participants paid attention to the cue and outcome, they were asked within 24 trials about their winning chance ('How many doors do contain a prize?', and in 24 different trials about the expectedness of the feedback, answered on a visual analog scale (anchored with 'very unexpected' to 'very expected'). All stimuli were shown against a grey background on a 21-in CRT screen and executed using E-Prime (V 2.0, Psychology Software Tools Inc., Sharpsburg, PA).

Procedure

Participants started with instructions and twelve practice trials. Five minutes of resting state with closed eyes were recorded before and after the first MIP as a baseline for the electro-dermal activity (EDA). The experiment consisted of four blocks of 92 trials. The three cue types were presented randomly, while there were 80 trials with medium and 144 trials with either low or high winning chance, respectively. Each block was interrupted by a short break. After each block, participants were informed about their current winning and the MIP was repeated.

Recording and preprocessing of electrophysiological data

EEG was recorded using a 64-channel Biosemi Active Two system (<http://www.biosemi.com>) with four additional electrodes measuring eye movements. EEG was sampled at 512 Hz and referenced to the Common Mode Sense active electrode Driven Right Leg passive electrodes. The EEG was preprocessed offline with EEGLAB 13.5.4b (Delorme and Makeig, 2004), implemented in Matlab R2013b, and included a 0.05/35 Hz high/low pass filter, re-referencing to the mastoids and FASTER guided automatic ICA component rejection (with a threshold of ± 3 s.d.) (Nolan et al., 2010). Individual epochs were extracted -900 to 1600 ms around the feedback onset and baseline corrected (-250 to 0 ms). A semi-automatic artefact correction procedure was applied to eliminate trials with voltage values exceeding ± 90 μ V or slow voltage drifts with a stronger slope than ± 90 μ V as well as based on visual inspection. For each subject separately, the EEG data corresponding to six conditions were extracted: Expected, no expectations and unexpected feedback (FB), separately for positive and negative FB. To account for different

signal to noise ratios, only a similar (randomly sampled) number of trials of the expected conditions was used ($M_{\text{Positive}} = 31.9$, s.d. = 3.97; $M_{\text{Neutral}} = 33.9$, s.d. = 2.70). The FRN was quantified at Fz as the difference between the most negative peak (within 140–300 ms) and the average voltage of the preceding and following positive peaks, to control for possible confounding effects of the overlapping positive components (i.e., P2 prior to and P3 following the negative component), as suggested by previous ERP studies (Yeung and Sanfey, 2004; Oliveira et al., 2007; Chase et al., 2010; Sallet et al., 2013). We also used two alternative scoring methods for the FRN. Either it was defined as a mean amplitude between 230 and 280 ms post FB onset, or as the difference between the most negative peak (N200) and the preceding positive peak (P200) (to reduce the possible contribution of the following P3 component).

Time frequency analysis was done using EEGLAB built-in `std_erspss()` function (3.5 to 24.5 cycles, 3 to 35 Hz (100 log-spaced frequencies), 200 time points per epoch). The time interval -500 to -200 ms before FB onset was used for baseline correction. Theta band power activity (4–8 Hz) was defined as the mean within 200–400 ms at Fz. The electrode Fz was chosen based on the local maximum of the mean voltage (200–300 ms, Fz and FCz) and the mean theta power (200–400 ms, Fz) (Figures 4E and 5B).

EDA was recorded continuously with a sampling rate of 512 Hz via two bipolar electrodes attached to the volar surface of the distal phalanges of the left index and middle finger. EDA was analyzed using Ledalab V.343 (Benedek and Kaernbach, 2010a, 2010b). Preprocessing included (8-point Gaussian) smoothing, 5 Hz low-pass Butterworth filter and visual inspection (interpolated artefacts: $M_{\text{Positive}} = 9.89\%$, s.d. = 11.45; $M_{\text{Neutral}} = 7.91\%$, s.d. = 11.07). The tonic skin conductance level (SCL) for each resting and task block was extracted. Additionally, phasic skin conductance responses (SCR) was quantified within 1 to 3 s after FB onset (minimum amplitude 0.05 μ S) (Boucsein et al., 2012). Finally individual data were standardized using a $\log(1+x)$ transformation (following Venables and Christie, 1980). Data to supplementary analyses that focused on reward anticipation, i.e. information cue related ERPs, and the separation of evoked and induced theta power, are available as Supplementary Materials.

Data analysis

For all analyses, significance alpha cutoff was 0.05. To check for the efficiency of the MIP, a mixed model ANOVA with mood

(positive vs neutral) as between-subjects factor and time (6 ratings) as within-subject factor was used, separately for all four mood assessments and SCL. Whenever the two-way interaction was significant, it was followed up by independent sample *t*-tests to compare mood levels between the two groups.

Behavioral performance was quantified by analyzing reaction time (RT) and exploration pattern. To measure exploration, we used an autocorrelation function of the trial-by-trial time series (Derrick and Thomas, 2004; Pacheco and Newell, 2015), analyzing the value of the first and the number of significant lags (until the 25th), where an auto-correlation value close to zero indicates a random distribution. Evaluations of the FB expectancy along the continuous scale were first transformed to percentages, arbitrarily setting one anchor ('very unexpected') to 0 and the other ('very expected') to 100. These evaluations were considered to be correct if the given rating fell within a $\pm 25\%$ range around the correct chance. We used this rather liberal criterion given the continuous scale, the small number of ratings collected per participant and condition, and since they primarily served to increase attention/processing of both the cue and the feedback. Accuracy of feedback and cue evaluation, RTs and exploration were compared between groups by means of independent sample *t*-tests.

For both EEG measurements and SCR separately, a mixed-model ANOVA with mood as between-subjects factor and feedback expectation (expected, no expectations, unexpected) as well as feedback valence (positive vs negative) as within subject factor was used.

Results

Manipulation checks

There was a significant interaction between time and mood for all ratings, except sadness ($F(5, 215) = 0.98, P = 0.83, \eta^2 = .006$); happiness: ($F(5, 215) = 14.43, P \leq 0.001, \eta^2 = 0.23$); pleasantness: ($F(5, 215) = 14.10, P \leq 0.001, \eta^2 = 0.22$); arousal: ($F(5, 215) = 6.764, P = 0.001, \eta^2 = 0.14$). Follow-up contrasts showed that there were no significant group differences for mood ratings at baseline (all $t_s(43) \leq 1.23, P \geq 0.06, d \leq 0.36$). After the MIP, the positive compared to the neutral mood group showed increased levels for happiness, pleasantness and arousal ($t_s(43) \geq 3.03, P \leq 0.004, d \geq 0.68$) (Figure 2).

EDA results

For the SCL analysis, a significant main effect of time was found ($F(5, 156) = 25.36, P \leq 0.001, \eta^2 = 0.39$), similarly in both groups ($F(5, 156) = .687, P = 0.64, \eta^2 = 0.010$). SCL increased after the first MIP and remained on a higher level compared to the baseline for both groups ($M_{\text{Resting Baseline}} = 2.94 \mu\text{S}$, *s.d.* = 0.35, $M_{\text{Resting after MIP}} = 3.09 \mu\text{S}$, *s.d.* = 0.36) (Figure 2). The auxiliary SCR analysis revealed only a significant main effect of expectation ($F(2, 86) = 42.1, P \leq 0.001, \eta^2 = 0.33$) (other $F_s(2, 86) \leq 2.89, P \geq 0.10, \eta^2 \leq .063$). The SCR was stronger for unexpected compared to expected FB [$t(45) = 6.87, P \leq 0.001, d = 1.03$], and for no-expectation compared to expected FB [$t(45) = 7.25, P \leq 0.001, d = 1.13$], irrespective of FB valence ($M_{\text{Unexpected}} = 65.9 \mu\text{S}$, *s.d.* = 17.79, $M_{\text{No-expectations}} = 63.78 \mu\text{S}$, *s.d.* = 15.0, $M_{\text{Expected}} = 43.0 \mu\text{S}$, *s.d.* = 21.5).

Behavioral results

Participants of both groups were equally fast in choice behavior [$t(43) = 0.39, P = 0.70, d = 0.12, M_{\text{Positive}} = 732 \text{ ms}$, *s.d.* = 305,

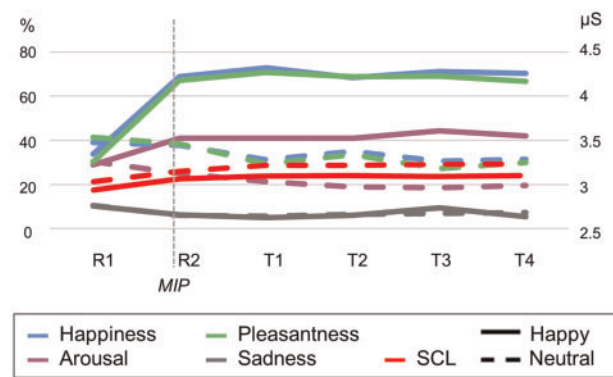


Fig. 2. Manipulation checks: mood ratings and SCL shown separately for the positive and neutral mood group as a function of time, including two resting state blocks (R1, R2) and four task blocks (T1–T4). After the first MIP (R2), participants in the positive mood group reported higher levels of happiness, pleasantness and arousal, while SCL increased for both groups. This increase remained stable over the task (from T1 to T4).

$M_{\text{Neutral}} = 701 \text{ ms}$, *s.d.* = 223] and showed a comparable exploration pattern (autocorrelation: $t(43) = 0.44, P = 0.66, d = 0.13$, $M_{\text{Positive}} = -0.01$, *s.d.* = 0.18, $M_{\text{Neutral}} = 0.13$, *s.d.* = 0.23; number of lags: $t(4) = 0.98, P = 0.33, d = 0.29$, $M_{\text{Positive}} = 2.45$, *s.d.* = 1.22, $M_{\text{Neutral}} = 3.56$, *s.d.* = 5.17). Participants of both groups did not differ in their accuracy for the cue (catch trials) [$t(43) = 0.023, P = 0.98, d \leq 0.01$; $M_{\text{Positive}} = 21.8$, *s.d.* = 1.00, $M_{\text{Neutral}} = 21.8$, *s.d.* = 1.30] or for the outcome [$t(43) = 1.77, P = 0.08, d = 0.53$; $M_{\text{Positive}} = 17.5$, *s.d.* = 3.74, $M_{\text{Neutral}} = 15.1$, *s.d.* = 5.11].

Electrophysiological results

The analysis of the FRN amplitudes showed a significant main effect of expectation [$F(2, 86) = 11.14, P \leq 0.001, \eta^2 = .037$] and valence ($F(1, 43) = 40.01, P \leq 0.001, \eta^2 = .32$). The FRN component was larger for negative compared to positive FB [$t(44) = 7.26, P \leq 0.001, d = 0.94$] and unexpected compared to both expected [$t(44) = 5.52, P \leq 0.001, d = 0.53$] and no-expectation FB [$t(44) = 4.28, P \leq 0.001, d = 0.42$]. The significant interaction between these two factors ($F(2, 86) = 4.01, P = 0.022, \eta^2 = .010$) showed that the difference of unexpected and expected FB was only significant for negative FB [$t(44) = 3.92, P \leq 0.001, d = 0.59$], but not for positive FB [$t(44) = 1.50, P = 0.14, d = 0.24$]. Importantly, there was also a significant interaction between valence and mood [$F(1, 43) = 4.58, P = 0.041, \eta^2 = 0.032$]. Participants in the positive mood group differentiated more between positive and negative FB (irrespective of expectation) than the neutral mood group [$t(43) = 2.11, P = 0.041, d = 0.63$]. The two groups did not differ from one another in their response to positive [$t(43) = 0.88, P = 0.38, d = 0.63$] or negative FB [$t(43) = 1.47, P = 0.15, d = 0.26$], but the effect sizes indicated that the interaction effect was mainly driven by a stronger response to negative FB in the positive mood group (Figures 3 and 4).

When using mean amplitudes to quantify the FRN, the analysis showed a significant main effect of expectation [$F(2, 86) = 4.38, P = 0.015, \eta^2 = 0.091$], valence [$F(1, 43) = 207.1, P < 0.001, \eta^2 = 0.82$], while the interaction between valence and mood did not reach significance [$F(2, 86) = 1.51, P = 0.23, \eta^2 = 0.006$]. However, given the morphology of the feedback locked ERP data, the use of mean amplitudes did not capture systematic changes occurring at the level of the FRN selectively, unlike peak-to-peak measurements (see Sallet et al., 2013 for a discussion). Moreover, using a peak (P2)-to-peak (N200)

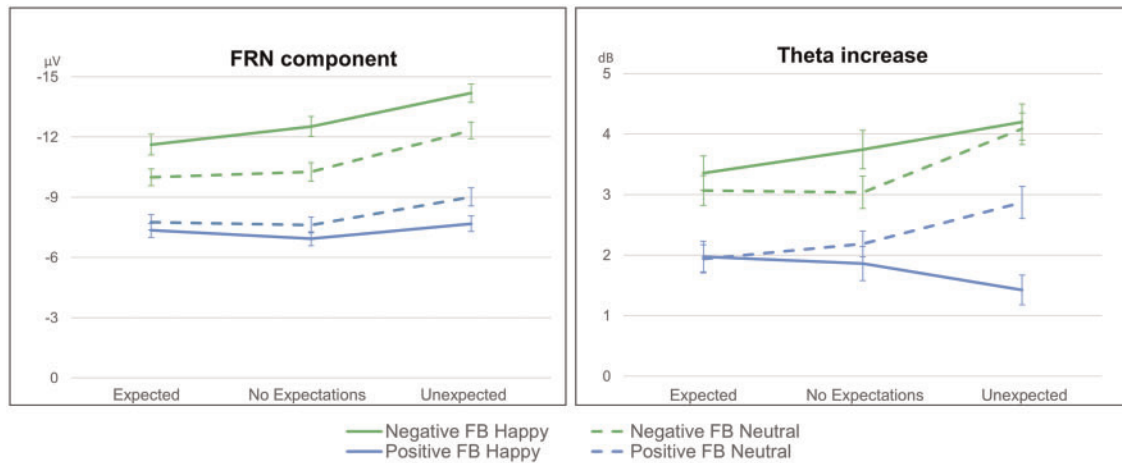


Fig. 3. Electrophysiological Results. Overview of mean FRN amplitudes (left panel) and mean theta power (right panel) (\pm standard error of the mean) at electrode Fz, separately for each group and each condition.

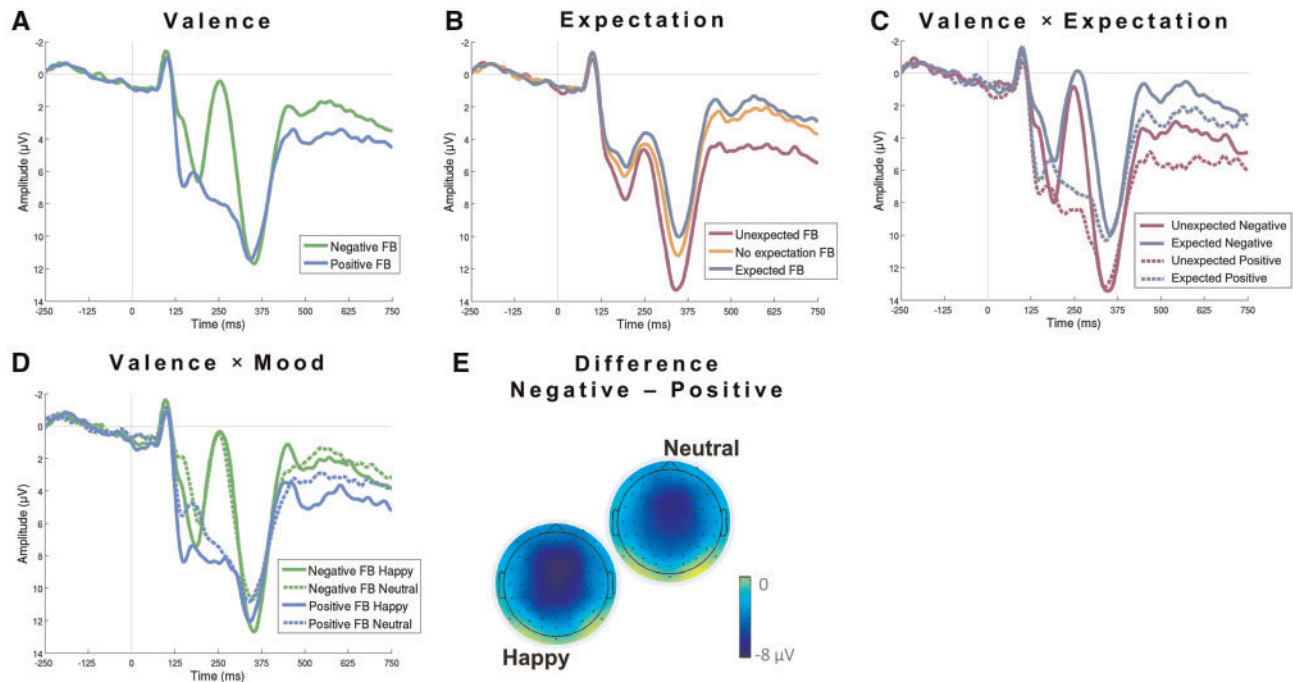


Fig. 4. FRN results. Grand averages feedback-locked ERP waveforms at Fz shown according to significant main effects and interactions. (A) The FRN amplitude was substantially larger for negative than for positive FB. (B) Unexpected FB led to a larger FRN component than expected FB. (C) The sensitivity of the FRN to expectation was the most pronounced for negative FB. (D) The FRN component of participants in the positive mood group differentiated better between negative and positive FB than in the neutral mood group. This effect was mostly explained by a stronger response to negative FB in the happy compared to the neutral mood group. (E) Topographical maps (horizontal view) of the FRN valence effect showing the mean activity during the 200–300 ms post feedback onset interval, separately for both mood groups, and confirming a predominant fronto-central scalp distribution for this ERP component.

approach, the main effect of expectation [$F(2, 86) = 16.1, P < 0.001, \eta^2 = .27$], valence [$F(1, 43) = 52.7, P < 0.001, \eta^2 = 0.52$] and the interaction between the valence and mood [$F(2, 86) = 5.81, P = 0.02, \eta^2 = 0.06$] were all significant, paralleling the statistical outcome evidenced using the peak-to-average-peak method.

The analysis performed on mid-frontal theta power showed a significant main effect of expectation [$F(2, 86) = 6.43, P = 0.002, \eta^2 = 0.033$], valence [$F(1, 43) = 75.54, P < 0.001, \eta^2 = 0.34$] and their interaction [$F(2, 86) = 4.69, P = 0.012, \eta^2 = 0.015$]. Moreover, each interaction term with mood reached statistical significance: mood and expectation [$F(2, 86) = 4.40, P = 0.015, \eta^2 = 0.023$], mood and valence [$F(1, 43) = 7.12, P = 0.011, \eta^2 = 0.032$], and the three-

way interaction [$F(2, 86) = 3.16, P = 0.047, \eta^2 = 0.010$]. To gain insight into this latter effect, two mixed-model ANOVAs were calculated separately for each group. While participants in the positive mood group showed a significant interaction of expectation and valence [$F(2, 44) = 6.75, P = 0.003, \eta^2 = 0.066$], participants in the neutral group did not [$F(2, 42) = 0.585, P = 0.56, \eta^2 \leq 0.001$]; only the two main effects were significant in this control group [expectation: $F(2, 44) = 12.77, P < 0.001, \eta^2 = 0.19$; valence: $F(1, 22) = 27.31, P < 0.001, \eta^2 = 0.28$] (Figure 3). Similar to the FRN results, theta power was stronger in response to negative compared to positive FB [$t(44) = 9.13, P < 0.001, d = 1.31$], and unexpected compared to both expected [$t(44) = 3.49, P = 0.002, d = 0.37$] and

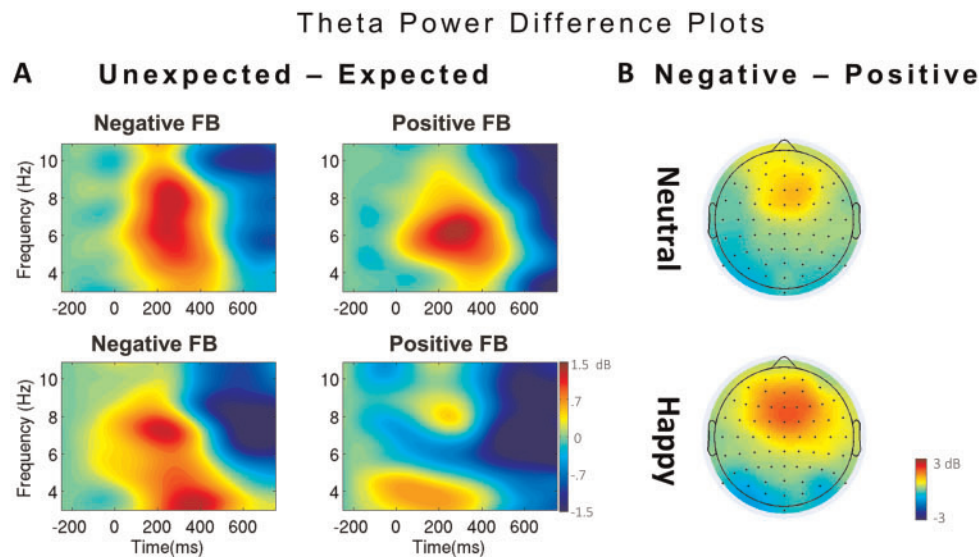


Fig. 5. Theta power results. (A) The difference in theta power increase for unexpected minus expected FB at Fz is shown separately for positive and negative FB, and for the neutral (first row) and the positive mood group (second row). While neutral participants showed a stronger theta response for unexpected than expected FB irrespective of their valence, happy participants showed this pattern for negative FB only, with a clear alteration of this expectation effect for positive FB. (B) Topographical maps of the theta power (difference between negative and positive FB) showing the mean power during the 200-400 ms post feedback onset interval, separately for both mood groups. This topography clearly confirmed a predominant fronto-central scalp distribution for this theta power effect, being reliably larger for happy than neutral participants.

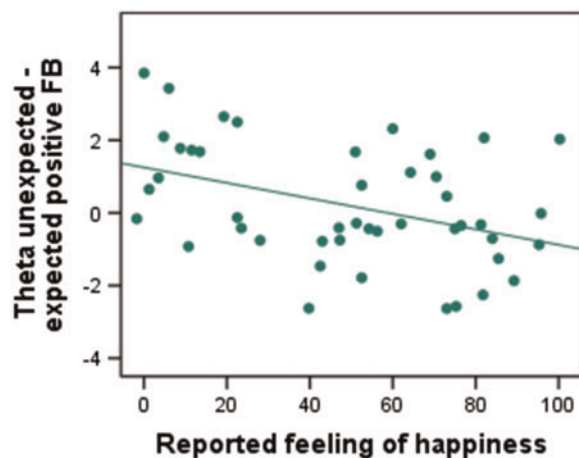


Fig. 6. Significant correlation between theta power effect for positive FB and levels of happy mood (as computed across all participants). In agreement with the significant three way interaction, the higher levels of happy mood, the lower the difference in theta power between unexpected and expected positive FB.

no-expectation FB [$t(44) = 2.73$, $P = 0.021$, $d = 0.45$]. Interestingly, participants in the positive mood group did not differentiate between expected and unexpected positive FB [$t(21) = 2.02$, $P = 0.057$, $d = 0.39$], although they did so for negative FB [$t(21) = 2.25$, $P = 0.035$, $d = 0.49$], while neutral participants showed this pattern for both positive [$t(22) = 2.84$, $P = 0.010$, $d = 0.60$] and negative FB [$t(22) = 3.76$, $P = 0.001$, $d = 0.79$] (Figure 5). Furthermore, direct statistical testing confirmed a balanced theta power response to expected positive feedback between the two mood groups [$t(43) = .09$, $P = 0.93$, $d = 0.03$], while the only significant group difference was found for unexpected positive feedback, where theta power was blunted for the positive mood group [$t(43) = 42.2$, $P = 0.002$, $d = 0.98$]. Moreover this altered RPE effect was related to the current mood state of the participant [$r(45) = -0.40$, $P = 0.006$], but not to the arousal level [$r(45) = -0.26$, $P = 0.085$] (Figure 6),

although these two correlations were not significantly different from each other ($z = 0.99$, $P = 0.32$). To confirm that mood, but not simply arousal, influenced this RPE effect, we also calculated a partial correlation between the mood state and the RPE effect controlling for arousal, revealing a similar significant result [$r(42) = -0.33$, $P = 0.031$]. The correlation between arousal and the RPE effect was non-significant when controlling for the mood state [$r(42) = -0.067$, $P = 0.67$].

Discussion

To explore modulatory effects of positive mood on PM and RPE, we induced either a positive or a neutral mood using guided imagery, while participants performed a gambling task and 64-channels EEG (as well as EDA) were recorded concurrently. This task enabled to manipulate feedback valence and expectation in a factorial design, making it possible, using adequate EEG methods (FRN and mid-frontal theta levels), to assess whether positive mood either blurred RPE during PM, or instead created compelling mood congruency effects. Our new neurophysiological results clearly lend support to the latter hypothesis, showing mood-related modulations of the FRN component and theta response: relative to a neutral mood group, participants in positive mood showed larger FRN amplitudes selectively for negative FB (as if negative feedback was always deemed as 'unexpected'), while mid-frontal theta results indicated an altered RPE signal to (objectively) unexpected positive FB (as if positive mood transformed unexpected reward to an expected event). Remarkably, this effect correlated with the individual level of positive mood, suggesting its pivotal role therein. Moreover, by disentangling the evoked from the induced component of the theta activity, i.e. removing the influence of the ERP signal from the frequency spectra (see Supplementary Material), we could demonstrate that this was not explained by the mere superposition of the ERP component on these oscillations. Importantly, this effect was evidenced in the absence of obvious differences at the behavioral level or the physical arousal (SCL), ruling out

the possibility that it was caused by uncontrolled changes in attention or involvement in the task.

To the best of our knowledge, our neurophysiological results are the first to show that positive mood does not simply create distraction during PM, but dynamically changes reward processing in a condition specific manner. Previous ERP studies already explored effects of positive mood on PM, with a focus on error-related ERP components, with some inconsistent results however (Larson *et al.*, 2006; van Wouwe *et al.*, 2011; Bakic *et al.*, 2014; Paul *et al.*, 2017). By comparison, no study to date showed a reliable effect of positive affect on PM when it is based on the use of external information and hence the FRN component (Bakic *et al.*, 2014; Riepl *et al.*, 2016). This apparent discrepancy between our results and these earlier studies likely stems from methodological differences and the specific cognitive process assumed to be changed by positive mood. While these earlier studies primarily sought to show modulatory effects of positive mood on PM using complex tasks, here we examined effects of positive mood on reward expectation, using a simpler task devoid of any learning or social component.

Our new results show that positive mood alters phasic and dopaminergic dependent reward prediction error signals (at the FRN and theta levels), which are instrumental to (de)code the degree of mismatch between the actual and expected outcome (Schultz *et al.*, 1997; Holroyd and Coles, 2002; Walsh and Anderson, 2012; Ullsperger *et al.*, 2014; Sambrook and Goslin, 2015; Schultz, 2015). The stronger FRN response for negative FB in the positive mood group suggests that negative FB was always—irrespective of the objective likelihood—coded as more unexpected, unambiguously translating a mood (in)congruent effect. Interestingly, theta results complement this by revealing a clear decrease for (objectively) unexpected positive FB, indicating that a positive outcome was probably expected a priori and hence not surprising in this mood group. Both results fit with previous research on mood congruent expectations (Mayer *et al.*, 1992; Loewenstein and Lerner, 2003; Sharot *et al.*, 2011; Eldar *et al.*, 2016), but they extend it substantially by revealing for the first time which neurophysiological mechanism (i.e., RPE) might be responsible for these behavioral effects. Furthermore, auxiliary analyses performed on anticipatory processes during reward processing (focusing on the CNV and SPN components) confirmed the assumption that positive mood dynamically changes reward expectation, creating in turn a strong bias in favor of reward delivery. This conclusion was supported by the observation of an enhanced CNV activity in positive mood for cases associated with a high reward probability, as well as the subsequent abnormal processing of reward uncertainty at the SPN level in this specific mood state (see Supplementary Material). Because these neurophysiological effects were observed in the absence of differences at the behavioral level (e.g., reward probability ratings), they suggest a dynamic change of reward expectations with positive mood state.

Our new EEG results confirm that although FRN and theta power covary tightly, they can be dissociated (Cohen *et al.*, 2007; Cavanagh *et al.*, 2010; Cavanagh, Zambrano-Vacquez, *et al.*, 2012), especially when effects of positive mood are considered. While the FRN seems more sensitive to negative RPE, i.e. worse than expected outcomes, theta power is rather linked to unsigned RPE in general (Hajihosseini and Holroyd, 2013; Osinsky *et al.*, 2016). Accordingly, depending on which electrophysiological marker is considered, different results could be found. Consistent with these earlier studies, here we found that positive mood mostly influenced negative RPE at

the FRN level, while it altered reward expectation at the theta level.

Some limitations warrant comment. As reported in a similar study (see Paul *et al.*, 2017), we found again a dissociation between arousal at the subjective level (that was increased in the positive compared to the neutral mood group) and the tonic activity (SCL) that did not show a group difference, suggesting that subjective arousal might contribute to the reported neurophysiological effects. However, we have good reasons to believe that subjective arousal was not the main determinant of the changes in RPE signals. First, albeit SCL increased after the MIP compared to baseline, confirming that this measure was sensitive to capture bodily changes in terms of autonomic arousal, it remained comparable between the two mood groups through the task. Also participants of both groups did show a stronger SCR to unexpected than expected outcomes, reflecting an orienting reaction (Siddle *et al.*, 1984; Barry *et al.*, 2011; Nieuwenhuis *et al.*, 2011). Second, we found a relation between reported levels of happiness and the change in RPE for positive feedback in theta activity, while we failed to evidence a relationship with (subjective) arousal. More generally, we believe that this discrepancy between subjective and objective arousal might stem from the different assessment methods for these two measures (see also Paul *et al.*, 2017). While the subjective ratings were performed immediately after the MIP, SCL was defined as the mean activity throughout the task. It has been shown previously that the induced arousal, but not valence, decreases over time (Gomez *et al.*, 2009). Therefore, a certain amount of activation is likely to be necessary to yield the expected change in positive mood. Because subjective reports of arousal and mood were strongly correlated in our study, it remained difficult to isolate the specific contribution of subjective arousal to the observed neurophysiological effects. Although we used a specific MIP meant to balance levels of arousal in the two mood groups (using physical activity-related memories during guided imagery for the neutral group), subjective arousal was still larger after the MIP in the positive compared to the neutral mood group. Therefore, we recommend using a similar experimental procedure in future studies, but with negative valence and enhanced subjective arousal as control mood condition (such as created by state anxiety for example) to assess which specific emotional component (either arousal or valence, or perhaps a blend of both) accounts best for changes in RPE signals with positive mood. A second caveat relates to the fact that we did not observe systematic changes in the actual expectation of reward at the subjective level with positive mood (see results for catch trials), whereas RPE brain signals were clearly influenced by this specific mood state. This dissociation could be explained by the fact that these catch trials probed the ‘objective’ probability of reward (based on the cue and feedback information), but were not suited to assess subtle changes in its mood dependent subjective valuation.

To sum up, the present neurophysiological results unequivocally add support to the assumption that positive mood carries important information for the organism, whereby negative feedback is perceived as a mood incongruent event (FRN results). Moreover, because reward is the default mode somehow with positive mood, when it is unexpected, it is not surprising nonetheless (mid frontal theta). More generally, these new findings show that phasic RPE signals can be shaped by the specific mood state of the participant, with dissociable effects found for the FRN and mid frontal theta activity as a function of positive mood.

Acknowledgements

K.P. was funded by a PhD fellowship from the Research Foundation Flanders (FWO). This work was also funded by grants of the FWO, the special research fund (Ghent University) and the Brain & Behavior Research Foundation (Independent Investigator Grant) awarded to G.P. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Conflict of interest. None declared.

References

- Bakic, J., Jepma, M., De Raedt, R., Pourtois, G. (2014). Effects of positive mood on probabilistic learning: Behavioral and electrophysiological correlates. *Biological Psychology*, **103**, 223–32.
- Bakic, J., De Raedt, R., Jepma, M., Pourtois, G. (2015). What is in the feedback? Effect of induced happiness vs. sadness on probabilistic learning with vs. without exploration. *Frontiers in Human Neuroscience*, **9**, 1–13.
- Barry, R.J., MacDonald, B., Rushby, J.A. (2011). Single-trial event-related potentials and the orienting reflex to monaural tones. *International Journal of Psychophysiology*, **79**, 127–36.
- Benedek, M., Kaernbach, C. (2010a). A continuous measure of phasic electrodermal activity. *Journal of Neuroscience Methods*, **190**, 80–91.
- Benedek, M., Kaernbach, C. (2010b). Decomposition of skin conductance data by means of nonnegative deconvolution. *Psychophysiology*, **47**, 647–58.
- Blanchette, I., Richards, A. (2010). The influence of affect on higher level cognition: A review of research on interpretation, judgement, decision making and reasoning. *Cognition & Emotion*, **24**, 561–96.
- Bohner, G., Chaiken, S. (1994). The role of mood and message ambiguity in the interplay of heuristic and systematic processing. *European Journal of Social Psychology*, **24**, 207–21.
- Botvinick, M.M., Braver, T. (2015). Motivation and cognitive control: from behavior to neural mechanism. *Annual Review of Psychology*, **66**, 83–113.
- Boucsein, W., Fowles, D.C., Grimnes, S., et al. (2012). Publication recommendations for electrodermal measurements. *Psychophysiology*, **49**, 1017–34.
- Bradley, M., Lang, P.J. (1994). Measuring emotion: the self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, **25**, 49–59.
- Bress, J.N., Hajcak, G. (2013). Self-report and behavioral measures of reward sensitivity predict the feedback negativity. *Psychophysiology*, **50**, 610–6.
- Broyd, S.J., Richards, H.J., Helps, S.K., Chronaki, G., Bamford, S., Sonuga-Barke, E.J.S. (2012). An electrophysiological monetary incentive delay (e-MID) task: a way to decompose the different components of neural response to positive and negative monetary reinforcement. *Journal of Neuroscience Methods*, **209**, 40–9.
- Cavanagh, J.F., Figueroa, C.M., Cohen, M.X., Frank, M.J. (2012). Frontal theta reflects uncertainty and unexpectedness during exploration and exploitation. *Cerebral Cortex*, **22**, 2575–86.
- Cavanagh, J.F., Frank, M.J., Klein, T.J., Allen, J.J.B. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *NeuroImage*, **49**, 3198–209.
- Cavanagh, J.F., Shackman, A.J. (2015). 'Frontal midline theta reflects anxiety and cognitive control: Meta-analytic evidence. *Journal of Physiology Paris*, **109**, 3–15.
- Cavanagh, J.F., Zambrano-Vacquez, L., Allen, J.J.B. (2012). Theta Lingua Franca: a common mid-frontal substrate for action monitoring processes. *Psychophysiology*, **49**, 220–35.
- Chase, H.W., Swainson, R., Durham, L., Benham, L. (2010). Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning. *Journal of Cognitive Neuroscience*, **23**, 936–46.
- Chiew, K.S., Braver, T.S. (2014). 'Dissociable influences of reward motivation and positive emotion on cognitive control.'. *Cognitive, Affective & Behavioral Neuroscience*, **14**, 509–29.
- Chwilla, D.J., Brunia, C.H.M. (1991). Event-related potentials to different feedback stimuli. *Psychophysiology*, **28**, 123–32.
- Cohen, M.X., Donner, T.H. (2013). Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *Journal of Neurophysiology*, **110**, 2752–63.
- Cohen, M.X., Elger, C.E., Ranganath, C. (2007). Reward expectation modulates feedback-related negativity and EEG spectra. *NeuroImage*, **35**, 968–78.
- Cooper, A.J., Duke, E., Pickering, A.D., Smillie, L.D. (2014). Individual differences in reward prediction error: contrasting relations between feedback-related negativity and trait measures of reward sensitivity, impulsivity and extraversion. *Frontiers in Human Neuroscience*, **8**, 248.
- Csikszentmihalyi, M. (1999). If we are so rich, why aren't we happy?. *American Psychologist*, **54**, 821–7.
- Delorme, A., Makeig, S. (2004). 'EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis'. *Journal of Neuroscience Methods*, **134**, 9–21.
- Derrick, T.R., Thomas, J.M. (2004). Time series analysis: the cross-correlation function. *Innovative Analyses of Human Movement*, 189–206.
- Dreisbach, G., Goschke, T. (2004). How Positive Affect Modulates Cognitive Control: Reduced Perseveration at the Cost of Increased Distractibility. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **30**, 343–53.
- Eldar, E., Rutledge, R.B., Dolan, R.J., Niv, Y. (2016). Mood as representation of momentum. *Trends in Cognitive Sciences*. Elsevier Ltd, **20**, 15–24.
- Faul, F., Erdfelder, E., Lang, A.G., Buchner, A. (2007). G* Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, **39**, 175–91.
- Fredrickson, B.L. (2001). The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. *The American Psychologist*, **56**, 218–26.
- Gomez, P., Zimmermann, P.G., Schär, S.G., Danuser, B. (2009). Valence lasts longer than arousal: Persistence of induced moods as assessed by psychophysiological measures. *Journal of Psychophysiology*, **23**, 7–17.
- Goschke, T., Bolte, A. (2014). Emotional modulation of control dilemmas: The role of positive affect, reward, and dopamine in cognitive stability and flexibility. *Neuropsychologia*, **62**, 403–23.
- Hajcak, G., Holroyd, C.B., Moser, J.S., Simons, R.F. (2005). Brain potentials associated with expected and unexpected good and bad outcomes. *Psychophysiology*, **42**, 161–70.
- Hajcak, G., Moser, J.S., Holroyd, C.B., Simons, R.F. (2007). It's worse than you thought: the feedback negativity and violations of reward prediction in gambling tasks. *Psychophysiology*, **44**, 905–12.
- Hajihosseini, A., Holroyd, C.B. (2013). Frontal midline theta and N200 amplitude reflect complementary information about expectancy and outcome evaluation. *Psychophysiology*, **50**, 550–62.

- Holmes, E.A., Mathews, A., Dalgleish, T., Mackintosh, B. (2006). Positive interpretation training: effects of mental imagery versus verbal training on positive mood. *Behavior Therapy*, *37*, 237–47.
- Holmes, E.A., Oughtrey, A.E., Connor, A. (2008). Looking at or through rose-tinted glasses? Imagery perspective and positive mood. *Emotion*, *8*, 875–9.
- Holroyd, C.B., Coles, M.G.H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*, 679–709.
- Isen, A.M. (2008) Some ways in which positive affect influences decision making and problem solving. *Handbook of Emotions*, 548–573.
- Koban, L., Pourtois, G. (2014). Brain systems underlying the affective and social monitoring of actions: An integrative review. *Neuroscience and Biobehavioral Reviews*, *46*, 1–14.
- Lange, S., Leue, A., Beauducel, A. (2012). Behavioral approach and reward processing: Results on feedback-related negativity and P3 component. *Biological Psychology*, *89*, 416–25.
- Larson, M.J., Perlstein, W.M., Stigge-Kaufman, D., Kelly, K.G., Dotson, V.M. (2006). Affective context-induced modulation of the error-related negativity. *Neuroreport*, *17*, 329–33.
- Loewenstein, G., Lerner, J.S. (2003). Role of affect in decision making. *Handbook of Affective Science*, *3*, 619–42.
- Mas-Herrero, E., Marco-Pallarés, J. (2014). Frontal theta oscillatory activity is a common mechanism for the computation of unexpected outcomes and learning rate. *Journal of Cognitive Neuroscience*, *26*, 447–58.
- Mason, L., O'Sullivan, N., Bentall, R.P., El-Deredy, W. (2012). Better than I thought: positive evaluation bias in hypomania. *PLoS ONE*, *7*.
- Mason, L., O'Sullivan, N., Blackburn, M., Bentall, R., El-Deredy, W. (2012). I want it now! neural correlates of hypersensitivity to immediate reward in hypomania. *Biological Psychiatry*, *71*, 530–7.
- Mayer, J.D., Gaschke, Y.N., Braverman, D.L., Evans, T.W. (1992). Mood-congruent judgment is a general effect. *Journal of Personality and Social Psychology*, *63*, 119–32.
- Mitchell, R.L.C., Phillips, L.H. (2007). The psychological, neurochemical and functional neuroanatomical mediators of the effects of positive and negative mood on executive functions. *Neuropsychologia*, *45*, 617–29.
- Nieuwenhuis, S., De Geus, E.J., Aston-Jones, G. (2011). The anatomical and functional relationship between the P3 and autonomic components of the orienting response. *Psychophysiology*, *48*, 162–75.
- Nolan, H., Whelan, R., Reilly, R.B. (2010). FASTER: fully automated statistical thresholding for EEG artifact rejection. *Journal of Neuroscience Methods*, *192*, 152–62.
- Novak, B.K., Novak, K.D., Lynam, D.R., Foti, D. (2016). Individual differences in the time course of reward processing: stage-specific links with depression and impulsivity. *Biological Psychology*. Elsevier B.V, *119*, 79–90.
- Novak, K.D., Foti, D. (2015). Teasing apart the anticipatory and consummatory processing of monetary incentives: an event-related potential study of reward dynamics'. *Psychophysiology*, *52*, 1470–82.
- Oliveira, F.T.P., McDonald, J.J., Goodman, D. (2007). Performance monitoring in the anterior cingulate is not all error related: expectancy deviation and the representation of action-outcome associations. *Journal of Cognitive Neuroscience*, *19*, 1994–2004.
- Olivers, C.N.L., Nieuwenhuis, S. (2006). The beneficial effects of additional task load, positive affect, and instruction on the attentional blink. *Journal of Experimental Psychology. Human Perception and Performance*, *32*, 364–79.
- Osinsky, R., Seeger, J., Mussel, P., Hewig, J. (2016). Face-induced expectancies influence neural mechanisms of performance monitoring. *Cognitive, Affective and Behavioral Neuroscience*, *16*, 261–75.
- Pacheco, M.M., Newell, K.M. (2015). Transfer as a function of exploration and stabilization in original practice. *Human Movement Science*, *44*, 258–69.
- Paul, K., Walentowska, W., Bakic, J., Dondaine, T., Pourtois, G. (2017). Modulatory effects of happy mood on performance monitoring: insights from error-related brain potentials. *Cognitive, Affective, & Behavioral Neuroscience*, *17*(1), 106–23
- Pornpattananangkul, N., Nusslock, R. (2015). Motivated to win: relationship between anticipatory and outcome reward-related neural activity. *Brain and Cognition*, *100*, 21–40.
- Riepl, K., Mussel, P., Osinsky, R., Hewig, J. (2016). Influences of state and trait affect on behavior, feedback-related negativity, and P3b in the Ultimatum Game. *PLoS ONE*, *11*, 1–16.
- Rusting, C.L. (1998). Personality, mood, and cognitive processing of emotional information: three conceptual frameworks. *Psychological Bulletin*, *124*, 165–96.
- Sallet, J., Camille, N., Procyk, E. (2013). Modulation of feedback-related negativity during trial-and-error exploration and encoding of behavioral shifts. *Frontiers in Neuroscience*, *7*, 1–10.
- Sambrook, T.D., Goslin, J. (2015). A neural reward prediction error revealed by a meta-analysis of ERPs using great grand averages. *Psychological Bulletin*, *141*, 213–35.
- Schultz, W. (2015). Neuronal Reward And Decision Signals: Reward Functions Learning. 853–951.
- Schultz, W., Dayan, P., Montague, P.R. (1997). A neural substrate of prediction and reward. *Science*, *275*, 1593–9.
- Schwarz, N. (1990). Feelings as information: Informational and motivational functions of affective states. *Handbook of Motivation and Cognition*, 527–61.
- Schwarz, N., Clore, G. (2003). 'Mood as information: 20 years later. *Psychological Inquiry*, *14*, 296–303.
- Seligman, M.E.P., Steen, T.A., Park, N., Peterson, C. (2005). Positive psychology progress. *American Psychologist*, *60*, 410–21.
- Sharot, T., Korn, C., Dolan, R. (2011). How unrealistic optimism is maintained in the face of reality. *Nature Neuroscience*, *14*, 1475–9.
- Sheldon, K.M., King, L. (2001). Why positive psychology is necessary. *The American Psychologist*, *56*, 216–7.
- Siddle, D.A.T., Remington, B., Churchill, M. (1984). Effects of stimulus change on the electrodermal orienting response. *Biological Psychology*, *18*, 33–9.
- Smillie, L.D., Cooper, A.J., Pickering, A.D. (2011). Individual differences in reward-prediction-error: extraversion and feedback-related negativity. *Social Cognitive and Affective Neuroscience*, *6*, 646–52.
- Ullsperger, M., Danielmeier, C., Jocham, G. (2014). Neurophysiology of performance monitoring and adaptive behavior. *Physiological Reviews*, *94*, 35–79.
- Vanlessen, N., De Raedt, R., Koster, E.H.W., Pourtois, G. (2016). Happy heart, smiling eyes: a systematic review of positive mood effects on broadening of visuospatial attention. *Neuroscience & Biobehavioral Reviews*, *68*, 816–37.
- Vanlessen, N., De Raedt, R., Mueller, S.C., Rossi, V., Pourtois, G. (2015). Happy and less inhibited? Effects of positive mood on inhibitory control during an antisaccade task revealed using topographic evoked potential mapping *Biological Psychology*, *110*, 190–200.

- Vanlessen, N., Rossi, V., De Raedt, R., Pourtois, G. (2014). Feeling happy enhances early spatial encoding of peripheral information automatically: electrophysiological time-course and neural sources. *Cognitive, Affective, & Behavioral Neuroscience*, *14*, 951–69.
- Vanlessen, N., Rossi, V., Raedt, R., Pourtois, G. (2012). Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex: Evidence from ERPs. *Cognitive, Affective, & Behavioral Neuroscience*, *13*, 60–79.
- Venables, P., Christie, M. (1980) Electrodermal activity. In: Martin, I. and Vanables, P. editors. *Techniques in Psychophysiology*. New York: Wiley & Sons, pp. 3–67.
- Walsh, M., Anderson, J. (2012). Learning from experience: event-related potential correlates of reward processing, neural adaptation, and behavioral choice. *Neuroscience and Biobehavioral Reviews*, *36*, 1870–84.
- Weinberg, A., Klein, D.N., Hajcak, G. (2012). 'Increased error-related brain activity distinguishes generalized anxiety disorder with and without comorbid major depressive disorder. *Journal of Abnormal Psychology*, *121*, 885–96.
- van Wouwe, N.C., Band, G.P.H., Ridderinkhof, K.R. (2011). Positive affect modulates flexibility and evaluative control.'. *Journal of Cognitive Neuroscience*, *23*, 524–39.
- Wright, W.F., Bower, G.H. (1992). Mood effects on subjective probability assessment. *Organizational Behavior and Human Decision Processes*, *52*, 276–91.
- Yeung, N., Sanfey, A.G. (2004). Independent coding of reward magnitude and valence in the human brain. *Journal of Neuroscience*, *24*, 6258–64.