

Research report

Computational EEG modelling of decision making under ambiguity reveals spatio-temporal dynamics of outcome evaluation



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HIGHLIGHTS

- Complex human cognition is reflected in dynamic spatio-temporal activity.
- We combined event-related potentials with computational modelling.
- A general linear model created a three-dimensional map of neural dynamics.

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ABSTRACT

Complex human cognition, such as decision-making under ambiguity, is reflected in dynamic spatio-temporal activity in the brain. Here, we combined event-related potentials with computational modelling of the time course of decision-making and outcome evaluation during the Iowa Gambling Task. Measures of choice probability generated using the Prospect Valence Learning Delta (PVL-Delta) model, in addition to objective trial outcomes (outcome magnitude and valence), were applied as regressors in a general linear model of the EEG signal. The resulting three-dimensional spatio-temporal characterization of task-related neural dynamics demonstrated that outcome valence, outcome magnitude, and PVL-Delta choice probability were expressed in distinctly separate event related potentials. Our findings showed that the P3 component was associated with an experience-based measure of outcome expectancy.

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1. Introduction

The Iowa Gambling Task (IGT; [1]) is a popular measure of decision making under ambiguous conditions. The IGT is an experience-based partial information paradigm that involves participants choosing among four decks of cards. Each deck yields an average monetary (or point) win and loss, with two of the four decks yielding a net gain over multiple trials (advantageous/good decks), and the other two decks yielding a net loss (disadvantageous/bad decks). Of the advantageous and disadvantageous decks respectively one deck results in less frequent but larger losses than

the other deck. The participants' goal is to maximize monetary or point gain after 100 trials. Advantageous performance on the IGT is therefore based on approximations of long-term consequences rather than exact calculations [2], and choice behaviour typically shifts across trials as participants learn to make more advantageous selections with increasing knowledge of the outcome contingencies [3].

The structure of the IGT allows for the examination of a number of questions relating to decision-making, including the role of memory, value updating, economic outcomes, and long-term calculations in choice selection [4]. As well as extensive research with healthy populations, decision-making deficits have been examined in a number of clinical populations using the IGT, including patients with frontal lobe damage [5], pathological gamblers [6], and people with schizophrenia [7]. Decision-making behaviour during the IGT is well suited to studying how task outcomes and prediction

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errors (i.e. unexpected outcomes) guide future behaviour, and has become a popular subject of reinforcement learning and heuristic computational models (e.g. [8–12,42,43]). These models consider factors such as the attention given to outcome valence (i.e., to wins vs. losses), how the recency of feedback affects future decisions, and how choices are influenced by experience (i.e., to what extent choices are random). Such parameter values have been used to examine how populations differ in terms of their decision-making processes [13,14].

One of the earliest models of choice behaviour in the IGT was the Expectancy Valence (EV) model [8]. However, this model often shows inadequate fit, and is consistently outperformed by other reinforcement-learning models such as the Prospect Valence Learning (PVL) Model [10]. The PVL-Delta model [9–11], a hybrid model combining elements of the EV and PVL models generates less accurate one step ahead predictions than the PVL model [15], but shows better simulation performance than other models [9]. Furthermore, the PVL-Delta model is able to account for most empirical choice patterns which tend to be observed in healthy decision makers [16,17]. This lends support to inferences about psychological processes underlying decision-making which are based on this model [18,40].

The nature of the IGT has also made it a target for neuroimaging studies investigating the neural underpinnings of adaptive decision-making [2,19]. While there is a large body of work investigating reinforcement learning using EEG (e.g. [20]), the IGT has almost exclusively been examined using fMRI. Functional MRI offers greater spatial resolution, but the high temporal resolution of event-related potentials (ERPs) extracted from the ongoing EEG signal is conducive to an examination of the temporal dynamics of decision-making. Indeed, ERPs associated with the anticipation and processing of wins and losses are sensitive to a number of parameters relevant to computational modelling of decision-making such as the valence, magnitude, and likelihood of the outcome [21–26]. However, EEG studies of feedback learning typically contrast average ERPs over different trial types (e.g., [27]) rather than modelling values on a trial-by-trial basis (see Larsen and O’ Doherty [41]; for an exception). Evaluating ERPs on a trial-by-trial basis makes it possible to capture outcome expectation and response to prediction error, thus permitting a more detailed analysis of the neural dynamics underlying complex decision-making.

In this study we used the PVL-Delta model to approximate participants’ subjective appraisal of their chosen deck and prediction errors. We then applied this subjective evaluation component as a trial-by-trial regressor to each participant’s EEG data with the goal of identifying elements in the ERP that are ostensibly associated with subjective outcome appraisal. We further evaluated whether this subjective element of outcome evaluation is associated with two ERPs which are well established markers of prediction error and choice evaluation: the Feedback related negativity (FRN) and the P3 potential. Our objective was to identify subjective components of decision making under ambiguity, and to identify if and how their neural signature differs from that of absolute task outcomes and trial characteristics. This analysis may therefore provide insight into the nature and time course of the interplay between key cognitive processes and task experience during decision making.

2. Materials and methods

2.1. Participants

Twenty healthy, right-handed adults (9 female), 19–38 years old (mean age = 24.9 years, $SD = 4.8$ years) participated and were reimbursed with £10 that was not contingent on performance. The Department of Psychology Ethics Committee, Swansea Univer-

sity, approved all procedures. One participant was excluded due to insufficient EEG data quality.

2.2. Iowa gambling task

We used a computerized variant of the original IGT [1] in which participants were instructed to select cards from four concurrently available decks (labeled A, B, C and D). Deck locations were randomly varied across participants. Trials were preceded by a 2 s choice appraisal interval, during which choices could not be made, as the four individual decks and the text, “Please consider your choice” appeared on screen. After this, choices were made using the mouse (the cursor was centred at the start of every trial). An initial ‘loan’ of £1000 virtual money, displayed at the bottom of the screen, was updated immediately following choices accompanied by text stating the amount of money gained and/or lost. Decks A and B (termed ‘disadvantageous’) resulted in long-term loss (£250 loss per 10 trials), whereas decks C and D (termed ‘advantageous’) resulted in long-term gain (£250 gain per 10 trials). Participants always won £100 if they selected a card from the disadvantageous decks, and £50 if they selected a card from the advantageous decks. Losses varied between £150 and £350 for deck A; £1250 for deck B; £25 to £75 for deck C; and £250 for deck D. Decks A and C resulted in frequent losses (on 50% of trials), whereas decks B and D resulted in infrequent losses (on 10% of trials). Onscreen feedback was displayed for 10 s, before a 2-s inter-trial interval. The task ended after 100 trials. After every block of 20 choices, subjective awareness ratings were made of the relative “goodness” or “badness” of each deck [28,29] using a slider-scale from 0 (‘very bad’) to 10 (‘very good’).

2.3. Behavioural performance during the IGT

The effect of task block on awareness ratings, selection of advantageous vs. disadvantageous decks, and selection of frequent vs. infrequent loss decks was investigated using a chi squared goodness-of-fit tests and a series of one-way repeated ANOVA. Furthermore, two Pearson’s correlations were carried out between the number of choices from advantageous and disadvantageous decks over each of the five task blocks and subjective awareness ratings.

2.4. The PVL-Delta model

The deck chosen on trial t is denoted $D(t)$. The reward received on each trial is denoted $R(t)$, and the loss on each trial is denoted $L(t)$, such that if deck D_3 (a disadvantageous deck) was chosen on trial $t = 9$ (i.e. $D(9) = D_3$) then $R(9) = £100$ and $L(9) = £1250$. The absolute monetary outcome on each trial is denoted $X(t)$.

An approximation of the subjective valence $u(t)$ on trial t is calculated using the prospect utility function, based on $X(t)$.

$$u(t) = \begin{cases} X(t)^\alpha & \text{if } X(t) \geq 0 \\ -\lambda * |X(t)|^\alpha & \text{if } X(t) < 0 \end{cases} \quad (1)$$

Subjective valence is calculated using a shape parameter α , and a loss aversion parameter λ .

The subjective valence value is then used to calculate the expected valence $Ev(t+1)_j$ for the selected deck j on the following trial.

$$Ev_j(t+1) = Ev_j(t) + \phi * (u(t) - Ev_j(t)) \quad (2)$$

Ev is calculated using the delta learning rule, which includes the recency parameter ϕ .

$$\theta(t) = 3^c - 1 \quad (3)$$

Finally, the probability $Pr[D(t+1)=j]$ that deck j will be selected on the next trial is calculated using a Softmax action-selection rule

in conjunction with a trial-independent sensitivity function, which includes the consistency parameter c quantifying to what extent participants make choices in accordance with the expected valence for each deck.

$$Pr[D(t+1) = j] = \frac{e^{\theta(t)Ev_j(t)}}{\sum_{k=1}^4 e^{\theta(t)Ev_k(t)}} \quad (4)$$

2.5. Model fitting

The hBayesDM package [30] was used to fit the PVL Delta, model. hBayesDM is an R package which uses hierarchical Bayesian analysis to fit computational models of reinforcement learning and decision making. The package utilizes a Markov Chain Monte Carlo (MCMC) sampling scheme to perform posterior inference. For each model parameter we used three MCMC chains, which were run simultaneously. Convergence of the MCMC chains was assessed visually, as well as using the R statistic [31]. R values close to 1.0 indicate that all chains have converged successfully to their stationary distributions, whereas values above 1.1 indicate inadequate convergence. We initialized MCMC chains randomly, and collected 1000 samples as well as 9000 burn-in samples. As the hBayesDM package did not include the modality of extracting model regressors, we employed a custom Matlab script (Supplementary materials), which calculated post hoc model fit for each participant using the parameters determined using hBayesDM.

As suggested by Steingrover et al. [18] we assessed the performance of the model when making predictions for the next trial based on previous choices (post-hoc fit) as well as the performance of the model when making predictions about choice behaviour without information about previous deck selections (simulation).

Based on one-step-ahead predictions the PVL-Delta model did not perform better than chance for either all deck predictions, or for both good vs. bad deck and frequent vs. infrequent loss deck predictions for five participants. The analysis of EEG data was therefore carried out both with the full sample ($n=19$), and with only the participants for which the PVL-Delta model outperformed a baseline model ($n=14$), and only findings which remained significant in the reduced sample are reported.

To evaluate whether the choice probability value captured an element of subjective awareness of deck contingencies two Pearson's correlations were carried out between the mean choice probability assigned to advantageous and disadvantageous decks over each of the five task blocks and subjective awareness ratings.

2.6. EEG acquisition and analysis

2.6.1. EEG recording

EEG data were recorded in a soundproofed room using the ActiveTwo Biosemi™ electrode system from 134 electrodes (128 scalp electrodes) organized according to the 10–5 system [32], digitized at 512 Hz.

2.6.2. EEG analysis

EEG preprocessing and artifact rejection was performed using the Fully Automated Statistical Thresholding for EEG artifact Rejection toolbox (FASTER; <http://sourceforge.net/projects/faster> [33], implemented in EEGLAB [34] under Matlab 7.12. EEG data were filtered (1–95 Hz, with a notch filter at 50 Hz). Epoch length was initially set to -3 s to 2 s for the choice appraisal interval (marker set to onset of appraisal interval) and the outcome evaluation phase (marker set to onset of outcome). EEG data from one participant was excluded due to poor data quality.

EEG data were processed in SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>). Data from each participant were transformed into two-dimensional sensor-space (interpolated from the 128 scalp

channels), over *peri*-stimulus times from -100 – 600 ms for the feedback processing phase, thus producing a three-dimensional spatio-temporal characterization of the ERP. Baseline was corrected from 100 ms before cue presentation. The EEG timeseries data were subsequently parcellated based on both spatial and temporal domains. Data were averaged in 64 spatial bins, and across time segments of 25.4 ms (resulting in 23 time bins in the outcome phase).

2.6.3. Outcome measures

For each participant, three variables were used as regressors in a GLM with the parcellated outcome data from the same trials: the valence (whether there was a net win or loss) and the absolute magnitude of the outcome (objective outcome measures), and the trial-by-trial choice probability for the selected deck calculated using the PVL-Delta model. The temporal and spatial properties of associations between regressors and the EEG timecourse across the whole outcome interval were examined. Associations between valence, magnitude and choice probability and two ERP components that consistently occur following feedback, the FRN and the P3, were examined.

2.6.4. Significance testing

A linear regression was carried out for each regressor individually. This resulted in a beta weight being generated for each regressor and each bin. The same calculations were also carried out using a random permutation of the model regressors (i.e. the values of each regressor were shuffled), which resulted in a baseline, or 'null' distribution. For each regressor and each of the bins a one-sample t -test was carried out using the beta values for each participant, as well as the beta values from the random label permutations. For each regressor the bins in which the test statistic was larger than the 95th percentile of the distribution of test statistic values for the beta weights generated using random label permutations were deemed significantly associated with the regressor.

3. Results

3.1. Behavioural data and awareness ratings

The mean number of times advantageous (C and D) and disadvantageous decks (A and B), as well as frequent (A and C) and infrequent (B and D) loss decks were selected per block of 20 trials was calculated for each participant. Task choices for good (advantageous) and bad (disadvantageous) decks across task blocks are presented in the left panel of Fig. 1. Task choices for all four decks across task blocks are presented in the left panel of Fig. 2.

The chi-square statistic was calculated for each task block to examine whether there were significant deck preferences. The test was found to be statistically significant ($p < 0.01$) in every task block (see Supplementary Table 1). The results indicate that the percentage of choices from deck B (a disadvantageous deck with infrequent losses) was higher in all task blocks than expected. From the third task block onward choices from deck D (i.e., an advantageous deck with infrequent losses) were also higher than expected, and in the final task block only deck A (i.e., a disadvantageous deck with frequent losses) was chosen less frequently than expected.

Two, one-way, repeated ANOVA found a significant ($p < 0.025$) effect of task block on awareness ratings for disadvantageous decks ($F = 12.21$, $df = 2.5$, $p < 0.001$, $\eta_p^2 = 0.404$; see middle panel, Fig. 1) but not for advantageous decks ($F = 1.72$, $df = 1.8$, $p = 0.197$, $\eta_p^2 = 0.087$). The number of choices was also only significantly associated with deck ratings for disadvantageous decks (see Table 1).

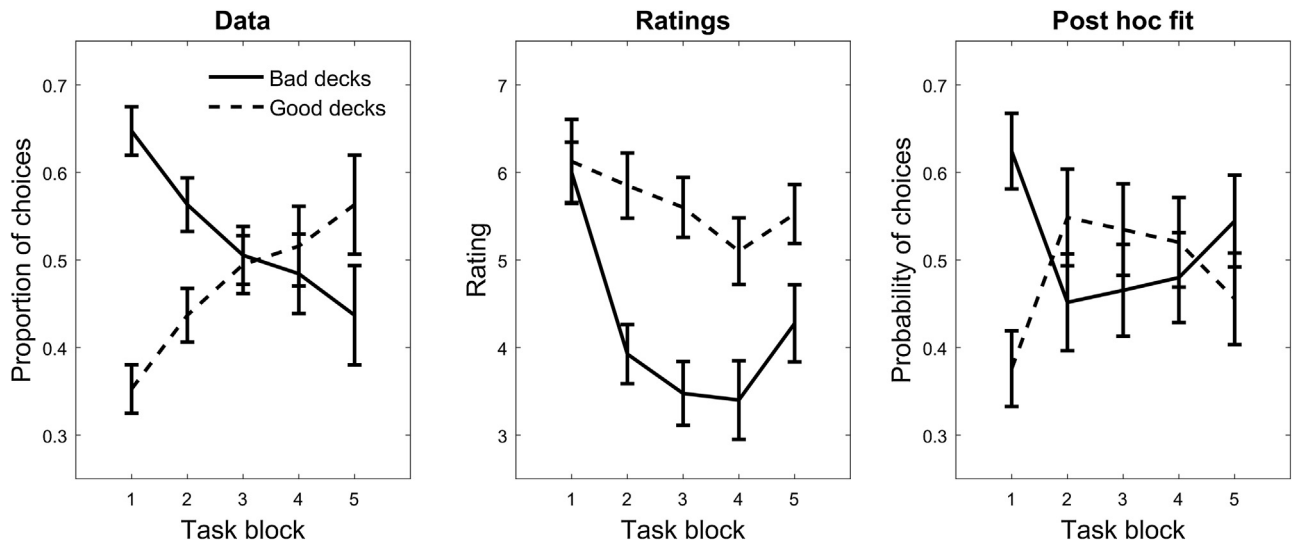


Fig. 1. Deck choice frequency, subjective awareness ratings, and PVL-Delta model choice probability (i.e. post hoc fit) for advantageous and disadvantageous decks. Error bars represent the standard error of the mean.

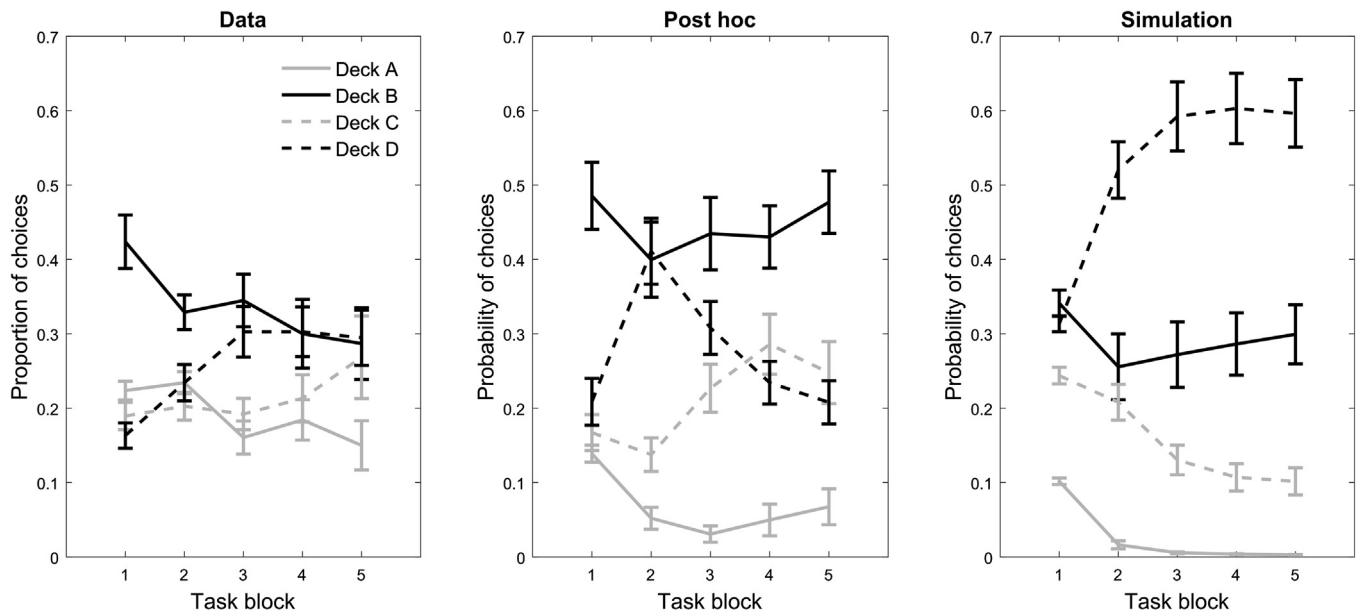


Fig. 2. Deck choice frequency, PVL-Delta model post hoc fit (i.e. choice probability), and simulation performance for all decks. Error bars represent the standard error of the mean.

Table 1

Spearman's rank correlations between choices, post hoc fit, and deck ratings for advantageous (good) and disadvantageous (bad) decks across task blocks (p values in brackets).

	Post hoc fit		Ratings	
	Good decks	Bad decks	Good decks	Bad decks
Choices	0.058 (0.58)	0.058 (0.58)	0.150 (0.17)	0.246 (0.01)
Ratings	0.209 (0.04)	0.141 (0.17)		

3.2. PVL-Delta model fit

The one-step-ahead predictions of the PVL-Delta model correctly predicted whether a good or bad deck would be selected 51.36% of the time, whether a frequent or infrequent loss deck would be selected 61.35% of the time, and which of the four decks would be selected 34.82% of the time. Both post hoc fit and simulation performance were best for decks A and D (see Fig. 2).

A series of Spearman's rank correlations revealed that post hoc fit averaged within task blocks (i.e. Pr) was not significantly associated with number of deck choices for good and bad decks ($r_{058}=0.058$, $p=0.57$), or for frequent and infrequent loss decks ($r=-0.011$, $p=0.91$). Post hoc fit was also not significantly ($p<0.008$) associated with awareness ratings for good or bad decks (see Table 1).

The distribution of the optimal values for each parameter from the PVL-Delta model across all participants is reported in Supplementary Table 2.

3.3. Associations between outcome measures and the EEG timecourse

Of the 1472 (64 spatial by 23 temporal) bins, 148 bins (10.05%) showed a significant association with at least one of the regressors, with almost all (140 bins, 9.51%) uniquely associated with one

Table 2
Percentage of all 1472 bins that were significantly associated with each regressor.

Regressor	Bins associated with the regressor (%)	Bins uniquely associated with regressor (%)
Outcome magnitude	2.04	1.63
Outcome valence	7.61	7.07
PVL-Delta Choice Probability	0.95	0.82

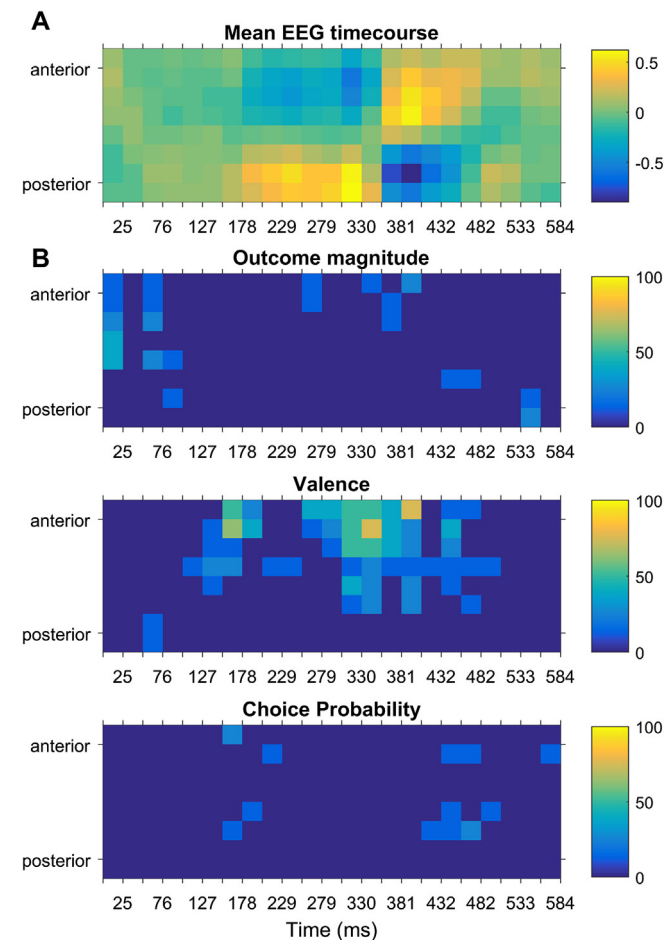


Fig. 3. (A) ERPs in each temporal bin from anterior to posterior, averaged over left and right. (B) Percentage of spatial bins from left to right in which each regressor (outcome magnitude, valence, and choice probability) was significantly associated with the ERP in each time bin at each of eight spatial locations from anterior to posterior.

regressor. Eight bins (0.54%) were associated with two regressors, and no bins were associated with all three regressors. The number of bins each regressor was significantly associated with is presented in Table 2 (see also Supplementary Table 3 for all bins which were significantly associated with a regressor).

3.4. Bins associated with objective task outcomes

ERPs associated with outcome magnitude occurred most strongly in the first 76 ms after feedback presentation (see Fig. 3B). Magnitude also showed some association with the ERP between 254 ms and 558 ms after feedback.

Valence was significantly associated with the ERP throughout most of the outcome processing interval, up to approximately 500 ms after feedback presentation (see Fig. 3B). The largest cluster of ERP activity associated with valence occurred between approximately 250 ms and 500 ms after feedback in a left anterior location.

During this interval, there was also a large cluster of activation in a right central location which was associated with valence. Similar clusters previously showed associations with valence between about 100 ms and 250 ms.

The ERP in 6 bins was significantly associated with both magnitude and valence, with most of these associations occurring between about 330 ms and 480 ms after feedback presentation (Supplementary Table 3).

3.5. Bins associated with PVL-Delta choice probability

Associations between choice probability and the ERP occurred in a number of left anterior and central midline locations. Choice probability was associated with the ERP between about 150 ms and 230 ms after feedback presentation, as well as from approximately 400 ms after feedback until the end of the feedback interval (see Fig. 3B). The largest cluster of activation associated with choice probability occurred between about 400 ms and 480 ms in a central/posterior midline location.

3.6. Bins associated with objective variables and PVL-Delta choice probability

Choice probability and valence were significantly associated with the ERP between about 150 ms and 180 ms after feedback presentation in a left anterior location (Supplementary Table 3).

3.7. Associations between outcome measures and predefined ERPs

3.7.1. Feedback related negativity (FRN)

Based on the observed EEG signal (Fig. 3A) the FRN was defined as the interval between 178 ms and 355 ms. During the FRN time interval, choice probability was associated with 2 bins, valence was associated with 54 bins, and outcome magnitude was associated with 3 bins of which one was shared by valence (Fig. 4A).

3.7.2. P3

Based on the observed EEG signal (Fig. 3A), the P3 was defined as the interval between 355 ms and 482 ms. During the P3 time interval, choice probability was associated with 8 bins, valence was associated with 86 bins, and outcome magnitude was associated with 9 bins of which 6 were shared by valence (Fig. 4B).

4. Discussion

We used a computational model approach of decision making during the IGT to reveal for the first time the electrophysiological dynamics of feedback processing in a spatio-temporal characterization of the ERP. The choice patterns generated using the PVL-Delta model and the best-fit parameters for each participant mapped closely onto choice frequency for decks A and D. The trial-by-trial values for choice probability calculated by the PVL-Delta model were subsequently used as regressors in a GLM of the EEG time-course during the feedback processing interval alongside outcome valence and outcome magnitude. This revealed that the ERPs associated with subjective choice probability do not overlap with the time interval of the FRN, which is generally considered to be associated with prediction error. However, in line with previous findings, subjective choice probability was associated with the ERP during the P3 time interval.

Across the entire outcome interval, valence was significantly associated with more than four times as many spatiotemporal bins of the ERP as the other model regressors. The PVL-Delta model choice probability variable was uniquely associated with 12 spatiotemporal bins. There was surprisingly little overlap between spatiotemporal bins associated with particular regressors, with

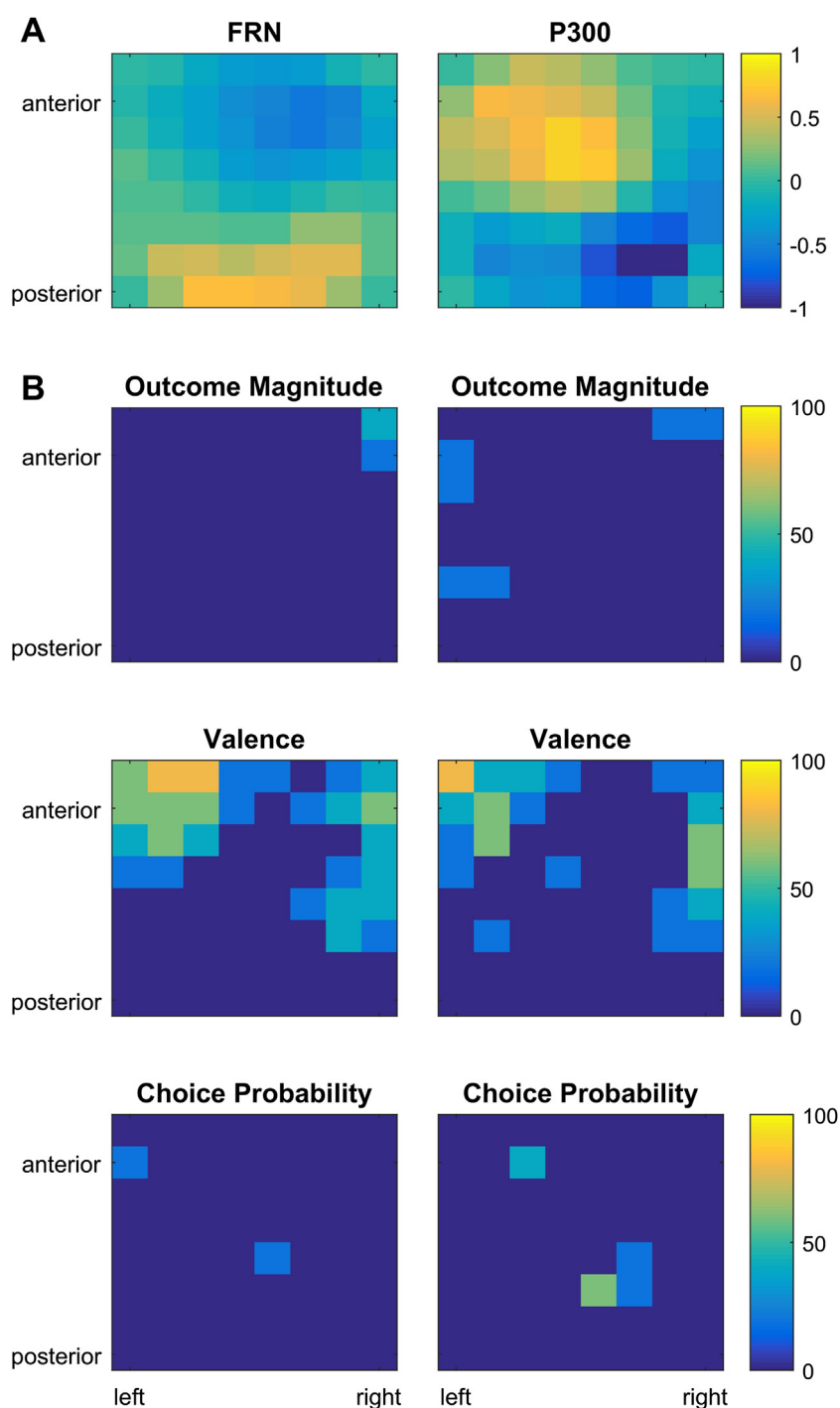


Fig. 4. (A) Feedback Related Negativity (FRN) ERP component with activation averaged across the FRN timecourse (178 ms after feedback to 355 ms after feedback), with percentage of time bins during the FRN time interval for which each regressor (outcome magnitude, valence, and choice probability) was significantly associated with the ERP. (B) P300 ERP component with activation averaged across the P3 timecourse (355 ms after feedback to 482 ms after feedback), with percentage of time bins during the P3 time interval for which each regressor (outcome magnitude, valence, and choice probability) was significantly associated with the ERP.

only eight bins in total showing significant associations with more than one regressor. This indicates that the three elements of feedback processing evaluated here (outcome valence, outcome magnitude, and subjective outcome expectations) show distinctly different temporal properties in terms of their expression in the ERP.

Past research has found that the FRN is associated with outcome valence [35,27], whereas the P3 appears not to be associated with valence [35]. This clear dissociation between the FRN and P3 is inconsistent with our findings relating to the expression of valence

in the ERP. Valence was strongly associated with the ERP between 250 ms and 500 ms after feedback presentation, which includes both a late component of the FRN, as well as the P3 ERP. Outcome magnitude showed only a small number of significant associations with the EEG timecourse across the entire outcome interval. While there were some significant association between outcome magnitude and both the FRN and the P3, the quantity of these associations was much smaller than those observed for valence. While previous research suggests that the P3 is sensitive to magnitude [35], there have been conflicting findings with regard to the effect of magni-

tude on the FRN. A recent meta-analysis suggested that the FRN does show a strong main effect of reward magnitude [20], while other studies suggest that the FRN is not associated with magnitude [35,27,36].

The choice probability value generated using the PVL-Delta model had, compared to valence, a relatively weak association with the ERP during the FRN time interval. The FRN is thought to be related to the probability of an outcome. For example, Holroyd and colleagues [21] have proposed that the FRN is a manifestation of an evaluative process which reflects the degree to which the experienced outcome was better or worse than expected. This so-called 'prediction error' signal is context dependent, and depends on which task dimension is made salient to the participant Nieuwenhuis et al. [44]. In line with this hypothesis, Fuentemilla et al. [26] found that FRN amplitude differed between task blocks in which outcome probabilities were manipulated, reaching a maximum when rewards were highly improbable. The FRN can be thought of as reflecting a reappraisal or updating of expectations about future task outcomes [22]. Fuentemilla and colleagues [26] also investigated to what extent an estimation of subjective outcome expectations incorporating a measure of learning from past trials is associated with the same components of the ERP as simple outcome probabilities. Mirroring previous findings by Mars et al. [37], Fuentemilla et al. observed that the magnitude of the P3 ERP increased with the subjective unexpectedness of the task outcome. While these studies used simple stimulus response tasks, our finding shows that a measure of 'subjective' expectedness of an outcome is also associated with the P3 ERP in more complicated decision situations. Interestingly, Fuentemilla et al. [26] also observed that variations in P3 amplitude were associated with individual differences in risk attitudes. In the context of the IGT a similar effect may have occurred whereby risky deck choices (i.e. deck selections where the associated choice probability value was comparatively low) were associated with higher P3 amplitudes. Overall, the finding of an association between the P3 and PVL-Delta choice probability supports a theory of the P3 as reflecting decision formation, incorporating awareness of a mistake having been made [38].

In conclusion, the present study used a well-validated model of choice behaviour in the IGT to map the spatiotemporal expression of subjective choice certainty in the ERP during outcome processing. This revealed that participants' subjective choice valuations were associated with the P3, expanding our understanding of how the P3 relates to decision-making and outcome evaluation. The degree to which objective measures of trial feedback such as outcome valence and magnitude are reflected in the well-established P3 component warrants further investigation. Our participants made choices for hypothetical rewards, which behavioural findings show, are like those on tasks presenting real rewards [39]. However, using hypothetical task outcomes may have resulted in a decrease in model fit; thus, an extension to money-earning variant IGTs may be helpful. It should also be noted that the choice probability values generated by the PVL-Delta model were not significantly correlated with awareness ratings. A replication of our EEG and computational modelling approach utilizing a larger sample, and seeking to predict trial-by-trial choices based on EEG data, would lend additional support to our conclusions and further elucidate the neural dynamics of complex choice behaviour.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.bbr.2016.12.033>.

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