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2 Temporal response modelling uncovers electrophysiological correlates 3 of trial-by-trial error-driven learning

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12 ABSTRACT

13 Humans learn from statistical regularities in the environment. There has been in-
14 creasing interest in recent decades regarding the mechanisms underlying such learn-
15 ing. We used Error-Driven Learning (EDL) to simulate participants' trial-by-trial
16 learning during exposure to a bimodal distribution of non-native lexical tones. This
17 gave us estimates of the degree of expectation of upcoming stimuli over the course of
18 the experiment. The expectation estimates were combined with Temporal Response
19 Function (TRF) fitting to predict the trial-by-trial ERP waveform. The expecta-
20 tion estimates of certain EDL simulations were significantly more informative about
21 the ERP signal than discrete stimulus conditions or overall stimulus probability.
22 These results show that trial-by-trial changes in neural activity can be captured
23 by EDL estimates of expectation. Hence, we tentatively conclude that learning of
24 statistical regularities, as reflected in neural activity, involves continual updating of
25 expectations depending on error-driven learning from cues in the environment.

26 KEYWORDS

27 error-driven learning, discriminative learning, Rescorla-Wagner equations,
28 temporal response modelling, event-related potentials, statistical learning

29 1. Introduction

30 Learning a non-native language requires learning to use acoustic cues differently to the
31 native language. Increasing evidence suggests that listeners learn implicitly from sta-
32 tistical regularities in the environment. However, there is still ongoing discussion about
33 what underlying learning mechanisms are involved. According to error-driven learning
34 theory, learning occurs through a process of prediction and feedback from prediction
35 error: expectations are constantly adjusted in response to incoming information to min-
36 imise prediction error (i.e. surprise) over time. The present study investigates whether
37 traces of error-driven learning occur in the trial-by-trial changes in event-related brain
38 potentials (ERPs).

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39 A wide range of studies have demonstrated that humans pick up on statistical regu-
40 larities in the environment (see Hasson, 2017; Perruchet & Pacton, 2006; Rebuschat &
41 Monaghan, 2019, for reviews). Various research traditions – including implicit learn-
42 ing (e.g. Reber, 1989), statistical learning (e.g. Maye, Werker, & Gerken, 2002; Saf-
43 fran, Aslin, & Newport, 1996; Saffran & Kirkham, 2018), artificial grammar learning
44 (e.g. Trotter, Monaghan, Beckers, & Christiansen, 2019), and neural adaptation (e.g.
45 Baldeweg, 2007; Frost, Winkler, Provost, & Todd, 2016) – have focused on different
46 aspects of learning. Perhaps as a consequence of this different focus, these paradigms
47 also differ somewhat in their interpretation of the underlying learning mechanisms
48 involved.

49 Most research in this area has focused on the question of how the *overall summed*
50 statistics, such as frequency or co-occurrence probabilities, influence the processing of
51 stimuli. Experimental studies have generally compared behavioural or brain responses
52 in tests before and after a training phase (pre-tests and post-tests; e.g. Wanrooij,
53 Boersma, & Benders, 2015) or compared post-tests between groups in different training
54 conditions (e.g. Maye et al., 2002; Wanrooij, Boersma, & van Zuijen, 2014), in order
55 to investigate how participants’ performance was influenced by exposure to statistical
56 regularities during training (but see e.g. Costa-Faidella, Grimm, Slabu, Díaz-Santaella,
57 & Escera, 2011; Koelsch, Busch, Jentschke, & Rohrmeier, 2016; Nixon, van Rij, Mok,
58 Baayen, & Chen, 2016). However, the reported effects found in post-tests resulting from
59 manipulations in training conditions are compatible with various different underlying
60 mechanisms. Investigating trial-by-trial changes in the neural signal can shed light on
61 the underlying mechanism, and in particular, the role that prediction error plays in
62 learning. We will return to the details of error-driven learning models below.

63 In the past, the methods typically used for analysing ERPs have made it difficult
64 to investigate incremental, trial-by-trial learning. ERPs and other neurophysiological
65 measures are generally noisy. They capture responses not only to the experimental
66 stimuli, but also to many other factors, such as muscle movement, regulatory processes,
67 emotional states and so on. Aggregation of measurements within conditions or in pre-
68 and post-test measurements reduces the influence of these factors, but also leads to
69 loss of information about individual stimuli and individual trials. Trial-by-trial analysis
70 of EEG has been done previously using generalised additive mixed models (e.g. de
71 Cat, Klepousniotou, & Baayen, 2015; Nixon, 2014; Nixon, van Rij, Li, & Chen, 2015;
72 Tremblay & Baayen, 2010). In the present study, however, we use the relatively new
73 statistical technique of temporal-response modelling (Brodbeck, Presacco, & Simon,
74 2018; Lalor & Foxe, 2010) which is able to test how well trial-by-trial predictions
75 capture ERP responses by fitting so-called *temporal response functions* (TRFs). TRFs
76 link an input signal with continuous measures placed in time to the recorded ERP
77 signal. The present study uses TRFs to investigate whether measures of trial-by-trial
78 expectations derived from error-driven learning models can be used to predict the
79 trial-by-trial EEG signal.

80 Below in the Background section, we first present the error-driven learning theory
81 and algorithm that we use to simulate the trial-by-trial learning and review the ERP
82 components that may reflect trial-by-trial learning. The EEG data section describes
83 the experimental paradigm and data preprocessing. The Method section provides a
84 brief overview of our methods, from the EDL simulations and TRF models to the
85 statistical tests. We then present in more detail the EDL simulations used to estimate
86 participants’ trial-by-trial expectations of the stimuli in the EDL simulations section.
87 The Analysis section shows 1) how TRFs are used to predict the ERP waveforms and
88 2) how the predicted ERP waveforms are tested against the observed ERP data. The

Results section presents the informative models and visualises how these models relate to the ERPs. Finally, in the Discussion, we examine what our results can tell us about trial-by-trial learning, the learning representations and cognitive tasks involved in this experiment and the timing and scalp distribution of the effects found in the ERPs. We also discuss the implications for learning and the potential benefits of our modelling method for future research.

2. Background

2.1. Error-driven learning (EDL)

Two main classes of learning algorithms have been proposed in the literature: generative models and discriminative models. The aim of *generative models* is to determine the underlying population distribution from a sample distribution. Generative models include distributional learning models and statistical models that are based on statistical measures, such as frequency or co-occurrence probability. Generative models have often been used in language acquisition and linguistics research (e.g. Maye et al., 2002; Saffran et al., 1996; Saffran & Kirkham, 2018). In contrast, error-driven learning models are *discriminative* (Bröker & Ramscar, 2020; Hoppe, Hendriks, Ramscar, & van Rij, 2022; Ramscar, Dye, & McCauley, 2013; Ramscar & Yarlett, 2007; Ramscar, Yarlett, Dye, Denny, & Thorpe, 2010). Discriminative learning models have a strong connection to information theory: Shannon (1948) described the problem of communication as selecting the appropriate intended message from a finite set of possible intended messages. Likewise, discriminative error-driven learning models use incoming information (cues) to select or discriminate between a set of possible outcomes. In the context of communication, these outcomes could be intended messages or parts thereof.

In discriminative, error-driven learning theory, rather than simply acquisition of knowledge, learning is considered to be a process of reduction of uncertainty (Baayen, Milin, Đurđević, Hendrix, & Marelli, 2011; Ramscar et al., 2013, 2010). To this end, potentially any discriminable cues in the environment can be used to predict important outcomes. If certain cues are repeatedly informative for predicting the occurrence (or non-occurrence) of an outcome, then over time encountering such cues will lead to an *expectation* of the occurrence (or non-occurrence) of said outcome.

Crucially, discriminative error-driven learning models involve *cue competition* (see Hoppe et al., 2022; Nixon, 2018, 2020; Ramscar et al., 2010, for further discussion). If multiple cues precede an outcome, each of these cues contributes to the expectation of the outcome: formally, each cue-outcome connection has a *connection weight*; the expectation or *activation* of an outcome is the sum of weights of all present cues. Weight adjustment is shared equally between all present cues: when an outcome occurs, the connection weights from all present cues to the outcome are increased with the same value; when the outcome does not occur connection weights decrease with the same value. Thus, cues compete for relevance in predicting outcomes. Importantly, however, the weight adjustment also depends on how much the present cues lead the learner to expect a particular outcome, based on previous learning. More learning occurs when an unexpected outcome occurs or when an expected outcome does not occur, compared to when an expected outcome occurs or an unexpected outcome does not occur. Thus, current learning depends on expectations developed over the course of previous learning. The next section presents the algorithm used for the error-driven learning simulations.

Figure 1. Example of EDL single layer network with cues and outcomes (a) and the associated matrix of connection weights (b). The red colored cues in (a) - C_1 , C_2 , C_3 - represent the present cues; the connections from all present cues to outcome O_4 (thick lines) are summed to derive the activation for outcome O_4 , which reflects the strength of expectation (i.e., the prediction) that this outcome will be observed given the present cues. The matrix of connection weights reveals that the activation of O_4 is 0.251 (i.e., the sum of the bold numbers).

2.1.1. The Rescorla-Wagner learning equations

In the present study, the EDL simulations provide an estimate of how expected the incoming sound was on each trial. As discussed above, these expectations are based on all present cues and, through trial-by-trial adjustments, develop over the course of learning. The simulations are based on the Rescorla-Wagner learning equations (Rescorla & Wagner, 1972; Widrow & Hoff, 1960/1988). This model consists of a simple feedforward two-layer network, fully connected and without any hidden layers. The nodes in the input layer represent the *cues*, observed events or information that elicits a prediction about upcoming events. The nodes in the output layer represent the *outcomes*, that is, the upcoming events or information. The connection weights w represent the prediction strength from individual cues to outcomes. The network can be represented by a matrix of connection strengths, as illustrated in Figure 1. The connection strengths between cue i and outcome j are incrementally updated at each observed event (trial) t , for all present cues and all outcomes, as described in Definition 2.1a.

Definition 2.1. Specification of error-driven learning (EDL)

- a. Update of connection weight matrix:

$$V_{ij}^{t+1} = V_{ij}^t + \Delta V_{ij}^t,$$

with V being the matrix of connection strengths.

- b. Learning rule for updating V_{ij} :

$$\Delta V_{ij}^t = \begin{cases} \eta(\lambda - act_j^t) & \text{if present}(C_i, t) \ \& \ \text{present}(O_j, t) \\ \eta(0 - act_j^t) & \text{if present}(C_i, t) \ \& \ \text{absent}(O_j, t) \\ 0 & \text{if absent}(C_i, t) \end{cases}$$

- c. Activation act_j^t :

$$act_j^t = \sum_{x \in Cues(t)} w_{jx}^t$$

The connections between cues and outcomes are updated at each event following the learning rule proposed independently by Rescorla and Wagner (1972) and Widrow and Hoff (1960/1988), specified in Definition 2.1b. In this learning rule, the update of weights is determined by three factors: (1) presence or absence of cues and outcomes, (2) the parameters η and λ , and (3) current activation, which is the sum of connection weights from all present cues to a given outcome.

Firstly, Equation 2.1b describes the change in weights for three different cue-outcome combinations: (i) for all cues present on the current trial, connection weight *increases* to all present outcomes; (ii) for all cues present on the current trial, connection weight *decreases* to all absent (but previously encountered) outcomes; (iii) for any cues not present during the current trial, no adjustment is made. Additionally, for outcomes not encountered previously, no adjustment is made. Importantly, in (i) and (ii) adjustment to cue weights is divided equally among all present cues, which creates cue competition.

Secondly, the parameters determine the speed of learning. The parameter η is the learning rate¹, set to 0.01. The parameter λ is the asymptote of the activation, which is typically (and in the present study) set to 1.

Finally, and critically, as mentioned in the previous section, when weights are adjusted, the amount of adjustment depends on previous learning. The *activation* of an outcome j is defined as the sum of connection weights from all present cues to outcome j (Definition 2.1c; see Figure 1a for an illustration). The weight update ΔV_{ij} depends on the activation. Higher activation values indicate a stronger prediction that outcome j will occur. For high activation values, the *prediction error* is small when outcome j is actually observed, but large when j is not observed. The learning rule in 2.1b aims to reduce prediction error over time. Therefore, the calculation of the weight update involves subtracting the activation from λ (and multiplying by the learning rate) when outcome j is observed, resulting in small updates for high activation values and large updates for low activation values. When outcome j is not observed, calculation of the weight update involves subtracting the activation from 0 (and multiplying by the learning rate), which decreases connection strength. The decrease in connection strength is large for high-activation (expected) outcomes and small for low-activation (unexpected) outcomes.

¹The Rescorla-Wagner equations allow for a separate parameter for the salience of cues, salience of occurring outcomes and salience of non-occurring outcomes. In the present study, we reduce these three model parameters to one, the learning rate.

Because the connection weights are updated based on the current activation and the observed information, the model does not need to remember the complete history of co-occurrences to capture statistical patterns in the input. Interestingly, this simple learning model can explain a wide range of cognitive and linguistic phenomena, such as order effects in language (e.g., Hoppe, van Rij, Hendriks, & Ramscar, 2020; Nixon, 2018, 2020; Ramscar et al., 2010), the Kamin blocking effect (e.g., Kamin, 1969; Nixon, 2020), learning about predictive relations in the environment (Nixon, Poelstra, & van Rij, 2022), distributional learning (Olejarczyk, Kapatsinski, & Baayen, 2018) and first language speech sound acquisition (Nixon & Tomaschek, 2020, 2021). We refer to Hoppe et al. (2022) for a thorough review of the dynamics of EDL and the phenomena it has explained and Nixon (2020) for comparison with other leading learning models. Here we will focus on how EDL models are used to simulate the online learning of non-native lexical tones.

2.2. ERP components related to prediction and learning

The ERP signal is derived from electro-encephalogram (EEG; voltage) measurements that are time-locked to an event (hence ‘event-related’ potentials), usually the presentation of a stimulus. Various ERP components have been found to reflect learning, adaptation and predictive processing. To facilitate interpretation of the results, we briefly summarise the candidate components, namely the mismatch negativity response, the P3, error negativity and the N400. They are divided into early and late components, in relation to the time-windows in our analysis.

2.2.1. Early components

The *mismatch negativity* component (MMN; e.g., Näätänen, Gaillard, & Mäntysalo, 1978; Näätänen & Kreegipuu, 2011) occurs when the brain detects a change in auditory stimuli, usually in the context of the oddball paradigm. In this paradigm, occasional *deviant* stimuli are presented within a sequence of a large number of *standard* stimuli. In response to deviant stimuli, the MMN occurs between 100-250 ms after stimulus onset, starting at the N1, which peaks around 100 ms, and overlapping with the P2, which peaks around 180-200 ms (see Näätänen & Kreegipuu, 2011, for a review). Because of the overlap with other components, the MMN is often (but not always) reported as the difference in the ERP signal between standard and deviant stimuli.

The MMN seems to capture violation of predictions and as such it may be an index of learning. The standard-deviant ratio influences the magnitude of the MMN, with a higher number of deviants reducing the MMN magnitude (e.g., Haenschel, Vernon, Dwivedi, Gruzelier, & Baldeweg, 2005). Koelsch et al. (2016) report that the occurrence and magnitude of the MMN depend on the conditional probability of a stimulus given the earlier two sounds, with low probability sounds eliciting the largest MMN magnitude.

The MMN has been used to investigate the learning of (non)native speech sounds. Because a difference between standards and deviants is only found in the ERPs when participants can detect the difference between standard and deviant stimuli, the MMN can be used to detect whether participants can discriminate between speech sounds. For example, after training with nonnative vowel contrasts, an MMN response may occur to the deviant vowels which were presumably not discriminated before training (e.g., Wanrooij et al., 2014; Winkler et al., 1999).

2.2.2. Late components

The $P3$ is a positive-going ERP component that is also associated with expectation and surprise (e.g., Polich, 2011; Rushby, Barry, & Doherty, 2005). Like the MMN, the $P3$ has often been investigated using an oddball paradigm. Two subcomponents of the $P3$ have been identified, namely the $P3a$ and the $P3b$. The $P3a$ occurs around 300-500 ms post-stimulus (Kopp & Wolff, 2000) and occurs with or without conscious attention to the critical stimuli (Polich, 1988; Snyder & Hillyard, 1976). The $P3b$ occurs around 500-700 ms post-stimulus (Kopp & Wolff, 2000) and requires attention to the target (Snyder & Hillyard, 1976). The $P3a$ is distributed over the central and parietal electrodes, while the $P3b$ is distributed more parietally (Polich, 2011).

The *error negativity* (N_E ; also called error-related negativity; ERN) is usually associated with overt responses. It is a negative-going component that peaks around 80 ms after participants make an incorrect response, but starts prior to the response (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; see Holroyd, Nieuwenhuis, Mars, & Coles, 2004, for a review). In addition to this *response* N_E , Miltner, Braun, and Coles (1997) discovered that a similar N_E component also appeared when participants received negative feedback. Holroyd et al. (2004) argue that the N_E is elicited when a prediction error is detected: if a participant makes an error and detects it prior to receiving feedback, an N_E appears. In contrast, when the participant does not detect the error at the time of the response, then negative feedback elicits a feedback N_E at around 250 ms after the onset of the feedback stimulus.

The $N400$ (Kutas & Hillyard, 1980) is a negative-going waveform that peaks at around 400 ms (see e.g., Kutas & Federmeier, 2011, for a review). $N400$ amplitude is greater in centro-parietal sites in response to surprising or incongruent events compared to expected events. The functional scope of the $N400$ is complex, but seems to relate to higher-level expectation or prediction, particularly in semantic processes. Several studies have failed to find $N400$ effects for lower-level surprising events, such as an orthographic switch to capital letters (Kutas & Hillyard, 1980) or notes that violated musical expectations (Besson & Macar, 1987). Increased $N400$ amplitudes have been found in response to surprising compared to expected items in word lists, sentence processing and broader discourse processing, as well as visual scenes in videos (e.g., Kutas & Hillyard, 1980; Nieuwland & van Berkum, 2006; Sitnikova, Kuperberg, & Holcomb, 2003).

2.3. Research questions and hypotheses

Previous research using the oddball paradigm has tested whether the ERP signal differs between discrete stimulus conditions, usually standard vs. deviant. In the present study, we address whether continuous trial-by-trial learning leaves traces in the ERP signal. In particular, we were interested in whether participants use *cues* encountered during the experiment to develop expectations about the occurrence of particular stimulus conditions (*outcomes*) on each trial. Furthermore, we also explored which input representations (cues and outcomes) are predictive of brain activity and which components of the ERP are involved. Therefore, the present study addresses three main questions.

Research question 1: Do participants' neural signals show evidence of trial-by-trial learning? We will test this question by investigating whether the activation values for stimuli, derived from the EDL simulations, contain information about participants' neural signals. Specifically, we compare the predictions of our EDL simulations to

control models based on a) discrete stimulus conditions and b) stimulus probabilities. Such models represent equivalent information bar the trial-by-trial learning simulated using the EDL paradigm. The hypothesis we test is that at least one EDL simulation is more informative about the ERP signal than control models (a) and (b).

Research question 2: What do participants learn in this task? In other words, which input representations (cues and outcomes) allow simulations that capture participants' trial-by-trial learning? We hypothesise that two main types of learning occur. Firstly, we expect that participants might use characteristics of each incoming stimulus to group the stimuli into categories, such as high vs. low lexical tone or standard vs. deviant. Secondly, we expect that participants might use information about the sequences of stimuli to predict upcoming stimuli. We will test these hypotheses by simulating both category learning and predictive sequence learning using various cue-outcome structures. These simulations are tested against control models as outlined for Research question 1; we hypothesise that at least one simulation of each type yields an input signal that is more informative about the ERP signal than a control model.

Research question 3: How does trial-by-trial learning as modelled by the EDL simulations modulate the timing, location, and shape of the ERP waveforms? To answer this question, we divide our analysis into two time windows, early (0-350 ms) and late (250-600 ms). The analysis also yields information about the scalp distribution as it is performed for each electrode independently. Specifically, we explore how the trial-by-trial modulation of the ERP waveform relates to the EDL simulations: Do different EDL simulations modulate the ERP waveforms differently? And vice versa, do EDL simulations that show a similar modulation of the ERP waveforms share input representations?

As explained in more detail below, we test the extent to which EDL simulations can be linked to ERP signals by using them as input for TRFs. The resulting prediction is hypothesised to be more informative than baseline models that only capture static properties of the stimuli, including a stimulus' overall probability. If this hypothesis is confirmed, it answers our first question whether participants' neural signals show evidence of trial-by-trial learning. To answer our second question, we implement fifteen EDL simulations with various cue-outcome structures. If only one of the EDL-derived models is significantly more informative than the baseline models, we take this as evidence for trial-by-trial learning in the neural signal in the way this informative EDL simulation produces its estimates. We correct our statistical tests for the number of models.

3. EEG data

EEG data were recorded as participants listened to tokens from a 13-step pitch continuum of the syllable /li/. The syllable (duration 285 ms) was recorded by a female speaker, then resynthesised using Praat (Boersma & Weenink, 2014). The continuum was based on Cantonese mid-level and high-level tones (hereafter, for simplicity, the tones are referred to as 'low' and 'high' tones, respectively). Presentation order was adapted from the oddball paradigm: A series of four standards was presented, followed by one deviant. However, instead of using identical stimuli for all standards and all deviants, the stimuli were sampled from a bimodal distribution with the mid and high tones each represented by a roughly Gaussian distribution of tokens 1-6 and 8-13, respectively (see Figure E1 in Appendix E). The experiment consisted of eight blocks of 42 *trial sets*, where each trial set consisted of five trials: four standards and one deviant (336 trial sets; 1680 trials). The standard was consistent within blocks (either the low

Figure 2. Examples of three trial sets in the odd blocks (standards of type B, high tone; deviants of type A, mid tone), left panel) and in the even blocks (standards of type A, mid tone; deviants of type B, high tone, right panel): each trial set consisted of four standard stimuli followed by one deviant. The stimulus sounds differed only in pitch (y-axis) and were sampled from a bimodal pitch continuum of 13 steps. ‘S’=standard, ‘D’=deviant.

or high tone) and alternated between blocks. The inter-stimulus interval was varied randomly between 600–800 ms. The experimental design is illustrated in Figure 2.

EEG data were collected from 20 right-handed, native German-speaking participants, four of whom were excluded due to excessive noise, leaving data from 16 participants. EEG was recorded from 32 electrodes in the standard 10-20 system. If there was too much noise in a channel during a trial, the channel was excluded for that trial (4.4%) and Independent Component Analysis (ICA) in Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) was used to exclude blinks and ocular artefacts. We filtered the data between 0.1 Hz and 15 Hz. The grand averages of electrodes FC6 and Pz are included in Appendix A as an illustration. The voltages in each channel were transformed to z-scores (per participant and channel).

Preliminary analysis suggests a mismatch negativity response (Boll-Avetisyan et al., 2018). The EEG experiment was followed by two offline behavioural tasks, which will not be discussed here (see Nixon et al., 2018).

4. Method

In the present study, EDL simulations yield estimates of how expected the incoming stimulus is for each participant on each trial. The specification of these simulations is described in more detail in Section 5. These expectation estimates provide a continuous measure, *activation*, rather than categorising each trial as expected or not. The present paper investigates whether EDL activation allows for better prediction of the ERP signal than two types of control models: (1) *baseline models*, based on the traditional ERP analysis, namely a binary categorisation of trials based on stimulus types, such as standard vs deviant or high vs low tone category, and (2) *probability models*, based on probability scores of each pitch stimulus over the whole experiment.

Schematic representations of the traditional ERP analysis method and our analysis method using TRF fitting are shown in Figure 3. In essence, TRF fitting shares with traditional ERP analysis that TRFs represent the change in the EEG signal over time in a window after stimulus presentation. The key difference is that estimates are fitted based on a range of expectedness (activation) values, rather than by comparing conditions or subtracting one condition from another. Details of the TRF modelling process are presented in Section 6. A TRF analysis with two stimulus conditions, such

as standard vs. deviant (shown in diagram in Figure 3a), can be seen as a special case of our model (shown in diagram in Figure 3b), in which all trials are classified as either fully unexpected or fully expected.

Our analysis procedure involves three statistical tests (Figure 4 gives an overview), which are described in more detail in Section 6. For each EDL simulation, we test the informativity of fitted TRFs as models of the process that generated the measured ERP waveform. The activation values obtained from the EDL simulations can be seen as a scaled ranking of all trials by expectedness, and informativity about the underlying process entails that the ranking corresponds to one or more ERP components that (linearly) increase or decrease along with the ranking. Hence, the more informative this ranking is about the underlying process, the more informative the predictions made by the TRFs will be about the ERP data. In traditional ERP analysis, it is possible to statistically compare the difference between the two categories of EEG recordings, thus testing whether the ERP difference wave is different from zero. However, for a TRF such a comparison is not directly possible. A TRF may not be zero because of components that are always present, irrespective of the expectedness of a trial. In addition, our EDL simulations, though designed to capture learning, may potentially lead to rankings that also reflect other properties of the trials. To address both issues conservatively, our statistical testing involves comparing our EDL-derived models to a set of control models (see Section 6 for more detail).

The EDL simulations in the present study capture the process of using cues to learn to discriminate the outcome stimuli. If the EDL simulations capture variation in the ERP signal, we need to ensure that this is not (only) due to the EDL activations capturing differences between the outcome stimuli, but rather due to trial-by-trial learning of the stimuli. In the simulations where there are only two different outcome types (i.e., ‘standard’, ‘deviant’ or ‘high’, ‘low’), baseline models are created in which the TRFs are based on a simple division of all trials into the two stimulus conditions, based on the outcome type. These baseline models are conceptually similar to comparing stimulus conditions in traditional ERP analysis, although here we do it with TRF modelling. **Test 1** comprises comparing the EDL models against these baselines. If the EDL models are more informative than their baselines, the continuous activation measure – a measure of expectation on each trial – is more informative about the neural response than discrete stimulus conditions based on static properties of the stimuli.

One group of EDL simulations (the ‘-val’ simulations, see Table 2, Section 5) learns to predict the individual steps on the pitch continuum. With this type of set-up, it is not meaningful to create a baseline model like those described above, because there are multiple (12) continuum steps, but no expected ordered effect of the continuum step – we do not expect a larger ERP response to higher values, for example. Therefore, in **Test 2**, we compare these models to a model that is not based on the outcome (the pitch value), but based on the probability of the outcome. Unlike the pitch value itself, the probability of occurrence of the pitch values does have an order that we might posit to affect participants’ expectation: if stimulus probability has an effect, higher probability stimuli are more expected. Hence, a model using only probabilities as input, but not trial-by-trial estimates of learning, is a good model for comparison with the ‘val’ simulations.

In addition to providing a comparison for the val models, these *probability models* also represent a theoretical model of learning. As discussed in the Introduction, distributional learning models posit that people learn from the frequency distribution of stimuli (e.g. Maye et al., 2002). According to these models, expectations should differ depending on stimulus probability. Therefore, the other EDL simulations (the HL and

Figure 3. Diagram comparing data treatment for traditional ERP analysis vs. the TRF approach, as in the present study. **Left:** In the classic ERP setup, trials are separated into (usually two) stimulus conditions (e.g ‘standard’ vs. ‘deviant’ or ‘high tone’ vs. ‘low tone’). The EEG signal is averaged and these averages are compared to obtain the ERP difference wave, marked in the diagram as ‘ERP’. **Right:** In our study, error-driven learning (EDL) simulations are run, yielding an estimate of the expectedness of the stimulus presented on each trial; the estimates are continuous values on an arbitrary scale. A function is fitted using brute-force, which captures the component in the EEG that gradually increases with the expectedness. Instead of a difference score, the result is a *predicted response signal* and a TRF fitted as closely as possible to the ERP for each trial. The quality of the fit allows us to estimate how informative the simulation (i.e. the expectation estimate) was. The TRF can be inspected to see the effect of activation on the ERP signal, such as the timing and polarity of the effect.

Figure 4. Overview of statistical tests and pruning steps. Note that the probability model acts in place of the baseline model for the EDL ‘-val’ simulations. Therefore Test 1 does not apply and Test 2 is used for pruning these models, but not for pruning the other EDL simulations.

SD models) are compared both to their own baseline (Test 1) and to the probability model (Test 2). Comparison to the probability model allows us to test whether the EDL models are more informative about the ERP signal than a model based on the statistical distribution of stimuli. The informativeness of each TRF, as used in Tests 1 and 2, is captured by its AIC value, as will be described in more detail in Section 6. A summary of each individual test is provided below. There are three tests, which are mostly independent tests. However, in rare cases, we conducted pruning based on Test 1, see footnote.² In general, if a model-channel-time window combination did not pass Test 1, it was not pruned, but instead still passed to Test 2 and/or 3.³

Test 1. Our analysis begins by testing each EDL model against its *baseline model* in each channel in each time window. Test 1 determines whether we are able to find evidence of trial-by-trial learning as captured by our EDL simulations, rather than only differences based on static properties of the stimuli. Technically, we perform a repeated test of the main hypothesis that for at least one channel in at least one time window at least one EDL model leads to a TRF model that is more informative than its baseline. Because the baseline model captures the temporal alignment and the static properties of the outcome stimuli, this means that if the EDL-derived TRF only fits the data due to these two factors, it will not pass Test 1.

Test 2. Our second test compares the EDL models to a *probability model*, which is a TRF based on the overall probability of the stimuli. As mentioned above, the ‘val’ models are not compared to a baseline model based on their outcome stimuli like the other EDL models, but are instead compared to the probability model. In addition, each EDL model that passed Test 1 is also compared to the probability model in each remaining channel in each time window. Test 2 determines whether we are able to find

²Pruning only took place in two specific cases: a) channel-time window combinations were pruned if *no EDL model* was more informative than its baseline in that channel-time window combination and b) EDL models were pruned if they were not more informative than their baseline *in any channel-time window combination*. This led to only one case of pruning under a).

³We thank an anonymous reviewer for making suggestions that lead us to include this test.

evidence that trial-by-trial learning as captured by our EDL simulations outperforms a model based on the statistical distribution of the stimuli. Technically, we perform a repeated test of the main hypothesis that for at least one channel in at least one time window at least one EDL model leads to a TRF model that is more informative than the probability model. In summary, the results of Test 2 allow us to determine which of the EDL models that passed Test 1 are also more informative than the probability model and in which channels in each time window. In addition, it also allows us to test the ‘-val’ simulations against a model with access to temporal information.

Test 3. Finally, for each combination (time window, channel) and for each EDL-derived model that beat its baseline, as well as for the val models that beat the probability model, an additional safety check was performed, comparing each individual EDL model in each channel in each time window to a set of *random* models.

By using conservative tests in Tests 1 and 2, we have confidence that, if any EDL-derived model passes the test(s), that EDL-derived TRFs may capture actual variance in the EEG data corresponding to our continuous activation measure – how expected the stimuli are – not just due to differences between stimulus types or the statistical distribution of stimuli. Because there is a range of activation values in the different simulations, while the trials can only be ranked in a limited number of ways, it is possible that a large enough selection of rankings accidentally contains one or more rankings that explains some variance. As estimating the number of meaningfully different rankings is difficult, we perform a simple, non-parametric test for each combination of EDL simulation, channel and time window not pruned in Tests 1 and 2: We test the hypothesis that the EDL simulation beats a randomly generated model more often than expected by chance. The activation values generated by all EDL simulations were simply randomly assigned, one to each trial, to create 5000 different random input signals, which are still time-aligned with the trials. These random input signals were then used to fit TRFs. The amount of variance explained by the random models was compared to that of each EDL-derived model. If the latter beat the random models (i.e., had a higher amount of explained variance), more often than expected by chance (i.e., significantly more often than 50% of the comparisons), we consider the EDL-derived model to have passed Test 3; the test is performed per channel/time window combination.

5. EDL simulations: obtaining trial-by-trial estimates of participants’ level of expectation

As described in Section 2.1, we use EDL simulations to generate an estimate of participants’ expectation of an upcoming stimulus; in the TRF derivation overview shown in Figure 3 the simulations are placed near the top, as a diamond shape. We generated one measure per participant per trial as an estimate of the participant’s expectation of the category (categorisation simulations) or upcoming stimulus (prediction simulations). This measure was the activation; that is, the sum of weights from all present cues to the outcome stimulus that occurred on the present trial. As each participant was exposed to a different sequence of stimuli, we simulated learning for each participant separately.

Determining the appropriate cues and outcomes as representation of the learning process is not trivial (see Bröker & Ramscar, 2020, for discussion). Furthermore, we assume that all discriminable cues might potentially be used to predict important events. This means that learning may occur on multiple levels simultaneously. There-

fore, the simulations investigated two types of cognitive task, four possible cue types (i.e. the information participants used to predict the outcomes) and three possible outcome types (the event that participants learned to categorise or predict).

5.1. Model specification: Cognitive task, cues and outcomes

The two types of cognitive task we investigated were categorisation (Table 1) and predicting the upcoming stimulus in the sequence (Table 2). In the categorisation simulations, various aspects of an incoming stimulus were used to categorise the *same* stimulus. That is, the cues and outcome were the same auditory stimulus. This is in contrast to the predictive models, in which various cues were used to predict an upcoming stimulus; the cues and outcome were different stimuli.

The reason for our choice of these two learning tasks is as follows. In terms of the categorisation task, the oddball design of the experiment (a series of standards followed by a deviant) provides structure that may lead to learning of standard vs. deviant or high vs. low tone categories. That is, the fine-grained acoustic differences may be downweighted with an increase in discrimination of the large-scale differences in lexical tone. In terms of the predictive simulations, on the other hand, previous EDL studies have shown that temporally earlier stimuli are used to predict temporally later stimuli (Hoppe et al., 2020; Nixon, 2018, 2020; Nixon & Tomaschek, 2020, 2021; Ramscar et al., 2010). The sequential presentation of stimuli in this experiment is likely to lead to learning through prediction of upcoming stimuli.

The cues used in the simulations were as follows. The *tone bigram cues* represent a sequence of cues. This is the only simulation type in which the input cues on each trial include information from more than one trial. Participants learn from a sequence of stimuli, namely a sequence of three overlapping lexical tone bigrams. Bigrams are created with a moving window over the stimulus sequence. For example, the stimulus sequence high_high_high_low produces the bigram cue sequence HH_HH_HL. The *pitch value cues* were the pitch value steps along the continuum (1-6, 8-13). As described in Section 3, the acoustic stimuli presented to participants were sampled from a pitch continuum of Cantonese tones. In a discrimination task, the participants were usually not able to detect differences of two steps along the continuum (although fine-grained effects were found in a continuous pitch estimation task; Nixon et al., 2018); therefore, the cues representing each pitch value were a *window of three* continuum steps. This added a ‘fuzziness’ or lower perceptual acuity to the learning, to account for the low sensitivity to single steps on the continuum. For example, if the stimulus presented on a particular trial was continuum step 4, the three input cues to the simulation would be 3, 4 and 5. The *pitch difference cues* are the number of steps on the continuum between the pitch value of the previous and current stimulus. For example, if the previous stimulus was 5 and the current stimulus 3, the pitch difference would be -2. The *window of three* is also applied to the pitch difference cues. Thus, in this example, the input cues would be -3, -2 and -1. The *position cues* represent the position of the current trial in the trial set. As described in Section 3, the trial sets consisted of five trials, of which there were four standards followed by one deviant. The letters A-E represent the positions 1-5.

The outcomes used in the simulations were as follows. The outcomes were either high vs. low lexical tone; standard vs. deviant stimulus; or pitch values. The pitch value outcomes were the same as above for the pitch value cues, except that they were a single value, not a window of three.

Table 1. Categorisation simulations. Overview of the different error-driven learning simulations in the categorisation analysis. For categorisation, the cue is always the *same stimulus* as the outcome. For example, a presented stimulus might be pitch value 10. In the Cat-val-HL simulation, the cues would be a window around 10 ('9_10_11'), the present outcome would be the lexical tone High and the absent outcome would be the lexical tone Low. The simulation learns to categorise Pitch 10 as High or Low. *Pitch diff* = Pitch difference, i.e. the change in pitch relative to the previous trial.

Simulation	Cue type	Possible input cues	Outcomes
Cat-val-HL	pitch value, window of 3	{'1_2', '1_2_3', ..., '12_13'}	{'Low', 'High'}
Cat-diff-HL	pitch diff, window of 3	{'-12_-11', '-12_-11_-10', ..., '11_12'}	{'Low', 'High'}
Cat-pos-HL	position in trial set	{'A', ..., 'E'} (stimuli 1-5 within trial set)	{'Low', 'High'}
Cat-val-SD	pitch value, window of 3	{'1_2', '1_2_3', ..., '12_13'}	{'Std', 'Dev'}
Cat-diff-SD	pitch diff, window of 3	{'-12_-11', '-12_-11_-10', ..., '11_12'}	{'Std', 'Dev'}
Cat-pos-SD	position in trial set	{'A', ..., 'E'} (stimuli 1-5 within trial set)	{'Std', 'Dev'}

Table 2. Prediction simulations. Overview of the different types EDL simulations in the predictive learning analysis. For predictive learning, the cue is always the *stimulus prior to the outcome*, except in the case of bigrams, where the cues are a series of the three bigrams before the outcome. Note that in the case of bigrams, in order to keep the table size to a minimum, example bigram cues are provided, rather than the full set.

Simulation	Cue type	Possible input cues	Outcomes
Pred-val-HL	pitch value, window of 3	{'1_2', '1_2_3', ..., '12_13'}	{'Low', 'High'}
Pred-diff-HL	pitch diff, window of 3	{'-12_-11', '-12_-11_-10', ..., '11_12'}	{'Low', 'High'}
Pred-bg-HL	tone bigrams	(e.g. 'HH_HH_HH', 'HH_HH_HL')	{'Low', 'High'}
Pred-val-SD	pitch value, window of 3	{'1_2', '1_2_3', ..., '12_13'}	{'Std', 'Dev'}
Pred-diff-SD	pitch diff, window of 3	{'-12_-11', '-12_-11_-10', ..., '11_12'}	{'Std', 'Dev'}
Pred-bg-SD	tone bigrams	(e.g. 'HH_HH_HH', 'HH_HH_HL')	{'Std', 'Dev'}
Pred-val-val	pitch value, window of 3	{'1_2', '1_2_3', ..., '12_13'}	{Pitch 1-6, 8-13}
Pred-diff-val	pitch diff, window of 3	{'-12_-11', '-12_-11_-10', ..., '11_12'}	{Pitch 1-6, 8-13}
Pred-bg-val	tone bigrams	(e.g. 'HH_HH_HH', 'HH_HH_HL')	{Pitch 1-6, 8-13}

In the categorisation simulations (Table 1), cues that are part of the outcome stimulus are used to categorise the outcome stimulus into different categories. Specifically, in six separate simulations, one of the cue types pitch value, pitch difference or position was used to categorise the outcome stimulus into either high vs. low or standard vs. deviant. In the prediction simulations (Table 2) incoming cues were used to predict the outcome in the upcoming trial. Specifically, in nine separate simulations, one of the cue types pitch value, pitch difference or tone bigram was used to predict one of three different outcome types, namely high vs. low tone, standard vs deviant or pitch value. Note that we do not expect the pitch value simulations to perform well, for the reasons explained above; namely, that the pitch differences of the continuum steps (even two steps apart) were usually too small to discriminate (Nixon et al., 2018). However, it is possible that even if participants did not discriminate these tokens in the behavioural data, the ERP response could still show evidence of prediction of the pitch value. The pitch value simulations test this possibility.

5.2. An illustrative example: Model predictions for *Pred-bg-HL*

To illustrate how our simulations predict participants’ expectations on each trial, Figure 5 visualises the activations for all experimental stimuli in the experiment generated by the *Pred-bg-HL* model for one participant. The trials are colour coded according to the position of the sound in a trial set, ranging from 1–5. (The colour coding is for visualisation purposes only; the simulation input does not include the trial set number.) This EDL model uses a sequence of bigram cues to predict whether the next stimulus will be a high or low tone. The unique cues and outcomes for this EDL model are presented in Table 3. What stands out from the activation pattern is that this EDL model generally has a stronger expectation for a standard stimulus to appear (i.e., stimuli 1–4) than a deviant (i.e., stimulus 5), with the activations for stimulus 5 considerably lower than for the other stimuli. Note that this occurs without the model having explicit information about which stimuli are standards or deviants. The reason is that the cues for the deviant stimuli do not uniquely predict the deviant outcome, but also appear with the standard outcome (i.e., cues ‘HH’ in the odd blocks and ‘LL’ in the even blocks) ; see Table 3). Further, the activations show a consistent change *within* each block. The activations of the standards are mainly determined by the cues ‘HL’ and ‘LH’, which predict the outcome High in the odd blocks and the outcome Low in the even blocks (see Table 3 below). Therefore, the learner needs to change their expectations based on these cues in every new block. The activations of the deviants, on the other hand, are determined only by the cues ‘HH’ in the odd blocks and ‘LL’ in the even blocks. Only one of these cue types occurs within each block. These cues occur more often with high tone outcomes in the odd block and low tone outcomes in the even block. Therefore, the expectation of each outcome is determined by cue competition. Note that outcome frequency also plays a key role, but the expectations

Figure 5. Activations (y-axis) for all stimuli of one experimental session (i.e., the trial order presented to one of the participants), generated by EDL model *Pred-bg-HL*. The legend shows the colour coding for the 5-trial sequence. In the odd blocks, stimuli 1-4 are high tones and stimulus 5 is a low tone; in even blocks stimuli 1-4 are low tones and stimulus 5 is a high tone. The cues are bigram tone sequences and the outcomes the tone of the next stimulus (e.g., ‘HH_HH_HL’ are the cues predicting stimulus 5). The activations represent the strength of expectation for this outcome to appear. The x-axis shows the order of incoming stimuli (5 pitch sounds per trial set $\times$ 42 trial sets per block = 210 stimuli per block $\times$ 8 blocks). The vertical dashed lines separate the blocks.

are learned through a discriminative process of prediction and prediction error, not direct frequency counts.

Thus, this EDL model predicts a difference in expectation between standards and deviants, and a repeating fluctuation in expectations that is associated with the switching of standards and deviants between the odd and even blocks. This fluctuation in expectations is not expected for generative models of statistical learning, because it is only predicted when *unlearning* of associations plays a role (which is not the case in models based on co-occurrence probabilities).

Stimuli	Cues	Outcomes	Blocks
1	'HH_HH_HL_x'	High	1, 3, 5, 7 (odd)
2	'HH_HL_LH_x'	High	
3	'HL_LH_HH_x'	High	
4	'LH_HH_HH_x'	High	
5	'HH_HH_HH_x'	Low	
1	'LL_LL_LH_x'	Low	2, 4, 6, 8 (even)
2	'LL_LH_HL_x'	Low	
3	'LH_HL_LL_x'	Low	
4	'LH_LL_LL_x'	Low	
5	'LL_LL_LL_x'	High	

Table 3. Cues and outcomes for the EDL simulation Pred-bg-HL. The 'x' cue is the 'background cue'. This is included in all trials in all simulations to capture the laboratory environment. The left column shows the position of the outcome stimulus (i.e. current trial) in the trial set. Outcomes were lexical tones, high or low. The cues consist of a sequence of trials implemented as overlapping tone bigrams (two trials of the lexical tone high (H) or low (L)). The 'x' cue is the 'background cue'. This is included in all trials in all simulations to capture the laboratory environment.

6. Analysis: Temporal response modelling

Analysis involved 1) generating trial-by-trial predictions of the ERP waveform using TRFs based on the EDL activations and 2) generating predictions of the ERP waveform for a set of control models for comparison. As outlined in Section 4, three tests were carried out to evaluate whether the trial-by-trial predictions of the ERP waveform derived from the EDL activation measure outperformed those derived from the control models in predicting the trial-by-trial EEG data. Below, we first explain how the trial-by-trial estimates of the ERP waveform are obtained for the EDL-derived models using Temporal Response Function (TRF) fitting. We then explain how each of the control models was generated and how they were used to test the EDL models.

6.1. Using trial-by-trial estimates to predict the ERP waveform

The EDL simulations give us an estimate of how expected the incoming stimulus is on each trial (i.e., the activation of the outcome). The next step is to fit TRFs, which give us a prediction of the ERP waveform based on the input signal provided by the EDL estimates per trial.

We use the MNE toolkit for Python (Gramfort et al., 2013) to fit TRFs for our dataset. For each EDL simulation, there is an input signal consisting of activation values from the EDL simulations, i.e., a unique series of activation values for each participant, one value per incoming sound. TRFs are fitted for each EDL model, for

each electrode, for each participant, and for the two time windows. We evaluate the fit of the TRFs for each EDL simulation, time window and electrode, hence aggregating over participants.

The TRFs are fitted so that the predicted response signal (the convolution of the input signal with the TRF) has an optimal fit to the ERP signal. Crucially, the input signal is not fitted, and hence the extent to which the TRF captures the ERP output signal is a measure of the relation between input and output.

6.1.1. Teasing apart the effect of expectation from the overall auditory response

Care was taken to avoid spurious fits (overfitting) and fitting to other properties of the signal. Because the EEG signal is highly variable, with many contributions to the variation, most of the EEG signal will not be predicted by any convoluted input. On the other hand, the mere occurrence of a stimulus likely leads to a predictable EEG response which will be captured by the TRFs. If the modelling approach does not account for a neural response to the onset of incoming stimuli in general, the TRF approach may be vulnerable to spurious fits. For analysis purposes, we can conceptualise this situation as a) an ERP component that occurs in response to any incoming stimulus and b) a modulation to that component depending on the level of expectation. We are interested in modelling the modulation, but because it is combined with the ERP response to the incoming stimulus, we need to tease them apart.

To tease apart the confound between the ERP component and the modulation of the component, two TRF shapes are generated using two-dimensional spikes. One dimension of the spike train is used to capture the brain's response to the onset of an (any) auditory stimulus. In this dimension, all spikes are of equal magnitude; thus, the dimension simply indicates stimulus onset and does not capture any variable properties of the stimulus. We call this the *constant* dimension. A second dimension is used to capture variation in the brain response, depending on how expected a stimulus is on a given trial. We call this the *variable* dimension. The use of two dimensions also allows us to avoid a potential technical difficulty. Because the ERP components measure error or surprise (low expectation), a priori we expect a *larger* (negative) ERP amplitude as activation/expectation increases. This inverse relationship would not be possible to model with a single dimension.⁴ Using two dimensions enables us to use the constant dimensions to predict the ERP component that occurs in response to unexpected stimuli, while the variable dimension can be used to predict how much smaller this component is as activation increases. Thus, larger spikes in the variable dimension can now be used to predict a decrease without generating an output signal that is overall positive.

Linking the two TRFs to our activation values, the TRF for the constant dimension represents minimum expectedness (activation of 0) and combining both TRFs (adding the TRF for the constant dimension together with the TRF for the variable dimension) represents maximum expectedness (activation of 1). The predicted response signal for all intermediate activation values is a linear interpolation between these two TRFs. Figure 6 illustrates the convolution: An idealised TRF is shown on the left (red line). A spike train of measures represents, per trial, the simulated activation of the presented

⁴ Recall that the input vector consists of a valued spike (height determined by the activation value) as the initial value (stimulus onset). Thus, if the TRF used only a single dimension, then when the input signal contained small values of the initial spike (i.e. activation values close to zero), the TRF would predict a waveform that is similar to when there is no stimulus and therefore no input signal, i.e. the baseline signal. If this were the case, small values of activation would produce a TRF that predicts a small ERP in response to low activation. In other words, there would be no way to model a large ERP waveform in response to unexpected stimuli.

Figure 6. Temporal response function (TRF) as a convolution. *Left:* An idealized TRF (red line), representing a positive response shortly after a stimulus and a negative response later. *Right:* The *predicted response signal* (blue line) is the convolution of the TRF function and the *activation spike* (i.e. the input signal). The height of the spikes represents the estimated activation of the stimulus, derived from the EDL simulations. As the spikes have no duration, the convolution is simply the multiplication of the TRF with the height of the spike. Three experimental *trial sets* of five trials are shown; for illustrative purposes, the standards are shown in grey, the deviants in black, and the start of a trial set as a hatched spike. Fitting (not shown) entails generating multiple TRF shapes and selecting the TRF shape that is closest to the (EEG) signal.

stimulus (right; black or grey vertical lines). This spike train is convoluted with the TRF. The output is a continuous *predicted response signal* (blue line).

6.1.2. Obtaining estimates for the timing and location of effects

An advantage of TRF fitting is that, while our simulations predict the level of *expectation* on each trial, the neural correlate of the expectation – the ERP component – does not need to be known in advance: it is derived from the data. Any relationship between the input signal (activation) and ERP data should be captured by the TRF. For example, if activation values are larger on trials that have a larger response at 200 ms and smaller on trials that have a smaller response at 200 ms, the model will capture this with a TRF that increases with activation value at 200 ms. The more the activation corresponds to the magnitude of the ERP signal (anywhere in the time window under analysis), the better the *predicted response signal* will fit to the observed ERP signal. If there is a linear relationship between the activation (spike magnitude) and the ERP component, there will be a good fit.

Thus, fitting TRFs not only allows us to detect whether there is a relationship between the trial-by-trial learning estimates and the ERP waveform, but also generates a prediction of the ERP waveform itself, for each trial in the dataset. Because separate TRFs are fitted for each electrode, the goodness-of-fit can be evaluated per electrode channel, revealing the location of the predicted effect. Although estimates of the ERP waveform are generated in a continuous manner anywhere in the window under analysis, the statistical *test of significance* is performed for the TRF as a whole. Therefore, given that either early or late ERP components or both may be involved in prediction and learning as outlined in Section 2.2, the present study separately fits TRFs in an early and a late window, 0–350 ms and 250–600 ms after stimulus onset, respectively. By separating the data into two time windows we can determine with more precision when the predicted effect actually fits the signal.

6.1.3. TRF fitting procedure

TRFs are fitted using five-fold cross-validation. All data gathered from one participant at one electrode channel, in one of the two time windows is split into five parts. Using four parts as training data, TRFs are fitted to maximize R^2 . The fitted TRF is then used to generate prediction for the remaining data, the test set, providing log-likelihoods for the test sets – which, over the five iterations of the cross-validation, comprise all the data. We then calculate the AIC of the fitted TRFs, and compare AIC values to assess whether the EDL-based TRF is more informative than a TRF fitted on a baseline model and a model based on probability, as in Ahmed (2021). The AIC/likelihood and R^2 scores are thus calculated only on the test sets (i.e., data not used for fitting). Note that all TRFs shown below are average TRFs over five iterations and over all participants.

6.2. Evaluation: Testing the EDL models against control models

Section 4 introduced three tests, of which the first two are against the baseline and probability models and the third is against a set of random models. Below, after a note about correcting for multiple comparisons, we provide more detail about how each of these models was created and how the tests were carried out. At the end of this process, we are left with a set of informative EDL models, which indicate what kind of learning predicts neural patterns in the ERPs; and a set of electrodes and time windows that indicate where and when the components related to trial-by-trial learning occur.

6.2.1. Multiple comparisons

As described in Section 5, the present study examined several possible EDL simulations. Note that, to avoid computational complexity, each different EDL simulation is used to generate a separate TRF model, rather than including multiple EDL simulations as input dimensions for one model. However, the EDL simulations are not considered to be independent, because the input for all the different models consists of spikes at certain time points (at the onset of the spike train, i.e. at stimulus onset) and zeros at all other time points. Therefore, because of the zeros, the input is highly correlated between models. In addition, there could potentially also be similarity between EDL simulations in the size of the onset spike itself. Further, we assume that different EDL simulations may capture different aspects of learning that are not mutually exclusive, but may take place in parallel. We therefore refrain from formally comparing different models based on different EDL simulations.

Because the statistical analyses test whether *any* EDL simulation can predict part of the ERP signal, they require corrections for multiple comparisons. In this respect, theoretically, all EDL simulations could turn out to represent exactly the same underlying construct; as such, the comparison of a control model with an EDL model may be a repeated test of the same hypothesis. Therefore significance is adjusted for multiple comparisons using Bonferroni corrections. Hence, α is divided by the product of the number of electrodes, time windows, and models (i.e., by 1280), to $\alpha = 0.000039$.⁵

⁵In a previous version of this article, we considered 20 models, but in the interest of clarity and space, we have dropped five uninformative models. We still correct for the original number of models, instead of the 15 described above.

697 6.2.2. Baseline models

698 On each trial, the *input* information that the EDL simulations use includes which type
699 of outcome stimulus has occurred (e.g. high or low tone, standard or deviant). The EDL
700 simulations learn to predict the outcome stimulus from the cues. The EDL *predictions*
701 are measured in activation, which represents how expected the outcome stimulus is on
702 each trial. However, if there are systematic differences between these stimulus types in
703 the ERP response, it is possible that the EDL simulations might spuriously pick up
704 on differences in the ERP response between these outcome stimuli. In this case, the
705 EDL models might appear to perform well simply because different activation values
706 correlate with differences in response to static properties of the stimuli, rather than
707 because they capture trial-by-trial learning.

708 Two *two-dimensional* baseline models were constructed to capture only the fit that
709 can be attained by separating the trials by outcome stimulus type and temporally
710 aligning the TRF input signal with the stimuli. The EDL simulations were evaluated
711 against these baseline models to assess whether the EDL predictions (activation) are
712 more informative about the ERP signal than just the model input (the type of outcome
713 stimulus). The High-Low (HL) baseline model serves as a baseline for the EDL models
714 that learned to categorise or predict the tone category (of which the name ends in
715 ‘-HL’) and the Standard-Deviant (SD) baseline model is for the EDL models that
716 learned to categorise or predict standard vs. deviant stimuli (of which the name ends
717 in ‘-SD’). Like the EDL models, each baseline model contains a constant dimension of
718 uniformly sized spikes, which captures the occurrence of a stimulus (time-aligned to
719 stimulus onset in the ERP data; see Section 6.1.1). In addition, the baseline models
720 also contain a variable dimension to capture the difference between the stimulus types:
721 This dimension contains a spike for each high tone (HL baseline model) or a spike for
722 each deviant (SD baseline model).

723 6.2.3. Probability model

724 As described in the Method section, the probability model served two purposes. Firstly,
725 it serves the comparison model for the pitch value simulations (the ‘-val’ simulations
726 in Table 2), since it is not meaningful to create a categorical baseline model like those
727 described above for this type of EDL model. This is because there are multiple (12)
728 continuum steps, but no expected ordered effect of the continuum step, such as a
729 larger ERP response to higher pitch values, for example. So for the val models, instead
730 of comparing to a model based on the outcomes per se, they are compared to the
731 probability model, which is based on the probability of the pitch value outcomes.
732 Secondly, the probability models are also used as an additional test for the other EDL
733 model types, since the probability model represents a theoretical model of learning. So
734 the probability models test whether the EDL models capture variability in the ERPs
735 that is not captured by statistical learning. As explained in Section 3, the stimuli
736 consisted of a bimodal distribution of pitch stimuli corresponding to two lexical tones.
737 To capture this statistical distribution, the probability models use a TRF for each
738 probability value (see Appendix E1).

739 6.2.4. Test against Baseline and/or Probability model

740 Informativeness – i.e., how well a TRF predicts the data – is calculated using Akaike’s
741 Information Criterion (AIC), considering the TRF together with the input signal as
742 a model, and the actual recorded EEG signal as data. The lower the AIC, the more

informative a TRF is. The AIC is low when the maximum likelihood of the data is high, but is penalised for each included parameter, because it is defined as two times the number of parameters k minus two times the maximum log likelihood of a model m : $AIC(m) = 2k - 2\ln L$. As k is constant for all our models, the AIC scores are reduced if the log-likelihood $\ln L$ is reduced. The total log-likelihood is the sum of the log-likelihood for all (unseen) test data in the five-fold cross-validation procedure described above. If two models (such as an EDL model and its baseline) are fitted on the same data, and the EDL model has a lower AIC than the baseline model, Equation 1 calculates the probability of the null hypothesis that the alternative (baseline) model and not the EDL model minimizes information loss.

$$p(\text{baseline}_x <_{\text{information loss}} \text{EDL}_x) = \exp\left(\frac{AIC(\text{TRF-EDL}_x) - AIC(\text{TRF-baseline})}{2}\right) \quad (1)$$

The p-values obtained in this way are used to evaluate significance, against $\alpha = 0.05$, with corrections for multiple comparisons, i.e., for the number of TRFs, which is equal to the product of the number of EDL models, electrode channels, and time windows.

6.2.5. Random models

As an added sanity check, for the models that beat the baseline and probability models, we also test whether the trial-by-trial activation values from our EDL simulations perform better than a random sampling of these values. This test provides an additional check to ensure that it is very unlikely that the EDL models spuriously capture variation in the EEG data. These random models are based on the activation values sampled from the set of all EDL simulations. Because the activation values are sampled from the EDL activations, correlation with the ERP response is still possible – and expected – in the random models. Therefore, we do not expect the EDL models to always outperform the random models. However, if the EDL-derived models perform well, they should achieve a *higher* correlation with the ERP response than the random models do.

To produce the spike values in the variable dimension for each random model, we sampled one activation value per trial for each trial of the experiment (1680 trials) from the activation values of all the EDL simulations. This was repeated 5000 times to produce 5000 random models. We fit TRFs for these random signals and compared the resulting models to the EDL models. The comparison uses explained variance, calculated as R^2 , for each channel at each time window. Since we cannot assume any specific distribution for the R^2 values, we perform a random comparison test: each EDL model is compared (at each time window and at each electrode separately) to all 5000 models. The outcome variable is the proportion of hits (beating a random model) against the total number of comparisons. Significance is calculated against the null hypothesis that the hits are as likely as the losses (a binomial test against 0.05), with the alpha level Bonferroni-corrected for the number of channels and time windows (64) to $p < 0.00078$. Note that the correction does not take the number of models into account, as we have already tested whether there are models that are more informative than a baseline model.

7. Results

Several EDL-derived TRF models passed all the relevant statistical tests in several channels. That is, they were significantly more informative than the baseline models (Test 1, for the ‘HL’ and ‘SD’ models), or the probability model (Test 2, for the ‘val’ models) and were likely to explain more variance than random models (Test 3). In addition, several of the ‘HL’ and ‘SD’ models also passed the extra test against the Probability model (Test 2). Hence, the information that the EDL simulations provide about trial-by-trial learning is predictive of the ERPs. Overall, the EDL-derived models were more often more informative than the baseline models for the early time window ERP than for the late time window. EDL-derived models also outperformed the probability model more often in the early time window. In contrast, only one model was more informative than the probability model in the late time window and in only a few channels. There was only one channel, FC5, in which none of the EDL models outperformed their baselines – and this was only the case in the late time window. This time window/channel combination was therefore pruned. Some EDL-derived models beat their baseline in a few channels in the late time window, but fewer than the early time window. Finally, two models never outperformed their baseline or the probability model: Cat-val-HL and Cat-pos-SDs these models are also pruned.

Figure 7 shows the model-channel-window combinations in which the EDL models outperformed the baseline model (i.e., Test 1 for the ‘-HL’ and ‘-SD’ simulations), or the probability model for the ‘-val’ simulations (Test 2) and also outperformed the random models (Test 3).

Early time window: The prediction models Pred-bg-HL, Pred-val-HL, Pred-diff-HL, and Pred-bg-VAL, Pred-val-VAL, Pred-diff-VAL show a broad and overlapping scalp distribution in the early time window. The distribution of the categorisation models Cat-diff-HL, Cat-pos-HL, Cat-val-SD and Cat-diff-SD each partially matches the electrodes of the prediction models. Together, the EDL models capture variance in the ERP signal over a wide scalp distribution in the early time window: frontolateral (F7, F8, FC5, FC6, T7, T8) and centroparietal/occipital electrodes (P3, P4, Pz, C3, CP1, CP2, CP5, PO3, Oz, O2). The categorisation models Cat-val-SD and Cat-diff-SD seem more localised, showing up frontolateral in case of Cat-val-SD, and central in case of Cat-diff-SD, though their absence in other regions is a null result and should not be over-interpreted as proof of absence. In the early time window, none of the EDL models outperformed random models in channels Fp1, AF3, F3, FC1, P7, O1, PO4, P8, CP6, C4, FC2, F4, AF4, Fp2, Fz, and Cz, so we refrain from interpreting these combinations.

The results for the comparison against the probability model (Test 2) are shown in Appendix C1. In the early time window, in almost all channels in which an EDL model outperformed its baseline, it also outperformed the probability model.

Late time window: Compared to the early time window, the EDL models seem to capture less additional variance in the ERP signal in the late time window, compared to the control models. Mainly the HL models – the models that learned the lexical tone category (categorisation models) or predicted the upcoming lexical tone (prediction models) – were more informative than their baseline in the late time window (except for categorisation model Cat-val-SD which is also found to be informative in two channels). In the late window, channels in which the EDL models were found to be more informative than their baselines were concentrated in the centroparietal-occipital electrodes Cz, CP1, CP2, Pz, P3, P4, PO3, PO4, O1, Oz, O2. In the late time window, none of the EDL models outperformed random models in channels F7, P7, P8, CP6,

832 T8, FC6, F8, and Fp2.

833 Appendix C1 shows the comparison against the probability model (Test 2). Although
834 several EDL models outperformed their *baselines* in the centroparietal-occipital elec-
835 trodes (Figure 7), they rarely outperformed the *probability model* in the late window
836 (Appendix C1). Only a few channels remain for Cat-diff-HL. This is in contrast to the
837 early time window, in which the informative EDL models generally outperformed the
838 probability model. This suggests that either statistical effects emerge later after stimu-
839 lus onset and that therefore, EDL-derived models are unlikely to be more informative
840 the probability model, or that EDL-derived models perform less well in the late time
841 window generally.

842 Results are also shown in Table 4. Due to space limitations Table 4 only shows
843 the models that beat the random models the most often in at least one channel. The
844 results for all models are presented in Appendix B1. The numbers shown in Table 4
845 represent the proportion of random models outperformed by each EDL model. The
846 scores were included in the table if the EDL models outperformed more than 50% of
847 the random models in that channel and time window; if not, the cell is left empty. As
848 these proportions of wins are always measured against the same 5000 random models,
849 higher proportions indicate numerically better performance; proportions are in that
850 sense comparable. However, proportion differences between models were not tested
851 statistically. Also note that the proportion of wins only measures *how many* of the
852 random models were beaten by the EDL model, not *how much better* the EDL model
853 was than the random models. That is, the proportion measure does not take mean
854 R^2 scores into account. Shown in bold are the models that beat the random model
855 most often for each channel and time window for each learning task: categorisation or
856 prediction.

857 7.1. Interpretation of the EDL simulations

858 The finding that some of the EDL models are more informative than their baselines
859 demonstrates that the EDL simulations captured variation in the signal resulting from
860 learning or prediction error, rather than merely from basic auditory processing of the
861 stimulus and rather than only to static properties of the stimuli. In addition, several
862 EDL models also outperformed the probability model, especially in the early time
863 window, indicating that these EDL models are also more informative about the ERP
864 signal than a model based on stimulus probability.

865 There is a substantial amount of overlap in the scalp distributions for the different
866 EDL models, as shown in Figure 7. It is possible that this overlap indicates that these
867 models (partly) capture the same patterns in the ERP signal. However, this is not nec-
868 essarily the case: the ERP signal is rich and variable, and the EDL models may capture
869 different aspects of the signal even within the same channel. To investigate whether
870 these overlapping scalp distributions were due to overlap in EDL activation patterns,
871 we analysed the similarity in activation patterns of the EDL models. Figure 8 shows
872 the correlation between the EDL activation patterns based on the stimuli presented to
873 a single participant. Note that although the activation values were calculated for each
874 participant individually, the correlations between activation values from various EDL
875 models are nearly identical between all participants (only for the 'val' models, small
876 differences are to be expected; note that the fact that the EDL input is nearly identical
877 does not mean the fitted TRFs have to be). The correlation matrix shows two groups
878 of EDL models with similar activation patterns. The first group are the models that

Table 4. Proportion of random models beaten for selected* EDL models, for channel/time windows combinations for which at least one EDL model beat its baseline model. Bonferroni corrected alpha level for 64 (32 channels $\times$ 2 time windows) comparisons, values only shown if $p < 0.00078125$. Boldface text indicates the best score for the electrode channel for each task, categorisation (Cat) or prediction (Pred). Italics indicate that a particular model beat its baseline model for that channel and time window. *Due to space limitations, this table presents only EDL models which beat the random models the most times in at least one channel and time window. For the full list, see Appendix B1.

Time window 0–350ms							
Channel	Model						
	Cat. Models			Pred. Models			
	diff-HL	diff-SD	val-SD	bg-HL	diff-HL	diff-SD	val-HL
F7	0.55	0.67	0.88	0.88	<i>0.79</i>	0.56	<i>0.78</i>
FC5	<i>0.61</i>	0.62	0.89	0.87	<i>0.78</i>	0.61	<i>0.83</i>
T7	0.51	0.63	0.69	0.68	<i>0.64</i>	0.59	<i>0.64</i>
C3	0.61	0.79	0.83	0.84	<i>0.77</i>	0.61	<i>0.82</i>
CP1	0.55	0.68	0.75	0.75	<i>0.74</i>	0.59	<i>0.73</i>
CP5	0.52	0.72	0.70	0.70	<i>0.67</i>	0.55	<i>0.64</i>
P3	<i>0.64</i>	0.69	0.67	0.68	<i>0.67</i>	0.53	<i>0.66</i>
Pz	<i>0.65</i>	0.62	0.65	<i>0.64</i>	0.66		<i>0.64</i>
PO3	<i>0.64</i>	0.66	0.65	0.64	<i>0.59</i>		<i>0.60</i>
Oz	0.66	0.60	0.57	0.57			<i>0.51</i>
O2	0.65	0.62	0.63	0.60			0.55
P4	0.56	0.67	0.67	<i>0.72</i>	<i>0.74</i>	0.55	0.76
CP2	0.59	0.74	0.70	<i>0.74</i>	0.78	0.56	<i>0.77</i>
T8	<i>0.57</i>	0.68	0.81	<i>0.86</i>	<i>0.81</i>	0.87	<i>0.84</i>
FC6	<i>0.62</i>	0.82	0.94	0.92	<i>0.89</i>	0.76	<i>0.89</i>
F8	<i>0.69</i>	0.68	0.86	0.84	<i>0.75</i>	0.76	<i>0.81</i>
Time window 250–600ms							
Channel	Model						
	Cat. Models			Pred. Models			
	diff-HL	diff-SD	val-SD	bg-HL	diff-HL	diff-SD	val-HL
CP1	<i>0.58</i>		0.59	<i>0.59</i>	0.51	0.64	0.53
P3	0.66	0.52	0.61	0.64	<i>0.60</i>	0.63	<i>0.62</i>
Pz	0.72		0.60	0.63	<i>0.52</i>	0.62	<i>0.57</i>
PO3	0.69	0.52	0.69	0.68	<i>0.55</i>	0.62	<i>0.60</i>
O1	<i>0.69</i>	0.56	0.73	0.73	<i>0.59</i>	0.62	<i>0.62</i>
Oz	0.68		0.63	0.62	<i>0.54</i>		<i>0.55</i>
O2	0.67	<i>0.57</i>	<i>0.66</i>	0.62	<i>0.55</i>		<i>0.54</i>
PO4	<i>0.66</i>	0.60	0.66	0.65	<i>0.63</i>	0.59	<i>0.62</i>
P4	<i>0.59</i>	0.56	0.66	0.72	<i>0.67</i>	0.65	<i>0.67</i>
CP2	<i>0.57</i>	0.55	0.59	0.66	<i>0.62</i>	0.65	<i>0.61</i>
Cz	<i>0.56</i>	0.53	0.57	<i>0.64</i>	0.55	0.70	0.53

a. Cat. Models:

b. Pred. Models:

Figure 7. Channel/time windows combinations for which EDL-derived models were more informative than their respective baseline models (for the models ending in -SD and -HL) or the probability model (for the models ending in -VAL), and were significantly more likely to be the model that explains more variance compared to a random model *Top row a)* shows the categorization models, *bottom row b)* shows the prediction models.

Figure 8. Matrix of Spearman's rho rank correlation coefficients representing the correlation between the activation values of the EDL simulations, ranging between -1 (blue) and 1 (red). The bold faced labels mark EDL models significantly more informative than their baseline (Test 1 or 2) and significantly more than 50% of the random models (Test 3).

predict the pitch value for the next stimulus, namely Pred-bg-VAL, Pred-diff-VAL, and Pred-val-VAL. Their correlations range between 0.83 and 0.91. The activation values of these three models are included in Appendix D, Figure D3. It is interesting that the val models were informative about the ERPs. This result is somewhat surprising given that these models predict the specific pitch value, yet participants usually did not discriminate the pitch values in an overt behavioural task (Nixon et al., 2018). It is possible that the ERPs pick up on a level of processing that is more sensitive than the behavioural discrimination task.

The second group are the models that predict the tone (high vs low) of the next stimulus, namely Pred-bg-HL, Pred-diff-HL, and Pred-val-HL. Their correlations range between 0.78 and 0.86. The activation values of these three models are included in Appendix D, Figure D1. In addition, two of the categorisation models – Cat-pos-HL and Cat-val-SD (Appendix D, Figure D2) – are strongly correlated with these prediction models. All these models have in common that they show lower activation values for the deviant stimulus than for the standards, and that the activation values of the standards show a strong increase over the course of each block. The model Cat-val-SD shows a similar pattern as the group of prediction models, even though this model simulates the learning of categorising an incoming pitch value as standard or deviant, rather than learning to predict whether the next stimulus is a high or low tone. In the odd blocks, the lower pitch values are associated with the standard stimuli and the

higher pitch values with the deviant stimuli. In the even blocks, the learner needs to switch this mapping and learn that the lower pitch values are now associated with the deviant stimuli and the higher pitch values with the standard stimuli. Thus, the pitch value *cues* and the standard vs deviant stimulus as learning *outcomes* captures the switching between blocks, which is also captured by the high vs low tone outcomes.

An important difference between this categorisation model and a prediction model such as Pred-bg-HL is that this Cat-val-SD model only categorises the current incoming stimulus, but cannot predict whether the next stimulus is going to be a standard or deviant. In other words, this model does not use the *sequence* of incoming sounds to predict the next stimulus – which we consider a highly plausible cognitive task in this experiment. This difference is visible in the trajectory of activation of the deviant stimulus over the course of the block, which increases for the categorisation model, but shows a ‘u-shape’ (decreasing-increasing) for the prediction models as a result of cue competition. This may be why the Pred-bg-HL model was informative over a larger number of electrodes and time windows than Cat-val-SD. However, our approach does not directly compare the different EDL models and, as a result, we cannot draw conclusions about which of the EDL model is most informative and whether the difference in explained variance would be significant. We consider the model Pred-bg-HL the most plausible from this group of models, because it is the only model that uses the sequence of stimuli as cues.

Two other models are worth mentioning: Cat-diff-HL and Cat-diff-SD. These two models show a correlation close to zero (-0.05), indicating that their patterns are not similar. In addition, these models do not show strong correlations with the other significant models (at most 0.51). Appendix D, Figure D2 shows the activation values for these two EDL models. These two models capture different aspects of the learning in this task from the informative prediction models described before. Both EDL models use the difference in pitch values between the preceding and current stimulus as cues, capturing the transition between sequential stimuli. When the difference in pitch is large, the incoming stimulus is likely a deviant stimulus, or the start of a new sequence of stimuli. When the difference is small, the incoming stimulus is likely to be another standard stimulus. As such, the EDL simulations show different activation patterns for the first stimulus, the last stimulus, and the other standards (i.e., stimuli 2–4). The two models learn to expect different outcome stimuli. On the one hand, model *Cat-diff-HL* learns to categorise high and low tones, and therefore also captures the switching of associations between the odd and even blocks: A large difference between two sequential pitch values (i.e., a low tone followed by a high tone, and vice versa) provides a clue to classify the incoming pitch value as a high or low tone, which is consistent over all blocks. On the other hand, a small difference between two sequential pitch values (i.e., two low tones with slightly different pitch values or two high tones with slightly different pitch values) does not provide a consistent cue for classifying the incoming pitch value as high or low tone, because its association to the tone is switching between blocks. A prominent difference in comparison with the other models discussed in this section is that the activation values for the deviant tone (i.e., stimulus 5) are in the same range as the activation values of the other standard stimuli (i.e., stimuli 2–4). On the other hand, model *Cat-diff-SD* learns to categorise standard and deviant stimuli based on the same cues as the model Cat-diff-HL, resulting in the opposite effect in the activation pattern: A small difference between two sequential pitch values (i.e., two low tones with slightly different pitch values or two high tones with slightly different pitch values) provides a reliable clue to classify the incoming pitch value as a standard stimulus, which is consistent over all blocks. In contrast, a large difference between two

sequential pitch values (i.e., a low tone followed by a high tone, and vice versa) does not provide a consistent cue for classifying the incoming pitch value as standard or deviant, because it differs per block whether a large negative difference is associated with a new sequence (i.e., the first standard) or with the deviant stimulus, and vice versa for a large positive difference.

Interestingly, the EDL models Pred-bg-HL, Pred-diff-HL, and Pred-val-HL are found to be informative in the same centroparietal electrodes as the models Cat-diff-HL and Cat-pos-HL in the later time window (see Figure 7), although they predict different activation patterns. This may be caused by these different models all capturing a similar aspect of the ERP response in these electrodes, such as the strong increase in activation for the standard stimuli 2–4, or the difference in activation between the first stimulus (i.e., stimulus 1) and last stimulus (stimulus 5, deviant). Alternative explanations may be that *different participants show different ERP patterns* that are captured by these different EDL models, or that the different EDL models capture variation at *different times* within the late time window. To gain more insight into how the EDL models are related to the ERP data, we will inspect the fitted TRFs.

7.2. Visualising the TRFs: Relation between EDL simulations and ERP waveforms

Figure 9 illustrates the TRFs that relate the activation patterns of EDL model Pred-bg-HL to the ERP measured in channel FC6 and Pz. Figure 9a (top left) shows the TRF for FC6 in the early time window between 0 – 350 ms after stimulus onset and Figure 9b (top right) shows FC6 in the late time window 250 – 600 ms after stimulus onset. The black solid line shows the estimated signal fitted by the constant dimension, which contains a uniformly sized spike for every incoming stimulus. The thick red line shows the estimated signal fitted by the variable dimension, which contains for each stimulus a variable sized spike. The size of the spike is determined by the activation value generated by the EDL model Pred-bg-HL on each trial. The scalp plots are shown for the early time window (top) and late time window (bottom).

As explained in Section 6.1.1, the constant dimension represents the estimated ERP waveform for stimuli with an activation value of 0.0 and the variable dimension represents the additive effect for different activation values: For stimuli with an activation value of 1.0, the ERP signal is represented by the sum of the constant and variable dimension (the dotted line in Figure 9). Thus, the variable dimension captures the difference between ERPs elicited by an activation of 1.0 and an activation of 0.0. For all intermediate values of activation, the variable dimension is scaled with the activation value to create a linear interpolation between the constant and variable dimension. Thus, an important assumption of this approach is that the differences in ERPs are linearly related to the differences in activation values.

In channel FC6, the difference in ERP amplitude as activation value increases is predicted to peak around 150 ms after stimulus onset (indicated by the yellow-marked time window in Figure 9a). The scalp plot shows the distribution of the differences in this time window over the scalp. Figure 9b shows the TRF for the same model and channel in the late time window ranging 250–600 ms after stimulus onset. The modulating effect of the activation values on the estimated ERP signal is much smaller in the late compared to the early time window. This is not surprising, because model Pred-bg-HL did not significantly outperform the baseline models in channel FC6 in the late time window (see Figure 7). Figure 9 also shows the TRFs for model Pred-bg-HL

TRFs EDL model Pred-bg-HL

Figure 9. TRFs fitting the activations of EDL model Pred-bg-HL to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing an activation value 0.0), the red thick lines show the variable dimension (representing difference between the activation values 1.0 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the activation value 1.0).

Panels a and c: TRFs early time window. The difference is predicted to peak around 0.150 s after stimulus onset, indicated by the yellow time window. *Panels b and d:* TRFs late time window. The EDL model only beats its baseline in channel Pz, but not in FC6. The scalp plot in *panel a* shows the distribution of the difference in the early, yellow-marked time window. The scalp plot in *panel d* shows the distribution of the difference in the later yellow-marked time window.

Figure 10. Relation between EDL activation values and the fitted TRF. *Left:* Activation pattern generated by model Pred-bg-HL (Section 5.2), with each learning event on the x-axis and the activation on the y-axis. For interpretation, we indicated the activation values 0.15 and 0.85 with blue lines. *Right:* TRF fitting the activation pattern generated by model Pred-bg-HL to the ERP measured in channel FC6, with on the x-axis the time in seconds, and on the y-axis the TRF amplitude (arbitrary value). The blue lines represent the estimated signals for activation values of 0.15 (solid line) and 0.85 (dash-dot line). The grey thick line shows the difference the two blue lines and equals $(0.15 - 0.85) \times \text{variable dimension}$ (see Figure 9a).

related to channel Pz, in which the model outperformed the baseline models in both the early (Figure 9c) and late time windows (Figure 9d). In the early time window, the timing of the peak in Pz is similar to the timing in FC6, around 150 ms after stimulus onset. In the late time window, the peak emerges around 450 ms and peaks around 525 ms after stimulus onset.

Figure 10 illustrates how the TRFs relate to the activation values in the EDL simulations. Each dot in the simulation figure (left) represents the activation on that trial; that is, the estimate of how expected the stimulus is (in this case, the expectation that the next stimulus will be a high or low tone) based on the cues (in this case, a series of bigram cues). The TRFs (right) provide an estimate of how the EDL activation values modulate the ERP signal. In EDL model Pred-bg-HL, the deviant stimulus (i.e., stimulus 5 in each sequence of sounds) generally has a low activation value (median: 0.15, interquartile range (IQR): 0.08–0.23), whereas the standard stimuli (i.e., stimuli 1–4) generally have higher activation values (median: 0.82, IQR: 0.73–0.85).

However, the relation between the stimulus characteristics and the activation values is different for each EDL model. The TRFs of all EDL models have in common that the constant dimension always implements the response to the occurrence of a sound, and the variable dimension implements the expectation (activation) of the incoming sound. We can compare the TRFs of the EDL models by comparing the variable dimension, as this dimension estimates how the activation modulates the ERP signal. Figure 11a compares the signals fitted by the variable dimensions of the most informative EDL models. Interestingly, the models with correlated activation patterns (i.e., Pred-bg-HL, Pred-val-HL, Pred-diff-HL, Cat-pos-HL and Cat-val-SD, see Figure 8) show a similar TRF, starting around 50ms and peaking around 150 ms after stimulus onset. However, the TRF of EDL model Cat-diff-HL (red dotted line) looks different, with a double peak between 75 ms and around 150 ms after stimulus onset.

To further investigate how to interpret this series of models, we examined how the models capture differences in the response to standards and deviants. Although not all simulations used standard-deviant information in the input representations, the oddball design – i.e. a series of four tones, followed by a change of tone on the fifth stimulus – was one of the most prominent aspects of the experiment design. The ERP

Figure 11. Evaluating TRF predictions. *Panel a:* Comparing the variable dimension of the TRFs for a group of EDL models with overlapping scalp distributions, namely Pred-bg-HL, Pred-val-HL, Pred-diff-HL, Cat-val-SD, and Cat-diff-HL. *Panel b:* The median activations for standard (grey bars) and deviant (black bars) stimuli, averaged over the complete experiment. *Panel c:* Estimated difference in ERPs (i.e., scaled variable dimension) between trials with the same activation as the median of standards (see panel b) and trials with the same activation as the median of deviants (see panel b) for EDL models Pred-bg-HL, Pred-val-HL, Pred-diff-HL, and Cat-val-SD. In addition, the thick red line shows the estimated difference between standards and deviants, as modelled by the SD baseline (i.e., unscaled constant dimension of SD model).

data also show different responses to standards and deviants (Appendix A). Therefore, we expect that at least some of the models might capture a difference between standard and deviant stimuli.

Firstly, we calculated the median activation for standards and deviants for each of the models. For the models with correlated activation patterns, Figure 11b shows higher activation values for the standards (range: 0.67–0.87) than for the deviants (range: 0.15–0.35). But for model Cat-diff-HL the median activation values for standards and deviants are the same (0.83 and 0.85 respectively). This means that, whereas the other EDL models have different activation values which predict a difference in ERPs between standards and deviants on average, model Cat-diff-HL does not predict any difference between standards and deviants (see also Appendix D, top left panel of Figure D2, for the trial-by-trial predictions for Cat-diff-HL).

Secondly, we investigated how the different EDL models predicted the ERP waveform and how these predicted ERP waveforms compare to a model that *only* used standards and deviants, namely the Standard-Deviant (SD) baseline model. Using the median activations in Figure 11b, we calculated the *difference* in median activations between standards and deviants for each EDL model. This difference in median activations was then used to produce a difference TRF that shows how the predicted ERP waveform changes between these activation values (the median activation value for standards and deviants, respectively). The difference TRF was calculated by scaling the variable TRF dimension by the difference in median activation. The difference TRFs are shown in Figure 11c for the same EDL models as listed above. This difference TRF tells us two things. If the difference TRF of the EDL model is similar to the variable TRF of the SD baseline model, this suggests that the EDL model is able to capture differences between standards and deviants. On the other hand, any differences compared to the SD baseline model suggest that the EDL model is capturing additional effects on top of the difference between standards and deviants. Therefore, Figure 11c also shows the (unscaled) variable TRF dimension for the SD baseline for comparison, which captures the estimated difference in ERP between standards and deviants (thick red line). Note that the estimate for model Cat-diff-HL is excluded,

1057 as this would be a straight line around 0, because the difference in median activation,
1058 which scales the variable TRF dimension, is 0.02.

1059 Interestingly, the TRF of the SD baseline model estimates that the difference be-
1060 tween standards and deviants starts around 100ms after stimulus onset, but the TRFs
1061 of the EDL models suggest that the difference starts earlier, around 50ms after stim-
1062 ulus onset. These results show that the EDL models do capture a different response
1063 between standard and deviant stimuli, but do not only capture the difference between
1064 standards and deviants. Instead, they capture *how expected* a stimulus is. On some
1065 trials, this will correlate with the difference between standards and deviants, but this
1066 is not always the case. The expectation of what will follow from the input cues changes
1067 over the course of the experiment, especially within the blocks. So both standards and
1068 deviants have both high- and low-activation trials (see Figure D1).

1069 Note that this effect of changing expectations over the course of each block is also
1070 captured by EDL model Cat-diff-HL. This model does not capture a difference between
1071 standards and deviants, but does show an early difference between high and low acti-
1072 vations in the estimated ERP signals in Figure 11a. What is interesting is that, since
1073 Cat-diff-HL does not pick up on differences between standards and deviants, this Cat-
1074 diff-HL model allows us tease apart a certain neural response pattern from that of the
1075 SD baseline model. When separated out, this pattern of results suggests that the EDL
1076 models are capturing two responses: an earlier response (50 – 200 ms after stimulus
1077 onset, as captured by EDL model Cat-diff-HL) and a later response (100 – 300 ms after
1078 stimulus onset, as captured by the SD baseline model). The EDL models Pred-bg-HL,
1079 Pred-val-HL, Pred-diff-HL, and Cat-val-SD capture both effects with their activation
1080 values. Taken together, we argue that the strength of participants’ expectations about
1081 the outcome stimulus is what modulates the ERP signal, which changes trial-by-trial,
1082 not just between standards and deviants.

1083 Appendix E provides a more extensive overview of the TRFs of the HL and SD
1084 baseline models, the probability model and the EDL models (Figures E5, E6 and
1085 E8). Based on the inspection of the TRFs we conclude that the EDL models that are
1086 found to be informative in the same centroparietal electrodes in the early time window
1087 (Pred-bg-HL, Pred-val-HL, Pred-diff-HL, Cat-val-SD, and Cat-diff-HL) partly capture
1088 the same patterns in the ERP data (stimuli 2–4), but also show differences (stimuli 1
1089 and 5). First, all EDL models that are found to be informative in multiple electrodes
1090 show a sharp increase in activations for stimuli 2–4 over the course of each block. The
1091 cues associated with these stimuli are informative for whether the standard stimulus
1092 is a high or low tone, but this switches every block and therefore the associations
1093 need to be updated at the start of each block. The EDL models explain the precise
1094 dynamics differently. Second, these EDL models also seem to capture different aspects
1095 of the ERP data. The EDL model Cat-diff-HL shows a qualitatively different TRF
1096 in comparison with the other EDL models, because it does not capture the difference
1097 between standards and deviants. The reason is that model Cat-diff-HL predicts the
1098 activation values for stimulus 5 in the same range as the the activation values for
1099 stimulus 2–4, whereas the other models predict lower activation values for stimulus 5
1100 than for stimuli 1–4.

1101 In the present experiment, we cannot say with certainty exactly what underlies these
1102 two different temporal patterns in the neural response. However, there are a number
1103 of possibilities that we believe might explain this pattern. Firstly, it might be that
1104 the early effect captured by the Cat-diff-HL model reflects differences in expectation,
1105 while the later effect, captured by the SD baseline model, reflects detection of large
1106 pitch differences (i.e. the switch between standard and deviant). The cluster of other

Figure 12. Grand averages in channel FC6 of the lowest 10% (blue lines) and highest 10% (red lines) of the activation values per participant with the error bars ± 1 standard error of the participant means. The grey lines show the difference between the averages of the trials with the lowest and highest activation values.

informative models (i.e., Pred-bg-HL, Pred-val-HL, Pred-diff-HL, and Cat-val-SD) captures both of these effects. Another possibility is that the difference in timing reflects a change over the course of the block. In the Cat-diff-HL model, activation increases over the block for all stimuli, including the deviants. So it is possible that the early effect picks up on a more general development that, as participants become more familiar with the pattern in a particular block, the ERP responses occur earlier.

Further work is needed to tease apart these possibilities. However, it is worth noting that disentangling the timing of effects was made possible by having a model, Cat-diff-HL, that was partly uncorrelated with the other models (see Figure 8). By generating a variety of EDL simulations and combining the EDL modelling with additional correlation analyses we were able to capture different parts of the ERP response signal. We see this as a fruitful path for future studies working with ERPs, which are a notoriously complex type of data.

As a final check we verified whether the patterns detected by the TRFs are also visible in the data. In order to do that, we added the activation values for EDL model Pred-bg-HL to the data. Note that for each individual experiment (i.e., a series of stimuli presented to an individual participant) a separate network was trained, so that for each unique participant-trial combination an activation value was calculated based on the cues and outcomes related to the presented stimulus and the current state of the network. To compare the TRFs to the data, we first calculated the 10% and 90% quantiles of the activation values per participant (mean values of 0.147 and 0.874 respectively). Based on these values, we selected the trials with activation values in the lowest 10% ($n=2429$) and the highest 10% ($n=2429$). Figure 12 shows the averages for the lowest (blue) and highest (red) quantiles and their difference (thin grey line). The patterns in the data are very similar to the TRF estimates in Figures 9a and b. The TRF variable dimension, however, seems to peak slightly earlier (0.150 s after stimulus onset) than the difference in the data (180 ms after stimulus onset). Note that the TRF variable dimension estimates the difference between activation values 1.0 and 0.0, whereas Figure 12 visualizes the difference between the activation values

1136 lower than 0.15 and higher than 0.87. To summarise, the EDL simulations predict how
1137 expected the outcome stimulus is for the participants in the experiment, based on stim-
1138 ulus characteristics and the state of the learning network. The TRFs are used to link
1139 these activation values to the ERP signal that was measured from participants as they
1140 were presented with stimuli, and estimate how the ERP signal changes with increasing
1141 activation. Therefore, we can consider TRFs to be a viable method for analysing ERP
1142 data by a continuous variable, such as EDL activation values. As the TRFs do not
1143 provide information about statistical significance, we used a strict procedure to deter-
1144 mine whether the fitted TRFs explain more variance of the ERP signal than baseline
1145 models that aggregate the data into categories such as high vs low tone and standard
1146 vs deviant stimuli, or stimulus frequency (i.e., the probability model).

1147 8. Discussion

1148 When listeners encounter speech sounds from an unfamiliar language, they often have
1149 difficulty discriminating them. However, discrimination can improve in the absence of
1150 explicit instruction, through implicit learning⁶. Recent evidence suggests that implicit
1151 learning occurs through a process of prediction and prediction error. The present study
1152 sought to determine whether evidence for such error-driven learning emerges in partic-
1153 ipants' trial-by-trial ERP signals as they listen to a sequence of lexical tones sampled
1154 from a bimodal pitch distribution. Below, we first discuss the results with the respect
1155 to our three research questions. We then discuss some implications for learning more
1156 generally, as well as our thoughts on the benefits of our method for ERP research.

1157 8.1. Trial-by-trial learning

1158 The first question we aimed to investigate in the present study was whether we could
1159 find evidence of trial-by-trial learning in the ERP signal. Error-driven learning simu-
1160 lations were used to obtain trial-by-trial estimates of participants' level of expectation
1161 of each incoming stimulus. These expectation estimates (activation values) were then
1162 used as input to the TRF modelling procedure, which generated estimates of the trial-
1163 by-trial ERP waveforms in an early and a late time window. Rather than comparing
1164 discrete stimulus conditions, such as for example, standard vs. deviant or expected vs.
1165 unexpected stimuli, our EDL models predict gradient differences in the ERP depending
1166 on *how expected* the incoming stimulus is on each trial.

1167 The TRF models derived from the EDL activations were compared to baseline mod-
1168 els, with an additional safety check against a set of random models. Several EDL models
1169 were found to be more informative than their baselines. This finding shows that the
1170 EDL simulations captured trial-by-trial changes in expectation that were predictive of
1171 brain activity. As predicted, ERP amplitude increased with decreasing activation. In
1172 addition, several EDL models were also more informative than the probability model.
1173 Particularly in the early time window, the EDL models outperformed the probability
1174 model in several channels. This finding suggests that, at least in the early time window,
1175 the variation in the ERP signal captured by our expectation estimates does not result
1176 from the statistical distribution of the stimuli, but from error-driven learning.

⁶We use the term 'implicit learning' in the broad sense here, to refer to learning that occurs implicitly, rather than the somewhat more specific research field/paradigm by this name.

1177 8.2. Learning representations and cognitive tasks

1178 The second question we aimed to investigate was what participants learn in this exper-
 1179 iment. We started with the assumption that participants could potentially be learning
 1180 on multiple levels simultaneously, as well as learning from potentially any discrim-
 1181 inable cues. We designed simulations to model two cognitive tasks, categorisation and
 1182 predicting the upcoming stimulus, with a variety of cues for estimating one of three
 1183 outcome types: lexical tone (high vs. low), standard vs deviant or the specific pitch
 1184 value (i.e. the pitch continuum step). Regarding this question, in some respects we
 1185 cannot draw strong conclusions from the present study. Several EDL models were in-
 1186 formative about the ERP signal and there was a substantial amount of overlap in the
 1187 estimates of the different EDL simulations (see Figure 8). Since we did not formally
 1188 compare the EDL models to each other, we cannot draw conclusions about which of
 1189 the informative models are most informative.

1190 However, we do note some patterns that are common between the informative mod-
 1191 els. Most of the informative EDL models predicted a gradual increase in expectation
 1192 for the standards (stimuli 1-4) over the course of each block. This increase in expec-
 1193 tation of the standard stimuli was captured by both the categorisation models (e.g.
 1194 Cat-val-SD and Cat-diff-HL) and the prediction models (Pred-bg-HL, Pred-diff-HL,
 1195 Pred-val-HL). Therefore, we cannot determine on the basis of this experiment whether
 1196 learning was based on categorisation of the current stimulus or predicting the upcom-
 1197 ing stimulus or both. However, the results do point to trial-by-trial learning that led
 1198 to an increasing expectation of the stimuli over the course of each block. Many of the
 1199 informative EDL models also predicted *unlearning*, i.e. a decrease in expectation, of
 1200 the deviant (stimulus 5) over the course of the block, particularly the prediction models
 1201 (Pred-bg-HL, Pred-diff-HL, Pred-val-HL).

1202 The present experiment used a version of the oddball paradigm, in which, within
 1203 each block, one stimulus is frequent and the other is comparatively rare. The founda-
 1204 tion of the design of this paradigm is the assumption that the frequent stimulus will be
 1205 expected and the rare stimulus will be unexpected. A wealth of literature (e.g. Frost
 1206 et al., 2016; Haenschel et al., 2005; Kopp & Wolff, 2000; Polich, 2011; Rushby et al.,
 1207 2005) has shown that examining differences between these frequent and rare stimu-
 1208 lus types gives us insight into the neural effects of expectation. However, the present
 1209 results demonstrate that the effect is not categorical, but evolves over the course of
 1210 the experiment and especially over the course of each block, as expectations develop.
 1211 A consequence is that there will be cases where the standard stimulus (usually seen
 1212 as an expected stimulus) is unexpected. And at least some of the EDL models, such
 1213 as Pred-bg-HL, also predict that there will be the opposite case, trials on which the
 1214 deviant stimuli are expected.

1215 Indeed, while researchers typically conceptualise the oddball stimuli as standards
 1216 and deviants, the participants in the experiment do not have direct access to these cat-
 1217 egories. The perceptual system only receives sensory information, such as the acoustic
 1218 properties of the stimulus. Expectations can only develop over time, as information
 1219 becomes available. The EDL modelling approach presented here allows us to model
 1220 the overall difference in expectations between the frequent standard stimuli and the
 1221 infrequent deviant stimuli, even when the models did not have access to these cat-
 1222 egories (as in all the HL models). Moreover, our EDL models not only capture the
 1223 difference between standards and deviants, but also capture the gradual development
 1224 of these expectations over time.

1225 An interesting result is that the models predicting the upcoming pitch value (the

val models, a subcategory of the prediction models) performed quite well in the early time window. In the present experiment, the pitch differences between continuum steps were very small. In fact, an offline test showed they were too small for a difference to be detected most of the time, even two steps apart on the continuum (Nixon et al., 2018). So it was interesting that models predicting the upcoming pitch value performed well. It is possible that these models pick up on perceptual sensitivity that is missed in the behavioural discrimination tasks, possibly even below the level of awareness. It should be noted that these models did not have the initial comparison against a baseline model, so the criteria for these val models were less strict than the other EDL model types. Nevertheless, they were found to be more informative than the probability models and outperformed the random models.

8.3. ERP components, timing and scalp distribution

The third question we aimed to investigate was the timing, location and shape of the ERP waveforms that are predicted by the trial-by-trial learning simulations. Generally speaking, evidence that the EDL models were more informative about the ERP response than the baseline models was found for the early time window, rather than for the late time window. In addition, we can draw some inferences based on the timing, polarity and scalp topography of the effects captured by our models. Both EDL types – the prediction simulations, such as Pred-bg-HL, which predict the upcoming stimulus and the categorisation simulation Cat-diff-HL, which uses pitch changes to categorise stimuli into high or low lexical tones – lead to TRF models that predict a more negative component starting around 50 ms and peaking around 150 ms after onset with decreasing activation estimates. That is, the more surprising the stimulus according to the EDL simulation, the greater the ERP amplitude. The timing, polarity and localisation of this early negative-going peak correspond to the mismatch negativity response (Näätänen et al., 1978).

In the later time window, the prediction model, Pred-bg-HL, captures a more positive signal for lower activation estimates, especially after 400 ms, at posterior and occipital electrodes. This is consistent with the P3a component (Kopp & Wolff, 2000), which has been found to increase in amplitude in response to the level of surprise evoked by a stimulus, including unattended stimuli. The timing and posterior localisation are consistent with the P3a (Polich, 1988, 2011; Snyder & Hillyard, 1976). This model was not more informative than the probability model, however.

Our models did not show evidence of predicting any effects akin to an N400, which is consistent with previous findings that the N400 is usually found in higher-level processing. Neither did we find evidence for effects comparable to error negativity (N^e /ERN) in any of the generated TRFs. The N^e is typically associated with response error, which may explain why it was not found in this passive listening task.

Overall, the pattern of ERPs over the scalp and over time suggests 1) an early MMN-like component, which increases the more surprising a stimulus is in terms of its categorisation as a standard or deviant stimulus and in terms of its predictability in the sequence and 2) a late positive P3a-like component, which increases the more surprising an upcoming stimulus is based on the previous sequence.

1269 8.4. *Implications for learning*

1270 Many studies have observed that the statistical structure of sensory or linguistic input
1271 can affect learning outcomes (Baldeweg, 2007; Frost et al., 2016; Maye & Gerken,
1272 2000; Maye et al., 2002; Nixon & Best, 2018; Nixon et al., 2016; Saffran et al., 1996;
1273 Trotter et al., 2019). The present study examined whether error-driven learning (EDL)
1274 could be the mechanism underlying such statistical effects. The results show that EDL
1275 simulations are able to predict variation in the ERP signal during learning. The ERP
1276 amplitude differed depending on how expected an incoming stimulus was, as predicted
1277 by the EDL activation measure.

1278 In the prediction task, neural activity was captured by a simulation that learned to
1279 predict upcoming lexical tones from a sequence of tones. In the categorisation task,
1280 neural activity was captured by a simulation that categorised pitch differences into
1281 lexical tones. Interestingly, despite the different input representations, these two mod-
1282 els made similar predictions for the frequent stimuli, the standards. In both cases,
1283 the simulations predicted a gradual increase in expectation over the block and surprise
1284 (low expectation) at the beginning of a new block. However, by comparing the TRFs of
1285 these models to the TRFs of the standard-deviant baseline model (Figure 11), we dis-
1286 covered two interesting findings. Firstly, the TRF of categorisation model (Cat-diff-HL)
1287 suggests an ERP waveform that is somewhat distinct from the other cluster of corre-
1288 lated models, with an earlier peak and inflexion. And secondly, the prediction models
1289 capture variance in the ERPs that overlaps with, but is distinct from the standard-
1290 deviant baseline model. This suggests the possibility that the categorisation model
1291 and the standard-deviant baseline model might be capturing two distinct processes,
1292 which are both captured by the prediction models. In any case, both types of models
1293 were able to capture evidence of trial-by-trial learning in the ERPs. Moreover, most
1294 of these models did not have standards and deviants as input to the simulations, and
1295 yet comparison of their TRFs to the standard-deviant baseline model suggests these
1296 EDL simulations were still able to capture variance in the ERP signal corresponding
1297 to differences in expectation between the standard and deviant stimuli.

1298 The results contribute to a growing literature suggesting that language is discrimi-
1299 native. For example, error-driven learning models have previously been used to model
1300 speech sound acquisition in the native language (Nixon & Tomaschek, 2020, 2021) or a
1301 non-native language (Nixon, 2018, 2020), as well as word learning (Ramscar & Baayen,
1302 2013; Ramscar et al., 2010), word segmentation (Baayen, Shaoul, Willits, & Ramscar,
1303 2016), morphology (Hoppe et al., 2020) and articulation (Tomaschek, Plag, Ernestus,
1304 & Baayen, 2021).

1305 Note that we did not formally compare these simulations to the other models and
1306 that weaker correlations with the ERP signal also do not necessarily indicate simula-
1307 tions are incorrect. Similarly, the fact that EDL simulations were often more informa-
1308 tive than overall statistics does not prove that overall statistics are not used at all; the
1309 probability model we used as a control model reflects a probability distribution over the
1310 whole learning phase. It is possible that after the learning phase, when participants
1311 have actually been exposed to the probability distribution, the probability model is
1312 more (and even most) informative of the ERP signal. It is possible that participants
1313 might slowly become more sensitive or less sensitive to the pitch continuum over the
1314 experiment (cf. Hoppe et al., 2022; Nixon & Best, 2018; Nixon et al., 2016), which
1315 might mean that different models capture the experiment better at different times. In
1316 the present study, investigating this possibility would have added too much complexity
1317 to the models. Therefore, we leave this question for future research.

1318 The present study sheds light on some divergent results in distributional and statis-
1319 tical learning studies. While many studies report effects of distribution type on learning
1320 (unimodal vs. bimodal; e.g. Maye et al., 2002), a number of recent studies have found
1321 that learning does not always follow the predictions of purely frequency-based statisti-
1322 cal learning. For example, Wanrooij et al. (2014) found differences in infants’ post-test
1323 behaviour after training with unimodal versus bimodal distributions, but no differences
1324 were found for adults. They argue that adults lose the ability to learn from statistical
1325 learning. Error-driven learning predicts this phenomenon, because the most learning
1326 is expected to occur when uncertainty is greatest. Since infants have much less prior
1327 learning than adults, perceptual input tends to be more surprising in general. As learn-
1328 ing occurs, the world becomes more predictable and there is less uncertainty left to
1329 drive learning. Secondly, it might be that adult participants use different information
1330 to what is being tested, because they have learned to pay attention to different cues or
1331 outcomes. That is, the actual cues and outcomes participants learn from might differ
1332 from those intended by the researchers.

1333 **8.5. TRF fitting**

1334 Our EDL simulations generated trial-by-trial estimates of listeners’ expectations about
1335 upcoming stimuli. Our results show that these estimates can be used to predict the
1336 brain activity of these listeners, represented by the amplitude of the ERP signal. This
1337 was made possible by combining our EDL simulations with the method of fitting TRFs.
1338 TRF fitting has been used previously to predict ERPs (Brodbeck et al., 2018; Brod-
1339 erick, Anderson, Di Liberto, Crosse, & Lalor, 2018); however, the present study is, to
1340 the best of our knowledge, the first to use TRF modelling to generate an ERP signal
1341 that changes dynamically over the course of the experiment, individually for each par-
1342 ticipant and each trial. The TRF fitting also allows us to investigate the timing and
1343 scalp distribution of the effects, discussed above.

1344 A second innovation of the present study in terms of the TRF modelling was that
1345 we used strict criteria to test whether the EDL model contributed to the fit of the
1346 TRF-convolved input signal, by estimating the information loss of baseline models, a
1347 probability model and models based on EDL simulations. Our modelling approach is
1348 useful for experimental paradigms in which no baseline or control *condition* is available;
1349 all ERP data is used to assess the learning process. Our results show that our EDL-
1350 derived estimates of the size of the spike (activation) in the input yield more informative
1351 TRFs than a baseline model spike (representing static properties of the stimulus), and
1352 in many cases also a probability model (representing the probability of the individual
1353 pitch stimuli). In addition, the sanity check against random models show that this is
1354 not because a better model is always possible, if one tries long enough. The fact that
1355 less (model, time window, electrode) combinations passed Test 3 than passed Test 1/2
1356 does not necessarily mean that random models are better than baseline models, but
1357 may very well reflect the limited power of the non-parametrized test against chance.
1358 Still, we argue the combination of tests used in the present study is valuable protection
1359 against spurious conclusions given the high (but unknown) degrees of freedom for both
1360 EDL simulations and TRF fitting.

1361 Our approach does not allow us to directly compare the EDL models against each
1362 other, because the EDL models are not considered independent. However, it is powerful
1363 enough to test twenty models at once, with a strong Bonferroni correction not elimi-
1364 nating all significance. Although the TRFs do not show which model fits best, they do

show for the models that predict the ERP signal *how* these models fit to the signal. In addition, our approach is novel in the strict control of the information explained by the EDL estimates alone. If we had only used an EDL-derived input signal, without the separate constant dimension, any significant fit might be (largely) explained by information provided by the time-locking of the spikes to the stimuli, making it impossible to determine the quality of the EDL simulation. This aspect of the modelling, which controls for the effect of the time-locking of spikes to any stimulus, is an improvement over previous studies that have used TRF modelling (see also Ahmed, 2021). Future studies that use TRF modelling could consider including a constant dimension to disentangle the effect of *any* stimulus from the particular predictor of interest under study.

8.6. Conclusion

In summary, the EDL simulations produced activation values that produced more informative models of the ERP signal than comparable models without EDL estimates. The extra information that allows for a better prediction of the ERP signal must thus be based on the error-driven learning predictions and is over and above changes in the ERP signal resulting from incoming auditory signal in general or static properties of the stimuli. In many cases, the EDL models also outperformed models based on distribution frequency.

Error-driven learning (EDL) simulations combined with temporal-response function (TRF) fitting allowed us to investigate the trial-by-trial effects of learning on ERPs. We were able to do this without a-priori assumptions about the ERP components. The EDL predictions successfully captured how trial-by-trial learning affects brain activity. In addition, the results suggest that learning may occur on multiple levels simultaneously. An innovation in our approach to TRF fitting enabled us to tease apart expectation and learning effects from mere acoustic processing and other effects on the ERPs. We propose that the combination of these two methods provides a promising approach to the investigation of neural processes underlying learning.

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1605 **Appendix A. EEG data**

1606 This section contains visualizations of the data.

Figure A1. Grand averages of the z-scores of the ERP data in FC6 (a) and Pz (b). ‘S: 1’ = first standard; ‘S: 2-4’ = standards, sounds 2, 3, 4; ‘D: 5’ = deviant, fifth sound.

Figure A2. Grand averages of the z-scores of the ERP data in FC6 (*top row*) and Pz (*bottom row*), for standards and deviants. Panels a and b show two (overlapping) analysis time windows. *Panel a*: Early time window from 0–0.35 s after sound onset. *Panel b*: Late time window from 0.25–0.6 s after sound onset.

Table B1. Proportion of random models beaten for each EDL model, in each time window and for each electrode selected in the previous step. Proportion of participants for whom the same comparison was also significant is given between brackets. Bonferroni corrected alpha levels for 64 (32 channels $\times$ 2 time windows) comparisons, values are only shown if $p < 0.00078125$. As this was never the case for model Cat-pos-SD, its (empty) column has been deleted. * Model Cat-val-HL never beat its baseline and thus is not considered further, but is left in for transparency.

Time window 0–350 ms														
Channel	Model													
	Cat-diff-HL	Cat-diff-SD	Cat-pos-HL	(Cat-val-HL*)	Cat-val-SD	Pred-bg-HL	Pred-bg-SD	Pred-bg-VAL	Pred-diff-HL	Pred-diff-SD	Pred-diff-VAL	Pred-val-HL	Pred-val-SD	Pred-val-VAL
F7	0.55 (0.6)	0.67 (0.8)	0.77 (0.8)		0.88 (1.0)	0.88 (1.0)	0.69 (0.8)	0.62 (0.6)	0.79 (0.8)	0.56 (0.5)	0.61 (0.6)	0.78 (0.8)	0.68 (0.8)	0.59 (0.6)
FC5	0.61 (0.7)	0.62 (0.5)	0.81 (0.9)		0.89 (0.9)	0.87 (0.9)	0.61 (0.6)	0.66 (0.8)	0.78 (0.8)	0.61 (0.6)	0.63 (0.6)	0.83 (0.9)	0.63 (0.6)	0.65 (0.6)
T7	0.51 (0.5)	0.63 (0.7)	0.63 (0.7)		0.69 (0.8)	0.68 (0.7)	0.67 (0.6)	0.60 (0.6)	0.64 (0.7)	0.59 (0.7)	0.63 (0.7)	0.64 (0.7)	0.59 (0.6)	0.65 (0.7)
C3	0.61 (0.6)	0.79 (0.8)	0.74 (0.8)		0.83 (0.9)	0.84 (0.9)	0.68 (0.7)	0.67 (0.7)	0.77 (0.8)	0.61 (0.6)	0.67 (0.7)	0.82 (0.8)	0.65 (0.6)	0.69 (0.8)
CP1	0.55 (0.5)	0.68 (0.7)	0.68 (0.7)		0.75 (0.8)	0.75 (0.8)	0.58 (0.6)	0.67 (0.8)	0.74 (0.8)	0.59 (0.6)	0.56 (0.6)	0.73 (0.8)	0.63 (0.6)	0.59 (0.6)
CP5	0.52 (0.4)	0.72 (0.8)	0.63 (0.6)		0.70 (0.8)	0.70 (0.8)	0.69 (0.8)	0.61 (0.6)	0.67 (0.7)	0.55 (0.6)	0.64 (0.8)	0.64 (0.6)	0.56 (0.6)	0.66 (0.7)
P3	0.64 (0.8)	0.69 (0.8)	0.64 (0.7)		0.67 (0.8)	0.68 (0.8)	0.61 (0.6)	0.60 (0.6)	0.67 (0.6)	0.53 (0.6)	0.53 (0.5)	0.66 (0.7)	0.57 (0.5)	0.53 (0.3)
Pz	0.65 (0.7)	0.62 (0.6)	0.63 (0.6)		0.65 (0.8)	0.64 (0.7)	0.58 (0.6)	0.57 (0.5)	0.66 (0.8)			0.64 (0.6)	0.55 (0.5)	
PO3	0.64 (0.6)	0.66 (0.7)	0.60 (0.5)		0.65 (0.8)	0.64 (0.8)	0.56 (0.6)	0.60 (0.6)	0.59 (0.6)			0.60 (0.6)	0.57 (0.5)	0.53 (0.6)
Oz	0.66 (0.6)	0.60 (0.6)	0.51 (0.4)		0.57 (0.6)	0.57 (0.6)		0.61 (0.6)				0.51 (0.4)		0.51 (0.4)
O2	0.65 (0.7)	0.62 (0.7)	0.52 (0.4)		0.63 (0.7)	0.60 (0.7)	0.56 (0.6)	0.54 (0.5)				0.55 (0.6)		
P4	0.56 (0.5)	0.67 (0.7)	0.69 (0.7)		0.67 (0.8)	0.72 (0.8)	0.60 (0.7)	0.61 (0.6)	0.74 (0.8)	0.55 (0.6)	0.53 (0.4)	0.76 (0.8)	0.58 (0.6)	0.55 (0.5)
CP2	0.59 (0.6)	0.74 (0.8)	0.72 (0.7)		0.70 (0.8)	0.74 (0.8)	0.61 (0.6)	0.62 (0.7)	0.78 (0.8)	0.56 (0.6)	0.56 (0.4)	0.77 (0.8)	0.59 (0.6)	0.53 (0.4)
T8	0.57 (0.4)	0.68 (0.6)	0.84 (0.9)	0.52 (0.5)	0.81 (0.9)	0.86 (0.9)	0.71 (0.6)	0.85 (0.9)	0.81 (0.9)	0.87 (0.9)	0.80 (0.9)	0.84 (0.9)	0.85 (0.9)	0.74 (0.7)
FC6	0.62 (0.6)	0.82 (0.9)	0.89 (0.9)		0.94 (1.0)	0.92 (1.0)	0.70 (0.7)	0.84 (0.9)	0.89 (0.9)	0.76 (0.9)	0.74 (0.7)	0.89 (0.9)	0.76 (0.9)	0.77 (0.8)
F8	0.69 (0.7)	0.68 (0.8)	0.76 (0.7)		0.86 (0.9)	0.84 (0.9)	0.67 (0.6)	0.84 (0.9)	0.75 (0.7)	0.76 (0.8)	0.73 (0.7)	0.81 (0.8)	0.64 (0.5)	0.76 (0.8)
Time window 250–600 ms														
Channel	Model													
	Cat-diff-HL	Cat-diff-SD	Cat-pos-HL	Cat-val-HL	Cat-val-SD	Pred-bg-HL	Pred-bg-SD	Pred-bg-VAL	Pred-diff-HL	Pred-diff-SD	Pred-diff-VAL	Pred-val-HL	Pred-val-SD	Pred-val-VAL
P3	0.66 (0.6)	0.52 (0.4)	0.62 (0.7)		0.61 (0.5)	0.64 (0.6)		0.62 (0.7)	0.60 (0.6)	0.63 (0.6)	0.61 (0.8)	0.62 (0.6)	0.59 (0.6)	0.60 (0.6)
Pz	0.72 (0.8)		0.58 (0.6)		0.60 (0.6)	0.63 (0.7)		0.63 (0.7)	0.52 (0.4)	0.62 (0.6)	0.59 (0.6)	0.57 (0.5)	0.56 (0.6)	0.57 (0.6)
PO3	0.69 (0.8)	0.52 (0.4)	0.62 (0.7)		0.69 (0.7)	0.68 (0.7)		0.67 (0.8)	0.55 (0.6)	0.62 (0.6)	0.62 (0.6)	0.60 (0.6)	0.61 (0.6)	0.64 (0.7)
O1	0.69 (0.7)	0.56 (0.5)	0.65 (0.8)		0.73 (0.8)	0.73 (0.8)		0.65 (0.7)	0.59 (0.6)	0.62 (0.6)	0.58 (0.7)	0.62 (0.6)	0.64 (0.6)	0.58 (0.6)
Oz	0.68 (0.7)		0.56 (0.6)		0.63 (0.8)	0.62 (0.6)		0.56 (0.6)	0.54 (0.6)		0.59 (0.6)	0.55 (0.6)	0.58 (0.5)	0.59 (0.8)
O2	0.67 (0.8)	0.57 (0.5)	0.59 (0.6)		0.66 (0.7)	0.62 (0.6)		0.51 (0.4)	0.55 (0.5)		0.57 (0.6)	0.54 (0.5)		0.52 (0.5)
PO4	0.66 (0.8)	0.60 (0.6)	0.65 (0.8)		0.66 (0.8)	0.65 (0.7)	0.56 (0.5)	0.62 (0.7)	0.63 (0.7)	0.59 (0.6)	0.59 (0.6)	0.62 (0.6)	0.61 (0.6)	0.63 (0.7)

1608 Appendix C. Comparison against the Probability model

1609 In Test 2, the EDL models were compared against the Probability model. Note that
 1610 the Probability model is the baseline model for the EDL models with the ‘val’ outcome
 1611 (i.e., predicting the pitch values), and therefore the results of Test 1 and Test2 are
 1612 identical for this group of EDL models.

a. Cat. Models:

b. Pred. Models:

Figure C1. Channel/time windows combinations for which EDL models beat the Probability model (i.e., Test 2), and significantly more than 50% of the random models (based on Bonferroni corrected alpha level for 64 (32 channels $\times$ 2 time windows) comparisons, values only shown if $p < 0.00078125$). *Top row a)* shows the categorization models, *bottom row b)* shows the prediction models.

1613 **Appendix D. Predictions of EDL models**

1614 Below are the activation patterns visualised for different EDL models:

- 1615 – Figure D1 shows a group of EDL models with similar activation patterns, which
1616 were found to be informative for the ERP data. (Note that one of these is included
1617 in Figure D2, *opleft* because of space limitations.)
- 1618 – Figure D2 shows a group of EDL models with activation patterns that were *not*
1619 correlated, which were found to be informative for the ERP data.
- 1620 – Figure D3 shows another group of EDL models with similar activation patterns,
1621 which were also found to be informative for the ERP data.

Figure D1. *Cluster 1*: Activation values for five EDL simulations with strong correlations. Activation values are based on the experimental stimuli for one participant in the experiment. Cat-val-SD is included in Figure D2 and is included in this group due to similar patterns for stimuli 1-4., but it does not capture *unlearning* of the deviant, stimulus 5.

Figure D2. Activation values for three other (not correlated) EDL simulations that outperform their baselines and the random models. Activation values are based on the experimental stimuli for one participant in the experiment. Note that model Cat-val-SD (*topleft panel*) is part of cluster 1, see Figure D1.

Figure D3. *Cluster 2:* Activation values for three EDL simulations with strong correlations. Activation values are based on the experimental stimuli for one participant in the experiment. Note that the range of activation values for these models is different from the EDL models presented in Figures D1 and D2.

1622 Appendix E. TRFs

1623 E.1. Baseline models

1624 Figures E2, E3, and E4 illustrate the TRFs for the baseline models High-Low (HL),
 1625 Standard-Deviant (SD), and the Probability model for the ERP data in channels FC6
 1626 and Pz. For all baseline models the **constant dimension** contains a constant spike for
 1627 each incoming stimulus (black solid line). The **variable dimension** differs between
 1628 the three models:

- 1629 – In the HL model (Figure E2) the variable dimension contains uniformly sized
 1630 spikes for each high tone. The ERP of the high tones is fitted by the sum of the
 1631 two dimensions, and hence, the variable dimension fits the *difference* between
 1632 high and low tones and the constant dimension fits the ERP of the low tones.
- 1633 – In the SD model (Figure E3) the variable dimension contains uniformly sized
 1634 spikes for each deviant stimulus. The ERP of the deviant stimuli is fitted by
 1635 the sum of the two dimensions, the variable dimension fits the standard stimuli,
 1636 and the constant dimension fits the ERP of the *difference* between deviant and
 1637 standard stimuli.
- 1638 – In the Probability model (Figure E4) the variable dimension contains spikes that
 1639 reflect the probability of the stimulus to occur (see Figure E1), based on the
 1640 frequency of occurrence in the experiment. The probability values range between
 1641 0.012 and 0.179. The ERP of the stimuli with a probability of 0.179 is fitted by
 1642 the sum of the constant dimension and $0.179 * \text{variable dimension}$.

Figure E1. Stimulus frequency (in probability values) for all presented pitch values.

TRFs baseline model High-Low

Figure E2. TRFs fitting the activations of baseline model High-Low to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing a low tone), the red thick lines show the variable dimension (representing difference between high and low tones), and the dotted lines show the sum of the constant and variable dimension (representing the high tones).

Panels a and c: TRFs early time window. *Panels b and d:* TRFs late time window. Note that only in the early time window the baseline model shows a small difference between high and low tones, around 0.175 s after stimulus onset, indicated by the yellow time window. Further, the TRFs do not predict any difference between high and low tones in channel Pz.

TRFs baseline model Standard-Deviant

Figure E3. TRFs fitting the activations of baseline model Standard-Deviant to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing the difference between deviant and standard stimuli), the red thick lines show the variable dimension (representing the standard stimuli), and the dotted lines show the sum of the constant and variable dimension (representing the deviant stimuli). *Panels a and c:* TRFs early time window. *Panels b and d:* TRFs late time window. Note that the difference between deviant and standard stimuli is much larger in the early time windows, peaking around 0.175 s after stimulus onset as indicated by the yellow time, than in the later time window.

TRFs Probability model

Figure E4. TRFs fitting the activations of the Probability model to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing the probability value 0.0), the red thick lines show the variable dimension (representing difference between probability values 0.2 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the probability 0.2). *Panels a and c:* TRFs early time window. *Panels b and d:* TRFs late time window. Note that the effect of probability starts only around 0.250 s after stimulus onset, and continues in the later time window.

1643 E.2. EDL models

1644 The TRF for EDL model Pred-bg-HL (Figure 9) was discussed in Section 6. The TRFs
 1645 of EDL models Pred-val-HL, Pred-diff-HL, and Cat-pos-HL are similar to the TRFs of
 1646 model Pred-bg-HL and therefore not included in this section. Below the TRFs for the
 1647 other models are included: Cat-diff-HL, Cat-val-SD, Cat-diff-SD, and Pred-bg-VAL.
 1648 The TRFs of the models are Pred-val-VAL and Pred-diff-VAL are similar to the TRF
 1649 of Pred-bg-VAL, and therefore not included.

TRFs EDL model Cat-diff-HL

Figure E5. TRFs fitting the activations of EDL model Cat-diff-HL to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing an activation value 0.0), the red thick lines show the variable dimension (representing difference between the activation values 1.0 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the activation value 1.0).

Panels a and c: TRFs early time window. The difference is predicted to peak around 0.125 s after stimulus onset, indicated by the yellow time window. *Panels b and d:* TRFs late time window. The EDL model only beats its baseline in channel Pz, but not in FC6. The scalp plot in *panel a* shows the distribution of the difference in the early yellow marked time window. The scalp plot in *panel d* shows the distribution of the difference in the later yellow marked time window.

TRFs EDL model Cat-val-SD

Figure E6. TRFs fitting the activations of EDL model Cat-val-SD to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing an activation value 0.0), the red thick lines show the variable dimension (representing difference between the activation values 1.0 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the activation value 1.0).

Panels a and c: TRFs early time window. The difference is predicted to peak around 0.125 s after stimulus onset, indicated by the yellow time window. *Panels b and d:* TRFs late time window. The EDL model only beats its baseline in channel Pz, but not in FC6. The scalp plot in *panel a* shows the distribution of the difference in the early yellow marked time window. The scalp plot in *panel d* shows the distribution of the difference in the later yellow marked time window.

TRFs EDL model Cat-diff-SD

Figure E7. TRFs fitting the activations of EDL model Cat-diff-SD to the ERPs in channels FC6 (top row) and Pz (bottom row). **Note that the EDL model does not beat its baseline in these channels, see Figure7, but we choose FC6 and Pz for comparison with other EDL models.** As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing an activation value 0.0), the red thick lines show the variable dimension (representing difference between the activation values 1.0 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the activation value 1.0).

Panels a and c: TRFs early time window. *Panels b and d:* TRFs late time window. The scalp plot in *panel a* shows the distribution of the difference in the early yellow marked time window. The scalp plot in *panel d* shows the distribution of the difference in the later yellow marked time window.

TRFs EDL model Pred-bg-VAL

Figure E8. TRFs fitting the activations of EDL model Pred-bg-VAL to the ERPs in channels FC6 (top row) and Pz (bottom row). As the TRFs are fitted on z-scores of the ERP data, the TRF scale has arbitrary units. The black solid lines show the constant dimension (representing an activation value 0.0), the red thick lines show the variable dimension (representing difference between the activation values 0.5 and 0.0), and the dotted lines show the sum of the constant and variable dimension (representing the activation value 0.5). Note that the range of activation values is smaller than for the other EDL models, therefore the variable dimension was adjusted to reflect the maximum activation (see Figure D3).

Panels a and c: TRFs early time window. *Panels b and d:* TRFs late time window. The scalp plot in *panel a* shows the distribution of the difference in the early yellow marked time window. The scalp plot in *panel d* shows the distribution of the difference in the later yellow marked time window.