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Abstract

Reinforcement learning (RL) theory posits that learning is driven by discrepancies between the predicted and actual outcomes of actions (prediction errors, PEs). In social environments, learning is often guided by similar RL mechanisms. For example, teachers monitor the actions of students and provide feedback to them. This feedback evokes PEs in students that guide their learning. We report the first study that investigates the neural mechanisms that underpin these processes. Neurons in the Anterior Cingulate Cortex (ACC) signal PEs when learning from the outcomes of one's own actions, but also signal information when outcomes are received by others. Does a teacher's ACC signal PEs when monitoring a student's learning? Using fMRI, we studied brain activity in human subjects (teachers) as they taught a confederate (student) action-outcome associations by providing positive or negative feedback. We examined activity time-locked to the students' responses, when teachers infer student predictions and know actual outcomes. We fitted a RL-based computational model to the behaviour of the student to characterise their learning, and examined whether a teacher's ACC signals when the student's predictions were wrong. In line with our hypothesis, activity in the teacher's ACC covaried with the PE values in the model. Additionally, activity in the teacher's insula and ventromedial prefrontal cortex covaried with the predicted value according to the student. Our findings highlight that the ACC signals prediction errors vicariously for others' erroneous predictions, when monitoring and instructing their learning. These results suggest that RL mechanisms, processed vicariously, may underpin and facilitate teaching behaviours.

Introduction

In reinforcement learning (RL) theory, learning is driven by prediction errors (PEs) (Sutton and Barto, 1998), which occur when the outcome of an action is discrepant from that which is predicted. A wealth of research has found neurons that signal PEs when the outcomes of one's own actions are unexpected (Rushworth et al., 2009). However, learning rarely occurs in a social vacuum. Often the learning of 'students' is guided by feedback provided by a 'teacher'. Such instructed learning is thought to be fundamental for the transmission of abstract, complex information between humans (Hoppitt et al., 2008). However, to date, there is no understanding of the neural or computational mechanisms that underpin teaching behaviours (Stanley and Adolphs, 2013; Gariépy et al., 2014; Ruff and Fehr, 2014). Does the brain of a teacher process the learning of a student under the computational principles of RL theory?

The Anterior Cingulate Cortex (ACC) is well known for its role in social behaviour (Singer et al., 2004; Ruff and Fehr, 2014). Lesions to the ACC disrupt the processing of social stimuli (Hadland et al., 2003; Rudebeck et al., 2006), neurons in the ACC are sensitive to rewarding stimuli that others will receive (Chang et al., 2013) and neuroimaging studies have shown that the ACC processes predictions about the value of others' actions (Behrens et al., 2008; Jones et al., 2011; Zhu et al., 2012; Apps et al., 2013b; Boorman et al., 2013; Apps and Ramnani, 2014). In contrast, theories of ACC function suggest that it processes PEs relating to the outcomes of one's own decisions, in a manner that conforms to RL principles (Silvetti et al. in press; Amiez et al., 2005; Alexander and Brown, 2011; Hayden et al., 2011; Kennerley et al., 2011).

How can these viewpoints be reconciled? It has been claimed that the ACC gyrus (ACCg) processes social information, but the computational principles that it instantiates parallel those of the adjacent ACC regions (Apps et al., 2013a). That is, the ACCg processes PEs about others' actions. However, no previous study has examined whether PEs are processed in the ACCg when monitoring, understanding and guiding the learning of others.

Using fMRI, for the first time, we examine whether activity in the brain of a teacher can be characterised by the computational principles of RL theory when monitoring and guiding the trial and error learning of a student. We examined activity in subjects ('teacher') whose role was to teach action-outcome contingencies to a confederate (‘student’) by monitoring their responses and providing positive and negative feedback. Teachers had pre-learnt the correct associations and therefore knew the actual value of each action. In addition, they could also model and simulate the students' prediction of each outcome. Thus, the teachers could process a PE at the time of students’ actions. We fitted a RL-based computational model to student’s behaviour, and tested the hypothesis that activity in the ACCg of teachers would covary with PEs from the model at the time of students' actions.

Methods

Subjects

Sixteen healthy right-handed participants were screened for neurological, psychiatric and psychological disorders (ages 18-32; 10 female). One subject failed to complete the whole scanning session and was excluded from the analyses. Each subject was paired with one of three confederate participants, who they believed were a naïve participant. All participants gave written informed consent. The studies were approved by the Royal Holloway, University of London Psychology Department Ethics Committee and conformed to the regulations set out in the CUBIC MRI Rules of Operation. The subjects were not paid for their participation but were given the incentive of receiving a picture of their brain for taking part. The subjects were informed that the other participant performing the task with them (the confederate) was being paid £5 for their participation since they were not being scanned, but that this payment was unrelated to task performance.

Task design

Subjects performed a task in which they acted as a 'teacher' providing a 'student' (confederate) with positive or negative feedback. The student learned the associations between a set of 10 arbitrary instruction cues and one of four responses on a keypad. The teacher had pre-learnt the same associations one day prior to scanning, and was therefore able to determine whether an action chosen for a particular visual cue was correct or incorrect. The teacher's task was to determine whether the student's actions were correct or incorrect and then use a keypad of their own to deliver this feedback to the student.

During the training the teacher was required to learn the arbitrary stimulus-response associations between ten instruction cues (coloured shapes that gave no indication of which response was correct) and one of four motor responses by trial and error (fig.1). That is, there was only one correct response for each instruction cue ensuring that learning the correct association for one instruction cue was not informative as to the correct associations for any other instruction cue. There were 100 trials in total, with ten presentations of each instruction cue. The instruction cues were presented in two blocks, five instruction cues in the first 50 trials and five in the last 50 trials. The cues were pseudorandomly presented, in a predefined sequence (see fig.1). A correct response was indicated by the presence of a picture of a one pound coin at time of the feedback screen and an incorrect response by a crossed out one pound coin. If the subjects did not respond within 750ms of the trigger cue, feedback was displayed as “missed”.

During the scanning session the teacher, monitored the student’s responses and provided them with feedback. The student learnt exactly the same associations as the teacher had learnt during the training session, with trials presented in the same order. The teachers were also informed of the identical nature of the trial structure. To maintain experimental control, we deceived teachers as to the nature of the student. Whilst the teachers believed they were performing the task with another genuine participant, the responses they saw were computer-generated and modelled on the behaviour of a participant in the pilot training session. The students were drawn from one of three confederates. This approach was necessary in order to maintain control over the performance of the third-person, such that the behaviour of the other person was consistent across participants.

During the teaching task the teachers saw two sets of information that were not presented to the student. Firstly, on one screen, the teachers were reminded of the correct association on each trial, before the student made a response (fig.1). This eliminated the possibility that trials would be lost, or that the student’s learning would be compromised by poor performance of the teacher, as a result of the teacher's failing to recall the correct association for each stimulus that they had learned in the previous session. It also ensured that participants were able to register the discrepancy between the student’s prediction and the actual value of their action, a key component of our hypotheses.

Procedure

Training session

Teachers were trained in two phases one day prior to scanning. In the first phase, the teacher was seated in front of a monitor, with a response keypad. This first phase of the training was designed to ensure that all teachers had learnt all the stimulus-response associations through trial-and-error. All teachers made at least two consecutive correct responses for the last two presentations of each instruction cue. All teachers had therefore learnt the correct associations for each stimulus. This enabled them to act effectively as a teacher during the scanning session.

In the second part of the training session, the teacher was required to become familiar with their role as a teacher, and therefore the task that they would perform in the scanner. During this session the participant lay supine within a mock MRI scanner and provided positive and negative feedback to the experimenter outside the mock scanner. They practised this role with the experimenter (see scanning session below) such that they became familiar with the task they would perform during the scanning session but were not teaching the student any information about associations that the student would need to learn in the scanning session – i.e. they learnt how to teach a student, without teaching a student stimulus-response associations that would be later used during scanning. In this part of the training, exactly the same setup was used as during scanning, but with the experimenter taking the place of the student and only a reduced number of trials (20) were used. It is important to note that given the requirement to maintain control of responses of the experimenter across subjects, the actions of the experimenter, as with the actual student, were actually a set of pre-programmed computer-controlled responses.

Scanning session

Before the teacher entered the scanner they were shown the student sitting in the MRI control room, in front of the monitor with a response keypad. The corner of the student's screen was covered, allowing information to be presented to the teacher inside the scanner that the student was not presented with (see trial structure below for more details). Crucially the teacher was made aware that they would have access to information in the corner of the screen that was not able to be seen by the student.

By obscuring that corner of only the student's screen (and not the teacher's screen) it was also possible to present the teacher's trigger cue and response to them without the student being able to observe this information. Hence, the teacher was also aware that the only feedback displayed to the student was that of a pound coin or a pound coin with a cross through it at the time of the final feedback. If the teacher failed to accurately indicate whether the response of the student was correct or incorrect, then the words "no feedback" were presented on the screen to the teacher and the student. This strategy ensured that teachers believed that the student was learning from the feedback that they were providing and ensured that they performed the task accurately. The teacher believed that the student was responding to the trials in real-time, but in fact the trials were computer-controlled, and the profile of responses were based on those of a participant during a previous pilot experiment. This participant was chosen due to a fast learning rate (see behavioural modelling below) and also as they missed only three trials. These trials were also shown to the teacher, thus ensuring that the pre-programmed behaviour of the student seemed genuine to the teacher. At the end of the scanning session the participants were asked standard debriefing questions, as used in previous studies (Apps et al., 2012; Apps et al., 2013b; Apps and Ramnani, 2014), to ensure that they had maintained a full belief in the deception throughout the experiment. Specifically, we asked four yes/no questions. (1) Are you surprised to read that you were deceived on the task (yes/no) ? (2) Did you believe that the responses that you were observing were those of the other person (yes/no)? (3)Did you believe the other person was learning the correct responses from your feedback (yes/no)? (4) Did you believe that the other person was learning the correct responses for the different shapes for the first time? (yes/no). A 'no' response on question one or a 'yes' response on questions two to four would have led to exclusion from the experiment.

Trial structure (see fig.1).

The teachers' trials consisted of an instruction cue (one of the ten that they had learnt associations for during training), immediately followed by the cue indicating the correct button (which reminded the teacher only – and not the student - of the correct association for that instruction cue), a student trigger cue and response (indicating to the teacher which response the student had made), a teacher trigger cue (to which the teacher pressed one button on a keypad for a correct student response and another for an incorrect student response – cued by the presence of a pound or coin or a crossed out pound coin switching pseudorandomly from left to right across trials) and then the feedback (indicating to the student whether the response was correct or incorrect).

Computational Modelling

Behavioural Modelling

The behaviour of the student was modelled using a simple Rescorla-Wagner (R-W) based reinforcement learning algorithm (Rescorla and Wagner, 1972) which has been extensively used to examine the behavioural and neural basis of arbitrary visuomotor associations (Dayan and Balleine, 2002; Schultz, 2006; Brovelli et al., 2008; Dayan and Daw, 2008). This model also bears considerable similarity to recent, influential models of ACC function (Silvetti et al., in press; Alexander and Brown, 2011). As the aim of this study was to examine brain activity in teachers, we maintained experimental control by ensuring that all subjects observed the same learning behaviour exhibited by the student. This requirement did not allow us to make comparisons between different computational models of behaviour, as model comparison cannot be meaningfully applied to a single subject's data. However, given the extensive use of the R-W model for associative learning tasks similar to that used here (Dayan and Daw, 2008), and the fact that most recent computational models of ACC function that we know of are underpinned by the same principles as a R-W model (Silvetti et al. in press), this approach was more than sufficient for meeting the aims of this study.

The R-W model assumes that the associative value of an action (or stimulus) changes once new information reveals that the actual outcome of a decision is different from the predicted outcome (Rescorla and Wagner, 1972). Thus, on each trial, an action has a predicted associative value, that is updated by a prediction error signal when the outcome reveals that this prediction is erroneous. The evolution of the associative values for each action are given by:

(1)

$$V_{a(n+1)} = V_{a(n)} + \eta \, x \, \delta$$

Where:

(2) $$\delta = \lambda_a - V_{a(n)}$$

In both (1) and (2), *n* is the trial number, *a* = 1 ….*k* with *k* representing the available actions and η is the learning rate. The asymptotic value (λ) of a correct action is greater than 0, but is a free parameter that is estimated, and is 0 for an incorrect response. A prediction error is therefore the student's prediction of its associative value ($V_{a(n)}$) subtracted from the actual value of the action (λ) known by the teacher. We instructed the students (and teachers on the first day) that 1 of the four finger movements could be correct for each instruction cue stimulus. Importantly, this also ensured that learning the correct association for one instruction cue was not informative as to the correct associations for any other instruction cue. Thus the associative values of actions for one instruction cue were not informative as to the value of an action for another instruction cue. The initial associative strength of each action for each stimulus was set to λ/4, given the equiprobability of each of the four actions being correct.

Model estimation

To model the action selection process of the student we transformed the associative values into probabilities using the softmax equation. This method is a standard approach used in reinforcement learning theory (Sutton and Barto, 1981). The probability of the action chosen by a subject is given by:

(3)

$$P_a\,(n) = \frac{exp(\beta\, V_a\ (n))}{\sum_{\mathrm{a}} exp(\,\beta\, V_a\ (n))}$$

This equation converts the associative values of the action chosen by a subject to a probability ($P_a\,(n)$). The coefficient β represents the stochasticity (or temperature) of the student's behaviour (i.e. the sensitivity to the value of each option). A high β (greater than 1) causes all actions to be nearly equiprobable, with a low β amplifying the differences in associative values. These two algorithms were used to model action selection by the student over time. The associative value the student placed on the chosen action ($V_a \;(n)$) was then updated in the R-W model, based on the feedback.

Crucially, in this study, the feedback was provided by a teacher (the subject being scanned). As the teacher had expert knowledge of all the associations –and was informed of the correct action on each trial- they knew the asymptotic value (λ) of each action chosen by the student. In this experiment, an aim was to examine whether the teacher modelled the learning of the student. It was therefore assumed that to instruct the student, the teacher would have to calculate the discrepancy between the student's prediction of the outcome $(Va_{(n)\ )})$ and the asymptotic value (λ) of the action chosen by the student. This asymptotic value would be known only by the teacher whilst the student would still be learning. Only when the student has learnt the correct stimulus-response associations for each cue would there be no discrepancy between the asymptotic value known by the teacher and the prediction made by the student. The aim of the teacher was therefore to provide the student with appropriate feedback to minimise the discrepancy between their own expert knowledge and predictions made by the student.

Within the R-W model and the softmax algorithm there are free parameters which need to be estimated. To identify the optimal set of free parameters for the student's behaviour (given the teacher's feedback), the learning rate, the stochasticity parameter β and the asymptotic value λ were varied. The output of the softmax algorithm is a series of probabilities, based on the values of each of these parameters and the actions chosen by the student. By varying the parameters, the probabilities output by the softmax algorithm differ. To select the parameters that best fitted the student's behavioural data (given the teacher's feedback) a maximum likelihood approach was used. By using a maximum likelihood algorithm it was possible to maximise the probabilities of the actions chosen by the student and identify the values of each of the parameters that produced them. The learning rate η was varied between 0 and 1in steps of 0.05, β between 0 and 5 in steps of 0.1 and λ between 0 and 5 in steps of 0.1. The likelihood of the chosen actions were found using:

(3) $$\mathrm{L} = \sum_n \ln\ P_a(\mathrm{n})$$

where the likelihood of each set of parameters (L) is determined by the log of probability of the performed action ($P_a(\mathrm{n})$) of the student at trial *n,* according to the model. If the model perfectly predicts the actions, the probability of every chosen action would = 1 and L would be 0. As the probabilities become less than 1 the log-likelihood L assumes negative values. The best fitting parameters were then selected using:

(4) $$\theta' = \arg\max \theta\ \ (\mathrm{L})$$

This identified the set of parameters for which L was closest to 0 i.e. the best fitting parameter set. Where θ is the parameter set and L is the log-likelihood. Importantly, in this study, the student's data was computer controlled and thus every teacher observed the same responses of the student. Variations in these parameters could therefore only be explained by changes in the feedback, i.e. if the teacher failed to give the student feedback on a particular trial. If this happened, then those trials were removed from the modelling and likewise, data at the time of the student's response on those trials was removed from the fMRI analysis. The maximum likelihood approach revealed that for the behaviour of the student, the best fitting parameters were a λ of 1, a learning rate η of 0.95 and a β values ranging from 2.3 to 2.7- reflecting the apparent differences in stochasticity of the behaviour given the teacher's feedback (see fig.1). Importantly, we used the behaviour of a participant from a pilot experiment as the 'student' behaviour. This student had a high learning rate (0.95) and thus, this ensured that any effects we observed in the ACCg could not be accounted for by teachers learning the learning rate of the student, as in Behrens et al. (2008).

Apparatus

Subjects lay supine in an MRI scanner (3T Siemens Trio, CUBIC, Royal Holloway, University of London) with the fingers of the right hand positioned on an MRI-compatible response box. Stimuli were projected onto a screen behind the subject and viewed in a mirror positioned above the subjects face. Presentation software (Neurobehavioral Systems, Inc., USA) was used for experimental control (stimulus presentation and response collection). A custom-built parallel port interface connected to the Presentation PC received transistor-transistor logic (TTL) pulse inputs from the response keypad. It also received TTL pulses from the MRI scanner at the onset of each volume acquisition, allowing events in the experiment to become precisely synchronized with the onset of each scan. The timings of all events in the experiment were sampled accurately, continuously and simultaneously (independently of Presentation) at a frequency of 1 kHz using an

A/D 1401 unit (Cambridge Electronic Design, UK). Spike2 software was used to create a temporal record of these events. Reaction times were calculated off-line, and event timings were prepared for subsequent general linear model (GLM) analysis of fMRI data (see event definition and modelling below).

Functional Imaging and analysis

Data Acquisition

Scans were acquired on a Siemens Trio 3T scanner. T1-weighted structural images were acquired at a resolution of 1×1×1 mm using an MPRAGE sequence. 1016 EPI scans were acquired from each participant. 38 slices were acquired in an ascending manner, at an oblique angle (≈30˚) to the AC-PC line to decrease the impact of susceptibility artefact in subgenual cortex (Deichmann et al., 2003). A voxel size of 3×3×3 mm (20% slice gap, 0.6 mm) was used; TR=3s, TE=32, flip angle=85°. The functional sequence lasted 51 minutes. Immediately following the functional sequence, phase and magnitude maps were collected using a GRE field map sequence (TE_1 = 5.19ms, TE_2 = 7.65ms).

Image Preprocessing

Scans were pre-processed using SPM8 (www.fil.ion.ucl.ac.uk/spm). The EPI images from each subject were corrected for distortions caused by susceptibility-induced field inhomogeneities using the FieldMap toolbox (Andersson et al., 2001). This approach corrects for both static distortions and changes in these distortions attributable to head motion (Hutton et al., 2002). The static distortions were calculated using the phase and magnitude field maps acquired after the EPI sequence. The EPI images were then realigned, and coregistered to the subject's own anatomical image. The structural image was processed using a unified segmentation procedure combining segmentation, bias correction, and spatial normalization to the MNI template (Ashburner and Friston, 2005); the same normalization parameters were then used to normalize the EPI images. Lastly, a Gaussian kernel of 8 mm FWHM was applied to spatially smooth the images in order to conform to the assumptions of the GLM implemented in SPM8.

Event definition and modelling (Student response)

Multiple GLMs analyses were performed to investigate activity time-locked to the teacher's observation of the student's response. These were performed to ensure that activations identified could only be accounted for by the uniquely explained variance of a parameter in the R-W model. Although each of the GLMs differed from the others, they shared several common properties. Each

GLM contained regressors modelling the instruction cue, the student response cue, the teacher trigger cue and the feedback cue. Regressors were constructed for each of these events by convolving the event timings with the canonical Heamodynamic Response Function (HRF). The effects of head motion were modelled in the analysis by including the six parameters of head motion acquired during preprocessing as covariates of no interest. In addition to these regressors defined for the event types, each GLM also contained regressors which were first order parametric modulations of the student response cue event. These modulators scaled the amplitude of the HRF in line with either the λ_a , V_a or δ parameters from the Rescorla-Wagner algorithm. The values of these parameters corresponded to the teacher's valuation (λ_a, the actual value of the action); the student's prediction ($V_{a\,,}$ the student's prediction of the value) and the prediction error (δ , the discrepancy between the student's prediction and the actual value) respectively. The prediction error could of course only be coded by the teacher at the time of the student's action, as the student would not have known the actual value of the action when they are learning. When a trial was missed by the student or when teachers delivered erroneous feedback or failed to respond, these parameters were all assigned a value of zero. Two sets of analyses were conducted in this study to examine responses at the time of the student's response:

(1) Nine separate GLMs were created in which the values of one of λ, V_a, and δ were used as first-order parametric modulators of the student response cues. These models enabled areas of the brain in which the BOLD response varied in the manner predicted by one of the parameters to be identified (see paragraph below). However, due to correlations between the values of these parameters in the R-W model and correlations due to these parameters being time-locked to the same event on each trial, additional analyses were required.

To examine activity that covaried with the prediction error parameter, we created three GLMs. The first contained only the values of the δ parameter as a parametric modulation of the student response cues. The second contained λ as a parametric modulator, with the values of the δ parametric modulator orthogonalised with respect to the values λ. The third contained V_a as a parametric modulator, with the values of the δ parametric modulator orthogonalized with respect to the values of the V_a parameter. Voxels were only considered if they were significant in an F-contrast in all three of these GLMs. This approach was then repeated for the λ and V_a parameters. Thus, nine GLMs were constructed to examine activity which varied with the values from the parameters of the R-W model. It is important to note that typically one would orthogonalise the parameter of interest with respect to both of the other parameters, in one GLM. However, this was not possible in the present study, because the prediction error parameter is a product of the other two parameters in the R-W model. Thus, orthogonalizing the prediction error (δ) parameter with respect to both of the other parameters in this model would have removed most of the variance that could be explained. The approach we have used provides a statistically conservative way to ensure that any variance that could be explained by the PE parameter is not due to its correlations with the student's prediction parameter or the actual value (the teacher's valuation).

(2) To control for other possible responses in the ACC at the time of the student's response, we created a GLM that contained alternative control parameters that varied with other plausible responses which were not components of the R-W model.

The hypothesis of this study was that the ACC would signal a PE at the time of another's action. In the R-W model these PEs are 'signed', such that during learning a negative outcome results in a negative PE signal and a positive outcome results in a positive PE. However, it is notable that there is empirical data that suggests that neurons in the ACC, and models of ACC function, have found both signed and unsigned PEs in the ACC (Alexander and Brown, 2011; Kennerley et al., 2011; Matsumoto et al., 2007). It was therefore crucial that we test the possibility that PEs in the ACC reflect not classical PE signals, as found in dopamine neurons in the midbrain, but may reflect 'unsigned' PEs that simply code for the magnitude of a PE and not whether it is positive or negative. We therefore created an unsigned PE parameter, that covaried with the magnitude of δ but was always positive.

Classical error detection accounts of the ACC suggest that the region has a generalised role in processing errors in information processing (Carter et al., 1998; Bush et al., 2000; Holroyd et al., 2004; Yeung and Nieuwenhuis, 2009), including the processing of errors which are elicited by the actions of others (Somerville et al., 2006; Shane et al., 2008; Yoshida et al., 2012). It is therefore possible that the ACC might have exhibited an unsigned and uniform magnitude signal whenever the student performed an incorrect action. To test this possibility we created a parameter that took on a value of 1 whenever the student performed an incorrect action and 0 when there was no error.

The error detection and unsigned prediction error parameters were fitted to the responses of the student and included in a GLM. In this GLM the parameters were not orthogonalized with respect to each other, allowing them to compete to explain variance. This allowed us to determine which parameter best explained activity in the ACCg at the time of the student's response. T-tests were then conducted between them to test which parameter best explained activity in a given voxel.

Outcome event

In addition to the main analysis, we examined activity at the time of the outcome event. We used the same strategy as that employed to examine activity at the time of the student's response, namely to fit the parameters from the model to the time of the outcome events.

Examining activity at the time of the teacher's response

Whilst our design enabled us to examine activity at the time of the teacher's response, it was suboptimal for asking questions about differences in how one's own compared to others actions are processed in the brain. Thus, we did not compare activity between the student and teacher motor events nor examine covariations with the BOLD response with parameter from the RW model at the time of the teacher's response. However, other studies have used tasks specifically designed to tackle such issues, which have nicely characterised responses in the brain comparing performing or observing actions (Burke et al., 2010; Ramnani and Miall, 2004).

Second-Level analysis

Random effects analyses (Full-Factorial ANOVA) were applied to determine voxels significantly different at the group level. SPM{t} images from all subjects at the first-level were entered into second-level full factorial design matrices. T-contrasts and F-contrasts were conducted in each of the GLMs. These contrasts identified voxels in which activity varied parametrically in the manner predicted by the parameters in the R-W model. Separate corrections for multiple comparison were used for the ACCg and the whole brain. To examine activity across the whole brain, FDR correction was applied. In contrast, activity in the ACCg was corrected for by using an 80% probability mask of the ACCg (see 'Anatomical Localization' below).

For the second set of analyses examining alternative models of ACC activity, the T-contrasts between the prediction error parameter and the control parameters were examined at a lower threshold. This was necessary due to the high covariance between each of these parameters. For these contrasts a threshold of $P<0.01$, uncorrected for multiple comparisons, was employed.

It was possible that there may be individual differences in activity at the time of the student's response, based on teacher's own learning history. To test this we input the learning rates from the

R-W model, which were estimated on the choices of the teacher in the initial training session, as covariates of interest at the time of student's response.

Anatomical Localization

To test our hypothesis, we used an 80% probability anatomical masks of the ACCg. To create each mask, subject-specific masks of the ACCg were constructed in FSL (http://www.fmrib.ox.ac.uk/fsl/). Although the cytoarchitectonic boundaries of the ACC have no corresponding gross anatomical landmarks, we defined the anatomical boundaries based on the location of these boundaries in previous literature investigating cingulate cytoarchitecture (Vogt et al., 1995). To define the posterior border of the midcingulate cortex, we used a boundary defined by a plane perpendicular to the AC-PC line that lay 22 mm posterior to the anterior commissure (Vogt et al., 1995). We included all voxels that lay within the ACCg extending anterior to this border, including subgenual cingulate cortex. The final ACCg mask included only voxels which were within the ACCg in 80% of our subjects. Importantly, this mask was of the ACCg only and did not extend into the adjacent sulcus.

Results

Behavioural Results

The teacher's task was to monitor the student's responses, determine whether the response was correct or incorrect, and deliver this as feedback to the student. The student's responses, unbeknown to the teachers, were computer-controlled replays of a real subject's responses during a pilot experiment, and included trials in which the student missed three trials (included such that the student's responses seemed realistic) and thus, teachers were required to respond on 97 trials. Teachers correctly gave feedback to the student on 95.2% (SD ± 2.9; range: 91-99%) of trials, indicating that all teachers understood the correct association for each stimulus and also understood whether the student's responses were correct or incorrect. In addition, responses to a standardised set of questions, revealed that none of the participants were aware of the nature of the deception. Thus, participants believed they were instructing another participants, and they were highly accurate at doing so.

Imaging results

Student's response

The main aim of this experiment was to examine activity in the brain of a teacher when they monitor the responses of a student. We tested the hypothesis that the ACCg would signal the discrepancy between a student's prediction and the actual outcome known by a teacher – a student prediction error (PE). In line with the hypothesis, activity was found in the ACCg (fig.2), putatively in midcingulate area 24a'/24b', which varied significantly with the PE (δ) parameter of the R-W model (MNI coordinates (x,y,z) 2, 30, 12; Z = 3.17; $p < 0.005$ svc). Activity in this area was also better explained by the signed R-W PE parameter than by an unsigned PE parameter, or by a parameter in which simple response errors (see methods) were modelled ($p > 0.01$ uncorrected). No other region in the ACC, even at a reduced threshold, showed a significant covariation with the PE parameter ($p > 0.01$ uncorrected). No portion of the ACC showed a significant effect of either the unsigned parameter or the parameter which modelled every erroneous response of the student, even at a reduced threshold ($p > 0.01$). No region of the ACC showed a significant effect of the student prediction parameter, or the actual value known by the teacher ($p > 0.01$). No other brain area significantly varied with the prediction error parameter when correcting for multiple comparisons ($p < 0.05$ FDR). At a reduced threshold, activity in an area consistent with the location of the Ventral Tegmental Area (VTA) and the head of the caudate nucleus covaried with the PE parameter from the R-W model ($P<0.005$ uncorrected).

Simulating the student prediction

At the time of the student's response, the predicted value according to the student could be modelled by the teacher. We examined whether activity in the brain of the teacher time-locked to the student's action covaried with the student's prediction parameter ($\mathrm{V}_{\mathrm{a(n)}}$). Activity which varied significantly with this parameter was found in a portion of the Ventromedial Prefrontal cortex (VmPFC; -14, 32, -10, Z = 5.06, p < 0.05 FDR, putatively BA 32) and in the right short insular gyrus (48, -4, -2, Z = 4.08 FDR, putatively area Idg; fig.3). These were the only regions in which the unique variance could be accounted for significantly by the predicted value according to the student.

The Teacher's valuation

At the time of the student's action, the teacher knew the actual value of the student's choice. We examined activity time-locked to the student's choice that covaried with the actual value of the chosen action. Activity which varied statistically with this parameter was found in the Superior Frontal Sulcus (SFS) bordering BAs 8,9 and 9/46 (-20, 32, 46; Z = 5.06, p < 0.05 FDR) and Posterior Cingulate Cortex (PCC; -14, -52, 32; Z = 5.57, p < 0.05 FDR) putatively in BA. These were the only regions in which the variance could be uniquely and significantly accounted for by the actual value of the action known by the teacher.

Individual differences in the brains of teachers

To test whether activity at the time of the student's response varied depending on the teacher's own learning history, we examined whether activity covaried with the learning rates of the teachers in the initial training session. No areas of the brain covaried significantly when correcting for multiple comparisons. However, at a reduced threshold (p < 0.001 uncorrected) we found activity in the three regions, including regions that also responded to the teacher's valuation in bilateral SFS (MNI 26, 0, 42; Z = 4.4; -34, -2, 40; Z = 3.87), and in the PCC (MNI -14, -22, 34; Z = 3.59), as well as in the intra-parietal sulcus (MNI -44, -38, 50; Z = 4.05). However, these results should be interpreted with caution, given the low sample size for exploring individual differences and that the results are reported at an uncorrected threshold.

Outcome events

In addition to the main analysis, we also examined activity time-locked to the outcome event. Activity was not found to covary with any of the parameters from the model at the time of the outcome when correcting for multiple comparisons. However, activity was found to covary with PE parameter from the model in several areas, Cerebellar Lobule VI (MNI -20, -38, 34, Z = 4.05), VmPFC (MNI 10, 54, 12, Z = 3.92), Hippocampus (MNI 36, -12, -20), and the left temporal pole (MNI -56, -10, -24; Z = 3.58), but only at a reduced threshold ($p < 0.001$ uncorrected).

Discussion

This study investigated activity in the brain of a teacher when monitoring a student’s responses, as the student learnt from feedback provided by the teacher. In line with our hypothesis, activity in a portion of the ACCg varied with prediction error (PE) values in a RL-based computational model. Activity in insula cortex and in the VmPFC varied with the predicted value of the action according to the student. These results suggest that the ACCg plays a specific role in signaling information about how erroneous another’s predictions about their actions are. In addition, we found that areas that are monosynaptically interconnected with the ACCg also play important roles in the processing of information about other people’s learning.

Anatomical evidence supports the notion that the ACCg is sensitive to information that guides reinforcement learning. The ACCg receives direct input from dopaminergic neurons in the Ventral Tegmental Area (VTA) (Williams and Goldman-Rakic, 1998). It has been well established that the firing properties of dopamine neurons in the VTA conform to the principles of RL. Specifically, they show an increased spike frequency to unexpectedly positive outcomes, a decreased spike frequency to unexpectedly negative outcomes and no activity change to predictable outcomes (Schultz and Dickinson, 2000; Schultz, 2006). As such the VTA is believed to signal PEs in a manner that drives one’s own learning of rewarding outcomes. Interestingly, we found that the BOLD signal in the ACCg showed similar response characteristics. However, whilst it is well known that dopamine neurons signal this information for one’s predictions about the outcomes of one’s own decisions, we have shown that the ACCg processes such PE signals when they pertain to others’ predictions and the outcomes of others’ actions as well.

Anatomical evidence also supports the notion that the ACC processes social information. The portion of the ACCg that was activated in this study (in the gyral, midcingulate cortex) has strong connections to the posterior portions of the superior temporal sulcus (pSTS), the temporal poles (TPs) (Markowitsch et al., 1985; Seltzer and Pandya, 1989; Barbas et al., 1999), and the paracingulate cortex (Pandya et al., 1981; Vogt and Pandya, 1987; Petrides and Pandya, 2007). These three regions are believed to form a core circuit that is engaged when processing information about the mental states of others (Ramnani and Miall, 2004; Frith and Frith, 2006; Hampton et al., 2008). In addition, the ACCg has monosynaptic connections to the portions of the insula and the VmPFC that were found to covary with the student’s prediction in this study (Mesulam and Mufson, 1982; Mufson and Mesulam, 1982; Morecraft et al., 1992; Cavada et al., 2000). Previous studies have shown that activity in the VmPFC, the insula, the pSTS, the paracingulate cortex and the TPs covaries with parameters from RL-based computational models during other forms of social interactions (Ramnani and Miall, 2004; Behrens et al., 2008; Hampton et al., 2008; Baumgartner et al., 2009; Klucharev et al., 2009; Cooper et al., 2013; Gariépy et al., 2014). Thus, input from areas which appear to process information in a manner that conforms to the principles of RL during social interactions and the input from midbrain dopaminergic nuclei both highlight the ACCg as a candidate for processing PE signals relating to the behaviour of others. Moreover, these results suggest that the ACCg may process information in concert with the VmPFC and the insula in order to vicariously process information about the predictions other people make when learning.

Functional evidence also supports the claim that an overarching functional property of the ACCg is that it processes information about rewards during social interactions (Apps et al., 2013a). Lesions to the ACCg in monkeys disrupt the processing of social stimuli (Hadland et al., 2003; Rudebeck et al., 2006) by reducing the typical delay present when reaching for a rewarding stimulus in the presence of another monkey. In addition, single-unit recording studies have shown that a large proportion of neurons in the ACCg code for a reward that a conspecific will receive. Crucially, these neurons do not change their firing rate when an identical reward is to be received by oneself (Chang et al., 2013). Imaging studies have also shown that the ACCg signals the net-value of rewards that others will receive (Apps and Ramnani, 2014), signals the unpredictibility of the relationship between another's advice and the outcomes of another's choices (Behrens et al., 2008), and signals when the outcomes of another's actions are unexpected (Apps et al., 2013b). These results all support the view that the ACCg signals information relating to reward-based decisions during social interactions. However, the new contribution that our study makes is to show that the ACCg processes information at the time of others' actions and does so when a subject's behaviour is aimed at guiding another's learning.

It has been argued that there are two major social frames of reference within which brain areas process social information. Whilst some areas process information when inferring the intentions and mental states of other people ('other' reference frame), other regions process information when updating one's own behaviour based on other's intentions or behaviour ('self' reference frame) (Hunt and Behrens, 2011; Baez-Mendoza et al., 2013; Baez-Mendoza and Schultz, 2013; Chang, 2013; Chang et al., 2013). Understanding the reference frames present in a task is therefore important for understanding the frame of reference within which a region, in this case the ACCg, processes social information. In this task, subjects were monitoring the learning of others in order to provide them with feedback. Importantly, the design of the task ensured that participants were not processing information about the relationship between their own actions and the reward they would receive themselves. Rather, they were processing information about the erroneous predictions of another. Interestingly, this supports recent claims that the ACCg (areas 24a'/24b') may in fact act as a nexus between these two frames of reference (Hunt and Behrens, 2011; Apps et al., 2013a). Specifically, it has been claimed that the area is engaged when processing information about (i) the rewards that others will receive, based on one's own or others' actions, and (ii) others' predictions about rewards, when others' predictions can be used to guide one's own behaviour (Apps et al., 2013a). Our results support this claim by showing that the ACCg processes the erroneous predictions of others (i.e. inferring information about others), in order that a subject can provide them with feedback (i.e. updating one's own behaviour based on another's intentions). Thus, the ACCg appears to process information in a way that acts as a nexus between the two major social reference frames.

The functional and computational properties of the whole ACC are still under considerable debate, however, one common feature of several recent accounts of the ACC is that they are underpinned by similar computational principles to those of RL theory (Silvetti et al., in press; Yeung and Nieuwenhuis, 2009). Several theories of ACC function have recently been developed that account for a diverse range of single-unit recording, EEG and fMRI data. Silvetti et al.'s (in press) reward-value and prediction model (RVPM) and Alexander and Brown's (2011) Predicted-Response Outcome (PRO) model both argue that the ACC acts as a 'critic', learning the value of stimuli or actions through PE signals. Similarly, Shenhav et al.'s (2013) Expected Value of Control (EVC) model is based around the notion that the ACC signals the value of the amount of cognitive control that will be required and updates this valuation when an outcome suggests this is required. Each of these models relies upon PE signals updating predictions. These models are largely supported by empirical evidence reporting from activity in areas 24c'/32', which lie in the sulcus of the ACC - a different region of the ACC from that found of this study. The area we identified was in the ACCg in areas 24a'/24b'. Thus, in line with other recent studies (Boorman et al., 2013; Apps et al., 2013b), our research has shown that this region may also process PEs, a key component of R-L based models and also of computational accounts of other ACC regions. Whether this PE is signalled by neurons that also signal fictive PEs – PEs for the outcomes of unchosen actions – that have been found in the ACC (Hayden et al., 2009) is yet to be determined. However, our results suggest that whilst the ACCg may have a degree of specialization for social information processing, the computational principles that govern its operation are similar to those of other regions of the ACC.

In summary, this study provided the first characterisation of the neural and computational processes that may operate in the brain of a teacher as they deliver reinforcement to a student. Our findings have highlighted a novel PE processed in the ACCg of a teacher that may play a key role in signalling how erroneous students' predictions are. Furthermore, our findings suggest that areas previously implicated in RL for oneself may also be important for vicariously processing and understanding the learning of others.

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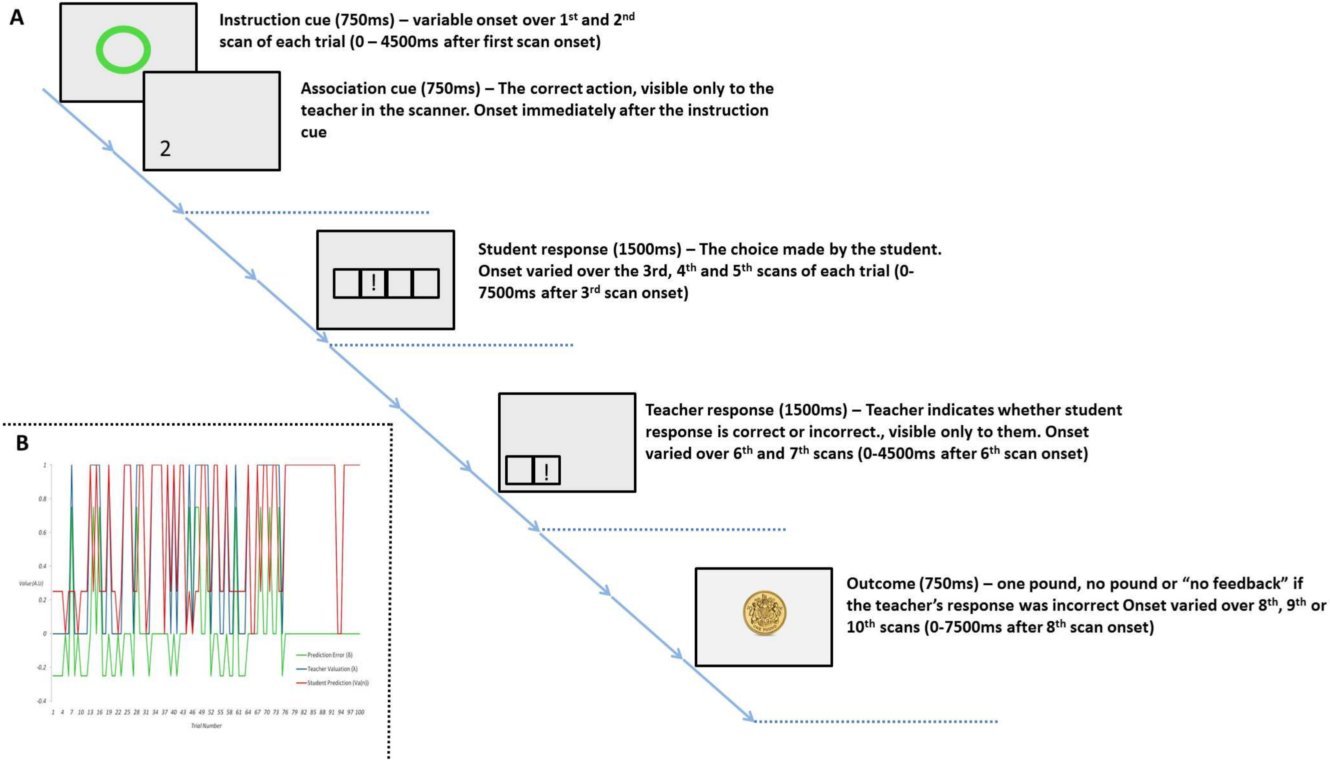
Figure Legends

Figure 1. (A) Trial Structure. Participants performed trials as a teacher, guiding the associative learning of a student. Each trial began a with a green instruction cue (one of ten that the teacher had learnt the associations for during training), followed by the association cue informing the teacher of the correct response for the stimulus. This was displayed in the corner of the teacher's screen. The corresponding corner of the student's screen outside the scanner was covered, such that this cue was shown only to the teacher inside the scanner. Following this, the teacher saw the student's response. They were required to indicate to the student whether this response was correct or incorrect. The teacher's indicated their response on a keypad at the time of a screen where a pound coin (correct) or a crossed out pound coin (incorrect) were presented. Participants had to select the corresponding stimulus to deliver to the student. This stimulus was also presented in the corner of the screen, ensuring that the student could not see the teacher's decision at that time. The chosen feedback was delivered to the student at the time of the outcome stimulus. **(B) Example model data.** Plot of the data of the example output from the R-W model. In this example the learning rate was set to 1 for clarity.

Figure 2. Student prediction errors. (A) Activity shown in the ACC time-locked to the student's response in which activity covaried with the prediction error parameter from the R-W model on the mean anatomical image. (B) Parameter estimates in the peak ACC voxel. Activity in this region correlated only with the prediction error parameter and not with the student's prediction or the actual value of the outcome. Activity in this region also did not significantly covary with the unsigned prediction error parameter or a parameter that simply coded for student erroneous responses. Error bars depict standard error of the mean. (C) Peristimulus time histogram (PSTH) of activity time-locked to the student's action in the brain of the teacher. Activity plotted for when the student's prediction was erroneously positive (light green triangles) or erroneously negative (dark green circles). The values of the prediction error were taken from the R-W computational model. Error bars depict standard error of the mean.

Figure 3. Simulating the student prediction. Activity shown in the ventromedial prefrontal cortex (A) and the right short insula gyrus (B) covarying with the predicted value according to the student, taken from the R-W model. Plots of the parameter estimates from the peak voxel in the VmPFC (C) and the insula (D) for the prediction error, the student predicted value and the actual value of the outcome known by the teacher. Parameter estimates for the predicted value parameter are for the unique variance explained by the regressor once orthogonalised with respect to the actual outcome parameter. Parameter estimates for the prediction error parameter and the actual outcome parameter are from regressors which have not been orthogonalised. Error bars depict standard error of the mean. PSTH plots from the VmPFC (E) and the Insula (F) time-locked to the student's prediction. Activity in these regions is broken down into low (<0.5) predicted value (light red triangles) vs high (>0.5) predicted value (dark red circles) according to the model. Error bars depict standard error of the mean.



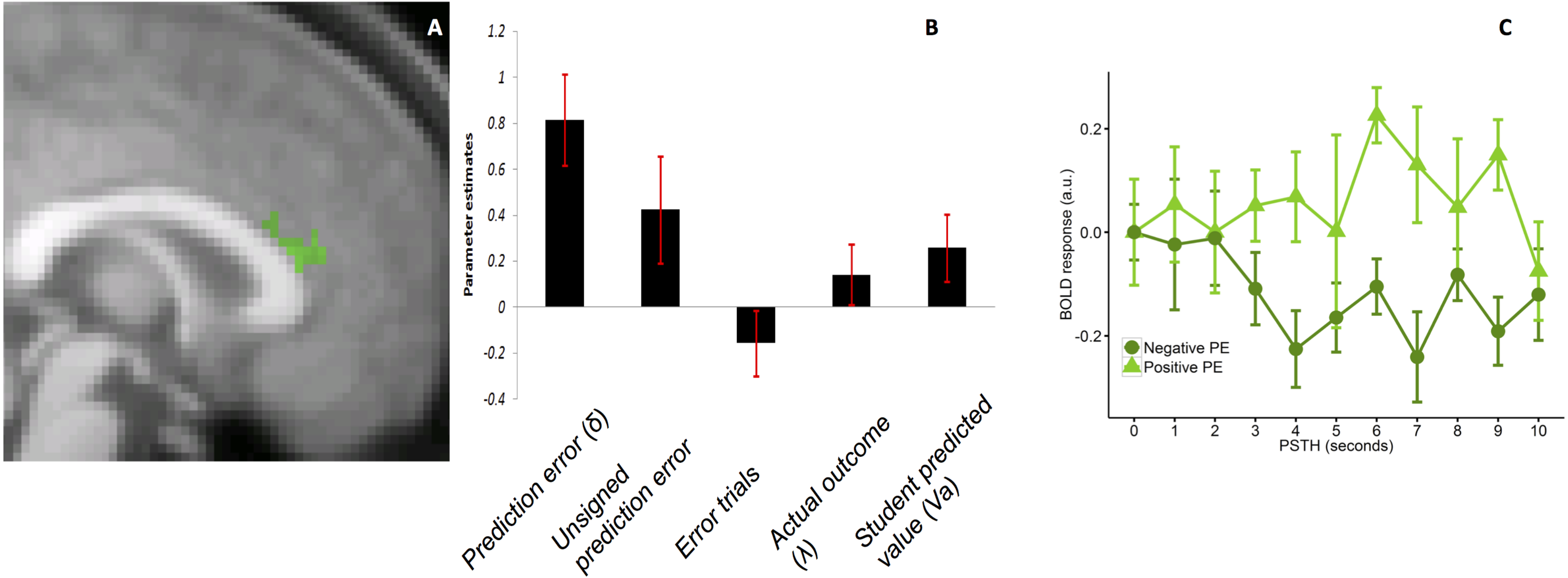
Instruction cue (750ms) – variable onset over 1st and 2nd scan of each trial (0 – 4500ms after first scan onset)

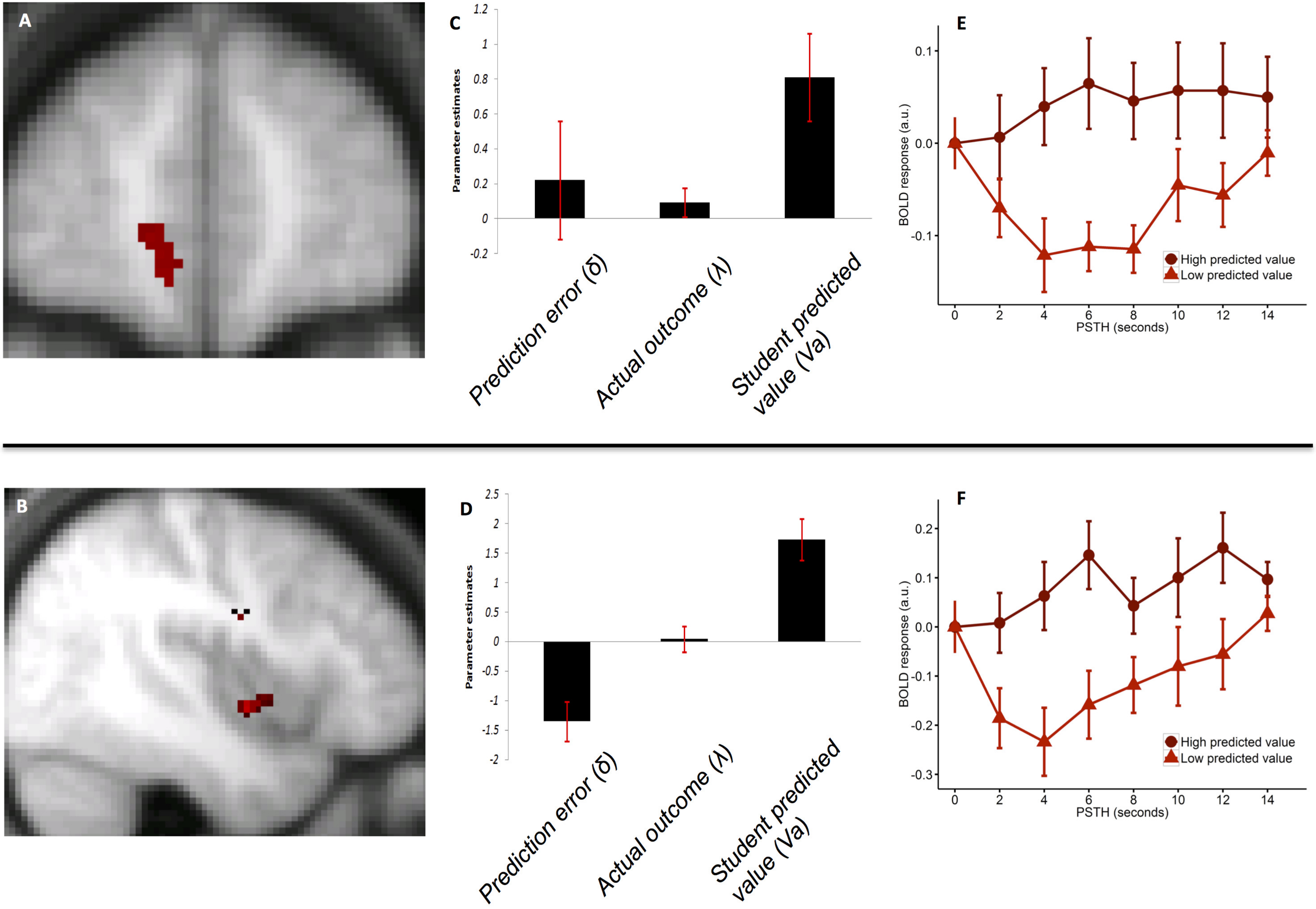
Association cue (750ms) – The correct action, visible only to the teacher in the scanner. Onset immediately after the instruction cue

Student response (1500ms) – The choice made by the student. Onset varied over the 3rd, 4th and 5th scans of each trial (0-7500ms after 3rd scan onset)

Teacher response (1500ms) – Teacher indicates whether student response is correct or incorrect., visible only to them. Onset varied over 6th and 7th scans (0-4500ms after 6th scan onset)

Outcome (750ms) – one pound, no pound or “no feedback” if the teacher’s response was incorrect Onset varied over 8th, 9th or 10th scans (0-7500ms after 8th scan onset)


A
B
C
Parameter estimates
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
Prediction error (δ)
Unsigned prediction error
Error trials
Actual outcome (λ)
Student predicted value (Va)
BOLD response (a.u.)
0.2
0.0
-0.2
0
1
2
3
4
5
6
7
8
9
10
PSTH (seconds)
● Negative PE
▲ Positive PE


A
C
Parameter estimates
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
Prediction error (δ)
Actual outcome (λ)
Student predicted value (Va)
E
BOLD response (a.u.)
0.1
0.0
-0.1
0
2
4
6
8
10
12
14
PSTH (seconds)
● High predicted value
▲ Low predicted value
B
D
Parameter estimates
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
Prediction error (δ)
Actual outcome (λ)
Student predicted value (Va)
F
BOLD response (a.u.)
0.2
0.1
0.0
-0.1
-0.2
-0.3
0
2
4
6
8
10
12
14
PSTH (seconds)
● High predicted value
▲ Low predicted value