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Research Report

Violation of auditory regularities is reflected in pupil dynamics

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ABSTRACT

The brain builds and maintains internal models and uses them to make predictions. When predictions are violated, the current model can either be updated or replaced by a new model. The latter is accompanied by pupil dilation responses (PDRs) related to locus coeruleus activity/norepinephrine release (LC-NE). Following earlier research, we investigated PDRs associated with transitions between regular and random patterns of tones in auditory sequences. We presented these sequences to participants and instructed them to find gaps (to maintain attention). Transitions from regular to random patterns induced PDRs, suggesting that an internal model attuned to the regular pattern is reset. Transitions from one regular pattern to another regular pattern also induced PDRs, suggesting that they also led to a model reset. In contrast, transitions from random patterns to regular patterns did not induce PDRs, suggesting a gradual update of model parameters. We modelled these findings, using pupil response functions to show how ongoing PDRs and pupil event rates were sensitive to the trial-by-trial changes in the information content of the auditory sequences. Expanding on previous research, we suggest that PDRs—as biomarkers for LC-NE activation—may indicate the extent of prediction violations.

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1. Introduction

The sensory input from natural environments exhibits statistical regularities over multiple temporal and spatial scales. A wide range of studies has observed that humans are sensitive to these statistical regularities and track them (Barascud et al., 2016; Canale, 2022; Frost et al., 2019; Paavilainen, 2013; Sherman, Graves, & Turk-Browne, 2020; Zhao et al., 2019) to improve their performance in perceptual and cognitive tasks (Bestmann et al., 2008; Krishnamurthy et al., 2017). However, statistical regularities in the environment are constantly violated, and new regularities emerge.

Zhao et al. (2019) observed that the violation of such statistical regularities (i.e., deviations from regular patterns) but not their emergence from random patterns led to sharp

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increases in pupil size (i.e., pupil dilation responses, PDRs in short). Based on earlier studies (Joshi et al., 2016; Reimer et al., 2016), Zhao et al. (2019) interpreted these PDRs as reflecting the activity of the locus coeruleus-norepinephrine (LC-NE) system, a vital part of the arousal system in the brain. The results were taken as suggesting that an internal model, reflecting a regular pattern, resets upon encountering a random pattern. Conversely, the internal model for a random pattern is not reset upon the onset of regularity, but instead undergoes a gradual update in its parameters, as the violation of randomness is statistically harder to determine. Hence, Zhao et al. (2019) suggested that the reset, but not the update, of internal models leads to PDRs.

Despite consistent observations, the influence of the violation and emergence of regular patterns on pupil responses (either constriction or dilation) has yet to be fully investigated. In this study, we first replicated and generalized the findings of Zhao et al. (2019), and then went on to quantify the relationship between the information content of the statistical patterns and the associated pupil responses. In the following sections, we will first highlight the empirical and theoretical background of this research and then describe our study in detail.

1.1. Expected and unexpected uncertainties

Internal models of statistical relationships in the environment are affected by changes that generate uncertainty by violating predictions (Dayan & Yu, 2003, 2006; Gershman & Niv, 2010; Wilson et al., 2013; Yu & Dayan, 2005). Two types of uncertainties can be defined: expected and unexpected uncertainties. Expected uncertainties arise because of modelled unreliability of predictive relationships and mirror the inherent stochasticity of the environment. When these uncertainties are epistemic rather than aleatoric,¹ they can lead to model update which is accompanied by a decrease in the expected uncertainty. Conversely, unexpected uncertainties invalidate models, requiring them to be replaced (Dayan & Yu, 2003, 2006; Nassar et al., 2012; Payzan-LeNestour et al., 2013; Yu & Dayan, 2005; Zhao et al., 2019), thus leading to model reset. Expected and unexpected uncertainties suppress topdown expectations and increase the importance of newly acquired information (Dayan & Yu, 2003, 2006; Farashahi et al., 2017; Soltani & Izquierdo, 2019).

Although uncertainties are subjective (Yu, 2012), they can be approximated from the perspective of an ideal observer model that learns optimal predictive relationships between events (Barascud et al., 2016; Pearce, 2005). The strength of these predictive relationships can be quantified by estimating the negative probability of events based on the history of the observer (MacKay, 2003). This measure is often referred to as information content, self-information or surprise. We now discuss how this measure illuminates the different types of uncertainties that we encounter. The dynamics of the information content varies with the different types of uncertainty. Known deterministic environments in which a single input sequence repeats are perfectly predictable, and so have zero information content. Thus, any change in these types of environments is a form of unexpected uncertainty, which is associated with an information content increase that is immediately apparent when predictions are violated. Such a change results in a reset of the model that is built for the sequence. If the result of the change is a different deterministic environment, the information content will then gradually decrease to zero as the perfect predictability becomes apparent.

Uniformly random environments, on the other hand, have maximal information content and full expected uncertainty, since they are completely unpredictable. When they change, for instance by becoming deterministic, the information content can only decrease. However, this change is difficult to pinpoint, because a repeating deterministic sequence is a possible, if increasingly unlikely, draw from the stochastic environment. Thus, there is no abrupt model reset, and only progressive model update. We will revisit this topic later when we examine the relationship between information content and PDRs.

1.2. Uncertainties, the LC-NE system, and PDRs

It has been suggested that the difference between expected and unexpected uncertainty is putatively accompanied by differences in the release of neuromodulators, as uncertainties signal when computation and plasticity are required. Thus, environmental changes can drive the brain's arousal systems. Expected uncertainty has been related to the neuromodulator acetylcholine (ACh) and unexpected uncertainty with norepinephrine (NE; Dayan & Yu, 2003; Bouret & Sara, 2005; Marshall et al., 2016; Nassar et al., 2012; Yu & Dayan, 2005).

In keeping with this suggestion, one role for the LC-NE system is regulating arousal via widespread NE release (Aston-Jones & Cohen, 2005; Carter et al., 2010; Joshi & Gold, 2020; Nassar et al., 2012; Sara & Bouret, 2012). Indeed, NE has been suggested as the medium by which unexpected uncertainties lead to a global reset signal across the brain (Bouret & Sara, 2005; Dayan & Yu, 2006; Yu & Dayan, 2005; Zhao et al., 2019); this then disrupts top-down cognitive processes and prioritizes the accumulation of bottom-up sensory information, thereby accelerating the discovery and establishment of models of new structure in the environment.

Neurological studies of animal models suggest that PDRs correlate with the LC-NE system's phasic activity (Strauch et al., 2022). For example, Reimer et al. (2016) found that phasic activity in NE was associated with PDRs in mice and Joshi et al. (2016) observed that the activation of the LC-NE system preceded an increase in pupil size. Further research based on fMRI (functional magnetic resonance imaging) suggested that pupil size was positively correlated with BOLD activity in the LC in humans (de Gee et al., 2017; Murphy et al., 2014). Therefore, from this perspective, PDRs can be considered a biomarker of the LC-NE system activity. The relationship of PDRs with arousal and learning rate further strengthens this idea (Nassar et al., 2012).

¹ Epistemic uncertainties stem from the incomplete knowledge of an observer and can be reduced by new information. By contrast, aleatoric uncertainties arise from irreducible stochasticity, for example, the outcome of a fair coin toss (Hüllermeier & Waegeman, 2021).

1.3. Information content and PDRs

In line with the suggested role of PDRs as a biomarker of the LC-NE activation, a wide range of studies has shown that PDRs were evoked in response to events with high information content (unexpected, surprising events; Alamia et al., 2019; Krishnamurthy et al., 2017; Payzan-LeNestour et al., 2013; Nassar et al., 2012; Preuschoff et al., 2011; Filipowicz, Glaze, Kable, & Gold, 2020; Zénon, 2019; Zhao et al., 2019). Most of these studies used tasks that required explicit tracking of the environmental statistics (Krishnamurthy et al., 2017; Nassar et al., 2012; Preuschoff et al., 2011; Filipowicz, Glaze, Kable, & Gold, 2020). Recent studies also explored PDRs in scenarios where no explicit tracking of the environmental statistics was required, thereby testing whether such PDRs can also be evoked spontaneously in response to events with high information content (Alamia et al., 2019; Bianco et al., 2020; Milne et al., 2021; Zhao et al., 2019). For example, these studies instructed participants to perform irrelevant, decoy tasks of passively listening to auditory sequences (Bianco et al., 2020), or to detect a target that was irrelevant to the statistical structure (Alamia et al., 2019; Milne et al., 2021; Zhao et al., 2019). Thanks to these efforts, a positive link between information content and spontaneous PDRs has been established.

However, several aspects of this link are still unclear. First, it is not fully understood how variations in information content-be they decreases or increases-affect the full-time course of PDRs. Indeed, recent studies suggest that it might be beneficial to investigate the full time-series of PDRs instead of focusing only on scalar values (like mean or maximum pupil size; Denison et al., 2020; Hershman et al., 2023; Fink et al., 2024). Such an approach would make it possible to determine the temporal characterizations of effects and outline temporal dynamics of cognitive and perceptual processing (Hershman et al., 2023) and thereby clarify the relationship between pupil dynamics and information content-for instance, the speed with which the pupil responds (Cai et al., 2023; de Gee et al., 2014; Denison et al., 2020; Hoeks & Levelt, 1993; Wierda et al., 2012). We also do not know whether performance on an irrelevant task influences the link between information content and PDRs, and if so with what effect.

1.4. Purpose of the present study

We measured PDRs in response to the violation and emergence of regular patterns in fast-paced auditory sequences (Zhao et al., 2019). Because we were interested in the spontaneous processing of statistical regularities, no task was associated with transitions between patterns. Instead, participants were instructed to perform the apparently irrelevant task of finding gaps in those patterns, just to ensure they maintained their attention on the auditory sequences.

Zhao et al. (2019) investigated transitions between regular and random patterns. We included a new condition with transitions from one regular pattern to another regular pattern. This new condition allowed us to verify that the resulting PDRs are not only due to the saliency of a new random pattern after a regular pattern per se, but instead are due to the violation of regularities. Both conditions have been shown to evoke a mismatch-negativity (MMN) in electroencephalography (EEG; Southwell, 2019), suggesting that the brain treats these transitions as unexpected events.

We also estimated the information content resulting from the violation and emergence of regularities. We did this using a variable-order Markov model called Information Dynamics of Music (IDYOM, Pearce, 2005; 2018). Violation and emergence of regularities (including our new regular—regular condition) led to different degrees of information content, suggesting different requirements for the computations that must be carried out in the brain to build models and make predictions (Dayan & Yu, 2003; Milne et al., 2021; Yu & Dayan, 2005; Zhao et al., 2019). Having observed that PDRs fluctuate over time with changes in information content, we modelled their relationships on a trial-by-trial basis using a convolutional approach based on pupil response functions (PRFs; Cai et al., 2023; de Gee et al., 2014; Denison et al., 2020; Hoeks & Levelt, 1993; Wierda et al., 2012).

Finally, although previous results showed that the PDRs arise spontaneously (Zhao et al., 2019), they did not quantify the effect of the irrelevant task on the link between information content and PDRs. We therefore assessed the extent to which pupil responses are spontaneous biomarkers of changes in predictive relationships in environmental statistics.

2. Material and methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/ exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The experiment and associated PDRs analysis for the replication were preregistered at AsPredicted (https://aspredicted.org/GSK_NHJ). Analyses linking information content and PDRs were not preregistered but were included at the suggestion of reviewers. The raw data, processed data, and analysis scripts were shared as an Open Science Framework project (https:// osf.io/KPW57).

2.1. Participants

Twenty-nine participants attended the study. As a result of the exclusion criteria based on the gap detection task specified in the preregistration, no data was collected for three participants whose accuracies after practice remained below 80%. However, due to the poor general performance of participants in finding gaps, we later deviated from the preregistration, letting all participants attend the main experiment and excluding outliers before the main analysis. Four participants with hit rates three standard deviations below or false alarm rates three standard deviations above the group mean were excluded, resulting in 22 participants (8 female, M_{age} : 24.43, SD_{age}: 3.28). Including the four excluded participants in the analysis did not change our results.

Zhao et al. (2019) reported Cohen's d_z of .8 in a withinsubjects design with a one-sided t-test for the effect on PDRs and determined that N = 12 yields adequate power $(1-\beta = .8)$ at α = .05. With the same effect size, we found that N = 20 increases the power to .964 (The current power of the study with N = 22 is 1- β = .976).

The participants were mostly university students and compensated with either course credit or 10 EUR per hour. The ethics committee of the Eberhard Karls University of Tübingen approved the study (Date of approval: 17.06.2020).

2.2. Materials

We used the same auditory stimuli as Zhao et al. (2019). Fig. 1 shows an example set of stimuli used in the experiment. All auditory stimuli were generated by concatenating 50 msec tones of various frequencies selected from a frequency pool consisting of 20 log-spaced values between 222 and 2000 Hz (namely, 222, 250, 280, 315, 354, 397, 445, 500, 561, 630, 707, 793, 890, 1000, 1122, 1259, 1414, 1587, 1781, 2000 Hz).

Ten tones selected from the frequency pool (with replacement) were used to create regularities (REG10). Similarly, ten tones selected from the frequency pool (with replacement) were shuffled to generate random patterns (RAND10). These



Fig. 1- Example stimuli. Note. Typical stimulus sequences used in the experiment. Each yellow bar represents a tone (each lasting 50 msec). RAND10: 10 tones were randomly selected from a pool of 20 tones and presented in a random order. REG10: 10 tones were randomly selected from the same pool and then these 10 tones were presented repeatedly in the same order. These conditions served as control conditions as they did not include a statistical change. RAND10-REG10: First the RAND10 pattern was presented, then there was a transition to a REG10 pattern. **REG10-RAND10: Transition from REG10 to RAND10.** REG10a-REG10b: Transition from one REG10 pattern to another REG10 pattern. Transitions between patterns are marked by a white vertical line (transition times were jittered in the experiment but are shown here as overlapping, for simplicity).

conditions, which did not involve a change in statistical structure, served as control conditions.

For trials involving a transition, ten tones were selected from the frequency pool for the first pattern, and the same tones were used to generate the second pattern to avoid introducing novel tones after the transition. There were three types of trials with transitions: (a) RAND10-REG10 involved a transition from RAND10 to REG10 and was used to investigate the effect of the emergence of regularity. As discussed earlier, this type of transition allows gradual model update and, in this case, a reduction of information content. (b) REG10-RAND10 involved a transition from REG10 to RAND10 and was used to investigate the effect of the violation of regularity. (c) REG10a-REG10b involved a transition from one REG10 pattern to another REG10 pattern and thereby also constituted a violation of regularity, and an increase, and then a decrease in information content. If PDRs are sensitive to unexpected uncertainties and are evoked due to model reset, transitions in (b) and (c) should elicit PDRs but not in (a).

Each participant observed 192 randomly generated trials corresponding to 48 RAND10, 48 REG10, 48 RAND10-REG10, 24 REG10-RAND10, and 24 REG10a-REG10b trials. The length of the auditory sequences varied randomly between 6 and 8 sec, at a granularity of 500 msec. Transitions occurred between 3 and 4 sec after the sequence onset. Specifically, REG10s consisted of 12–16 repetitions of the same auditory sequence (120–160 tones in total), and REG10s in REG10-RAND10 and REG10a-REG10b were violated after 6–8 repetitions (60–80 tones in total) presented. Inter-trial intervals (ITIs) were 5 sec.

A gap detection task was provided to keep participants' attention and lead them to engage with the auditory stimuli (Milne et al., 2021; Zhao et al., 2019). The gap detection task was irrelevant to the transitions. It required participants to detect possible gaps that could occur in 20% of trials and at any time between 250 msec post-onset and 750 msec pre-offset. Each condition involved the same number of gaps, but their durations were determined to be three missing tones (150 msec) for RAND and two missing tones (100 msec) for REG to equate the difficulty of the gap detection task (in line with Zhao et al., 2019). Trials involving a gap or receiving a false alarm response were removed from the analysis to avoid any effect of the gap or the motor response.

The auditory stimuli were presented by a headphone (Beyerdynamic DT-770 M 80 Ohm) connected to the monitor (ViewPixx/3D System, screen diagonal: 24-inch/60.96 cm). Participants were provided with a RESPONSEPixx connected to the monitor and could respond with any of the five buttons (according to their preference). The participants' right eyes were tracked using an EyeLink 1000 system (SR Research) at a 1000 Hz sampling rate.

2.3. Procedure

Participants sat in a luminance-controlled, dimly lit room (5 cd/ m^2) to ensure that non-luminance-evoked pupil dilation could be observed. They were instructed to place their chin on a chinrest 50 cm away from the monitor to maintain a fixed distance between the eye and the monitor. They were asked to fixate on a white cross (13.2 cd/m²) in the centre of a grey background, which remained constant throughout the

experiment. The eye tracker was positioned below the monitor and continuously tracked the gaze position and the right eye.

Sounds were presented diotically at a comfortable intensity level the participants selected before the experiment. Participants were shown several examples of auditory sequences, including a gap, and a short practice session was carried out. They were instructed to monitor the sequences for gaps and respond by pressing a button. The end of trials was indicated by a fixation cross changing to green for 400 msec. The main experiment involved four blocks, each taking approximately 9 min with 3-min optional breaks. Participants observed trials coming from different conditions within the same block. A calibration phase was applied before each block to calibrate the gaze locations detected by the eye tracker.

2.4. Analysis

Our preprocessing pipeline closely paralleled that of Zhao et al. (2019) but was implemented using different programming languages and software packages. We note minor deviations throughout the analyses section.

2.4.1. Analysis of gap detection performances

Participants' performance in the gap detection task was transformed into hit and false alarm rates. Hit and false alarm rates were then arcsine transformed for the subsequent parametric and Bayesian statistical analyses.

2.4.2. Analysis of pupil size values

The area of the pupil of the right eye was measured during the experiment, and the data were converted to diameter for further analysis (pupil area led to the same results). The pupil size data were analysed at 1000 Hz.

Participants' gaze directions were analysed to avoid any effect of gaze on pupil size by checking deviations of more than three standard deviations from the group mean. By this criterion, we found that none of the participants' mean gaze locations exceeded the group mean more than this amount.

As noted, trials involving a gap or receiving a false alarm response were removed from the analysis to avoid any effect of the gap or the motor response. The pupil sizes measured for RAND10-REG10, REG10-RAND10, and REG10a-REG10b conditions were separated into epochs according to the transition time; namely, the data were segmented by considering 1 sec before and 3 sec after transitions to investigate their effects. For the control conditions REG10 and RAND10, which lack a transition, dummy transition times were randomly selected between 3 and 4 sec. The segmented data were analysed to investigate the effect of transitions on PDRs. Considering that the first ten tones in REG10 were indistinguishable from random sequences of tones, transitions from RAND10 to REG10 were shifted one repetition (10 tones, 500 msec).

Complete or partial blinks in the segmented pupil size data were reconstructed by piecewise cubic interpolation. Trials having 50% missing data because of blinking or involving missing data after interpolation were removed from the analyses (\approx 1.15% of all trials). After blink construction, the data were smoothed with a 150 msec Hanning window.

To be able to compare the conditions, the data were zscored by computing each participant's mean and standard deviation for each block separately across all conditions. To assess the effect of transitions on pupil size, baselines were determined for each trial as the mean of a 1-sec interval before the transitions.

Following the preregistration associated with the replication of Zhao et al. (2019), we calculated separate linear regressions for each participant, condition, and timepoint (each timepoint represents 1 msec) to predict pupil size from baseline, with the residuals from these regressions being used for estimating the effect of transitions. This method replicated the target study closely (Figure S2); however, it brought minor timing and magnitude differences between REG10-RAND10 and REG10a-REG10b in response to transitions (see Figure S3 for a comparison). Upon observing that subtracting baselines led to more consistent results, we used this method in our analyses.

We conducted a series of two-tailed t-tests to compare transition and control (no transition) conditions after downsampling the data to 20 Hz. Bayes factors (BF₁₀) were calculated from t values with Jeffreys, Zellner, and Siow (JZS) priors using the Pingouin package in Python (Vallat, 2018). Unless stated otherwise, the transformation was conducted with a Cauchy scale factor of .707. As a complementary frequentist analysis, we detected significant clusters (p < .05) by a nonparametric cluster-based permutation procedure (5000 iterations with a threshold of p < .05) using the MNE package in Python (Gramfort et al., 2013; Larson et al., 2023; Maris & Oostenveld, 2007). To counteract the multiple comparison problem, we also utilized orthogonal Chebyshev polynomials (the first kind) to model the time course of PDRs (Section S7). Orthogonal polynomials have previously been used in pupillometry research to investigate differences in linear and nonlinear trends in pupil size data (Geller et al., 2019; Kuchinsky et al., 2013).

All these statistical analyses revealed consistent results. For simplicity, we therefore show only BF_{10} in the figures (as coloured horizontal lines). The other statistical tests based on the non-parametric cluster-based permutation procedure and orthogonal polynomials can be found in Figures S3 and S7.

To estimate the possible baseline differences between regular and random patterns (i.e., REG10 versus RAND10), RAND10 and REG10 conditions were segmented by considering 1 sec before and 6 sec after sound onset. Then, similar analysis steps as above were applied to REG10 and RAND10 separately. For correction of these signals, the mean of the 1sec interval before the sound onset was computed and subtracted from each trial to investigate the effect of patterns.

Finally, as an exploratory analysis, we asked for individual participants whether violations of regularities and whether performance in the gap-detection task were associated with any change in baseline and mean pupil responses. Baseline pupil responses were determined for each trial as the mean of a 1-sec interval before transitions. We then determined mean pupil responses for each trial by averaging the changes in baseline corrected pupil diameter during the .6 sec–3 sec interval following a transition, a time frame where mean PDRs were visible and BF₁₀ > 1 for both REG10-RAND10 and REG10a-REG10b. We further investigated their relationships with performance variables (RTs and d' of the gap detection task) to

assess the impact of the irrelevant task performance on pupil responses.

2.4.3. Pupil event rate analysis

To determine the effect of transitions on pupil responses, as an exploratory analysis, we used a method proposed by Joshi et al. (2016) and applied by Zhao et al. (2019). This method finds pupil events by focusing on either positive (i.e., pupil dilation) or negative (i.e., pupil constriction) changes in pupil size independent of the magnitude. Unlike averaging, which emphasises macro-events and slowly varying pupil responses, this method detects micro-events such as micro-dilations and micro-constrictions.

The slope of the change on each trial was computed by a set of linear regression algorithms trained sequentially on a 150 msec window to recover the pupil's behaviour at specific time points, using time as a predictor of pupil size. The locations of micro-dilations were defined as local maxima; conversely, those of micro-constrictions were defined as local minima between two selected sequential zero-crossings.

Sequential zero-crossings were selected based on exceeding two different thresholds on their separation in time (Joshi et al., 2016). Events were determined according to 75 and 300 msec thresholds for each trial in the average PDRs analysis (see Fig. 2), and event rates were computed using a 500 msec sliding window for each participant for each condition (based on the mean of participants). Finally, we performed the same statistical procedure we employed for comparing PDRs to compare event rates across conditions.

2.4.4. Information content analysis

The IDYOM model (Pearce, 2005, 2018) was used to evaluate changes in information content (to estimate model update and reset). This fits a variable-order Markov chain with multiple viewpoints (i.e., features). Based on previous observations, it calculates information-theoretic values for each tone within a sequence (e.g., information content and entropy). This model was used in previous research to estimate



Fig. 2— Micro-dilations and constrictions. Note. A sample trial that involves micro-dilations and constrictions detected by the algorithm. (A) Events determined according to a 75 msec threshold and (B) 300 msec threshold. The red line represents dilations, and the red dot shows where dilation events are temporally located, whereas the blue line and dot represent constriction events.

information-theoretic values within auditory sequences (Barascud et al., 2016; Bianco et al., 2020; Milne et al., 2021; Zhao et al., 2019).

We applied this model to the auditory sequences that were presented to participants during the experiment. Since we were interested in statistical relationships between tones, we used "pitch" as a viewpoint ("cpitch" in the IDYOM model terminology). To capture the long-term effects of the entire experimental session and short-term effects of statistical structure (mimicking perception and learning), we used the combination of short (STM) and long-term memory (LTM). This parameter corresponds to "both" in the IDYOM model terminology.

After receiving information content values from the IDYOM model for each trial, we subtracted the information content of the previous point from the corresponding current point; thereby calculating the change in information content. We assumed that the information content in ITIs was 0, as no stimuli were displayed in these ranges except for a constant fixation cross. We down-sampled PDRs to 20 Hz, corresponding to the sampling rate of information content.

We developed two pupil models using information content changes: the pupil size and the pupil event model. The pupil size model predicts the magnitude of pupil responses within trials from information content changes. In this way, it approximates continuous pupil behaviour. By contrast, the pupil event model models micro-dilation and micro-constriction rates (see 2.4.3 Pupil Event Rate Analysis) using the accompanying information content changes whilst ignoring slow pupil responses. These two models complement each other, since the number of pupil events, rather than the magnitude of PDRs, might be associated with changes in information content if, for example, the number, but not the size, of microdilations was affected.

We focused our modelling on the transitions between patterns (i.e., REG10a-REG10b, REG10-RAND10, RAND10-REG10) since these are expected to offer the strongest effects. Furthermore, the violation of regularities (REG10a-REG10b and REG10-RAND10) and the emergence of regularities (RAND10-REG10) occurred on similar numbers of trials in the dataset. The models were required to fit pupil size and microevent rates for the entire auditory sequence across whole trials. We describe the size and event models in turn.

Pupil size model. The pupil response to a particular event can be modelled by a convolutional approach based on a linear model (Cai et al., 2023; de Gee et al., 2014; Denison et al., 2020; Hoeks & Levelt, 1993; Wierda et al., 2012). Following this approach, we treat information content change as an internal event that changes the pupil response in a way that is described by a pupil response function (PRF). The predicted overall dynamics of the pupil then arise from a convolution of the information content change signal and the PRF.

This approach makes several assumptions as to how the pupil responds to events. In the context of our model, these include that the same information content change leads to the same PDRs, the relationship between information content change and PDRs does not vary over time, and, in the simplest case, the information content change is linearly related to PDRs. These properties have been shown to capture pupil responses to isolated events such as simple visual and auditory stimuli (Hoeks & Levelt, 1993) and have been utilized to model PDRs in previous studies to investigate attention and decisionmaking (Cai et al., 2023; de Gee et al., 2014; Hoeks & Levelt, 1993; Wierda et al., 2012) even when relevant events are close in time (Denison et al., 2020).

The PRF has been specified in the literature (Hoeks & Levelt, 1993) as

$$h(t) = t^n e^{-nt/t_{\text{max}}} \tag{1}$$

In this equation, *h* is the pupil size, t is the time in sec, t_{max} (also in sec) determines the peak time of the PRF, and *n* controls the width of the PRF (see Fig. 3). Hoeks and Levelt (1993) specified parameters of this PRF (n = 10.1 and $t_{max} = .93$ sec) and pointed out that *n* is quite variable between participants ($n = 10.1 \pm 4.1 \sigma$). We will call this the literature-based PRF.

We fitted the actual pupil responses recorded in the experiment with a linear model (in our case, a linear-mixed model for each participant) based on the convolved signal. We discuss the independent variables in the model and the fitting procedure in detail in the following sections.

Pupil size model types. We built five models with varying complexities which make different assumptions as to how information content changes determine PDRs.

(a) The first model converts information content changes to pupil responses using convolution with the literature-based PRF (IClit in short). (b) The second model is an extension of the first model that converts information content changes to pupil responses by a unique PRF for each participant (ICfit in short). These PRFs used the same functional form as in Equation (1), but with individual values for *n* and t_{max} which were found by an optimization procedure.

Models (a) and (b) specify identical sensitivities of pupil responses to positive and negative information content changes. The remaining models allow these to differ based on separating information content changes into positive and negative channels, symbolised as IC_{\pm} . (c) The third model convolves these channels with the literature-based PRF (IC \pm lit in short). (d) The fourth model convolves these channels by a unique PRF for each participant (IC \pm fit in short). (e) The fifth, and the most complex model, allows these channels to have different PRFs (IC \pm fit \pm in short).

By comparing these models, we estimated any differential effects of positive and negative information content changes (IC versus IC \pm) on PDRs, individual variabilities within PRFs (IC \pm lit versus IC \pm fit), and possible differences between PRFs across channels (IC \pm fit versus IC \pm fit \pm).

The IDYOM model estimates information content within sound sequences. However, it may not accurately capture the predictability of trial onset, as it does not account for participants' predictions during the ITI. To address this, we added a parameter to the models specified so far to estimate the effect of trial onset (called IC_{start}). We assume that the trial onset is always surprising (i.e., presents only positive information content) and has an effect that can be captured by the same PRF used for information contents of sound sequences. We appended an asterisk (*) to indicate the involvement of this parameter; for example, IClit* corresponds to the model that estimates the effect of the trial onset with this additional parameter and then convolves the information content changes with a literature-based PRF.

Pupil size model fitting. We used the function in Equation (1) for all PRFs. We used literature-based values for (n = 10.1 and $t_{max} = .93$ sec) for IClit and IC \pm lit. For the other models, we used a Bayesian optimization procedure (using scikit-optimize in Python; Section S10) to fit values for individual subjects. We conducted a search between 1, 20 for *n*, .2 sec-2 sec for t_{max} , and from 0 to 20 bits for IC_{start}

By convolving information content changes with the resulting basis PRFs, we computed predictive signals. Then we mapped these predictive signals to actual pupil responses using a linear-mixed model (using the statsmodels package in Python; Seabold & Perktold, 2010) to find the best fitting parameters for each participant by determining the maximum of average R² across trials.

IClit and ICfit (and the variants with an *) models assume that positive and negative information content changes affect pupil responses to the same degree (but in opposite directions, given positive sensitivity, the convolution of a positive signal with a basis PRF results in positive values, i.e., pupil dilations, whereas for a negative signal, the result is negative values, i.e., pupil constrictions). They include one predictive signal for information content changes that is convolved with a basis



Fig. 3– Pupil Response Function Examples. Note. An example set of PRFs (Pupil Response Functions). (A) PRFs with n = 10.1 for different peak responses (t_{max}). (B) PRFs with the parameter $t_{max} = .93$ sec for different n values.

PRF (symbolised as IC) with a random effect across trials. The linear-mixed model used for them had the following form (in Wilkinson notation; Wilkinson & Rogers, 1973):

$$\begin{aligned} \text{PupilSize} &= \text{IC} + \text{PupilBaseline} + \text{PupilDrift} + \text{BlockOrder} \\ &+ (1 + \text{IC}|\text{Trials}) \end{aligned} \tag{2}$$

We included *PupilBaseline*, the mean pupil size of a 1-sec interval before the auditory onset, as a predictor to investigate its effect on pupil responses. Additionally, we included time in a trial to estimate spontaneous negative or positive linear changes in pupil behaviour within a trial; this regressor is called *PupilDrift*. We also included the order of experimental blocks (i.e., *BlockOrder*) to assess the potential impact of time throughout the experiment.

IC \pm lit, IC \pm fit, and IC \pm fit \pm (and the variants with an *) allow positive and negative information content changes to affect pupil responses to different degrees. They include a predictive signal for each channel estimated by a convolution operation with a basis PRF (symbolised as IC+ and IC-) with a random effect across trials. The model used for them had the following form (\pm within terms are given as a subscript in the formula for visual clarity):

$$\begin{aligned} \text{PupilSize} &= & \text{IC}_{+} + \text{IC}_{-} + \text{PupilBaseline} + \text{PupilDrift} \\ &+ \text{BlockOrder} + (1 + \text{IC}_{+} + \text{IC}_{-} | \text{Trials}) \end{aligned} \tag{3}$$

Models predicted the shape and magnitude of baseline corrected PDRs across entire trials (i.e., both before and after the transition) based on information content changes. We then segmented and corrected the model predictions to visualise sustained and transition-evoked PDRs (like actual PDRs, see 2.4.2 Analysis of Pupil Size Values). We compared candidate models by their average Bayesian Information Criterion (BIC) and average R² scores across participants.

Pupil event model. In a separate but complementary analysis, we modelled the rate of micro-dilations and constrictions in response to information content changes. We again down-sampled pupil size, computed slopes (using np.gradient from Numpy in Python), and detected the location of pupil events. Since 75 and 300 msec result in similar rate patterns (3.5 Pupil Event Rate Analysis), we selected the 300 msec threshold for modelling.

Micro-events within a sequence might have many determinants: time-related factors, such as the duration of the trial or experiment; response-related factors, such as whether a pupil response occurred before, and stimuli history-related factors, whether the pupil has already responded to changes in information content in the past. These factors must be accounted for to establish the link between information content changes and pupil events.

To account for these factors, we used a generalized linear model (using the statsmodels package in Python; Seabold & Perktold, 2010). A Poisson regression model is the usual choice for rate models; however, in our data, the occurrences of pupil events were sparse (see Section S10). Upon the observation that the Poisson model determined unusual rates due to the excessive number of zeros, we used zeroinflated Poisson regression (Lambert, 1992). Similarly, in the data, the number of events per bin (each 50 msec) never exceeded 1 due to the down-sampling operation. Thus, the predictions from the Poisson regression can be interpreted as probabilities.

The model had two components with separate logistic link functions: a logistic model for 0s (i.e., the inflation) and a Poisson regression model for event counts (i.e., Poisson model). Apart from the random effect of information content changes, we included the same regressors in this model as those used in the pupil size model. (a) To estimate the temporally varying effect of information content changes, we convolved them with PRFs. To identify model components, we applied the same model comparison procedure used for the pupil size model. We included (b) pupil baselines, (c) pupil drift to estimate spontaneous changes in event rate within a trial, and (d) block order to account for time-related effects.

We fit two models: one for identifying the rate of microdilations and one for micro-constrictions. To specify model components, we ran an optimization procedure (see Section S10) and found parameter sets that minimized the negative log likelihood of the model for each participant. We did not use R^2 as it is not a proper metric for count models.

For both pupil size and event models, we used the fixedeffect coefficients to determine the link between pupil behaviour and the factors of interest (information content, intercept, pupil baseline, pupil drift, and block order). T values were calculated by comparing participant-specific coefficients to 0, and BF_{10} were calculated as a measure of evidence.

3. Results

3.1. Behavioural performance in gap detection task

Participants reached similar performances on gap detection during RAND10 (with the longer gaps) and REG10 (Fig. 4; see Section S1 for a comparison with Zhao et al., 2019). Paired twosided t-tests over hit and false alarm rates did not reveal a



Fig. 4— Hit and false alarm rates of participants in the gap detection task. *Note.* Gap detection performance of participants in the current study. Single points correspond to the performance of individual participants. Error bars indicate bootstrapped 95% CIs.



Fig. 5– Pupil dilation responses in the experiment. Note. Pupil size over time. (A) PDRs were induced by violation of regularities. This could either be a transition from a regular pattern to a random pattern (REG10-RAND10), or from one regular pattern to another regular pattern (REG10a-REG10b). In contrast, the transition from a random to a regular pattern (RAND10-REG10) did not induce PDRs—similar to the control conditions without transition (REG10, RAND10). Pupil size is given as normalized change from baseline (which extended from -1 sec to 0 sec before the transition). Coloured horizontal lines indicate Bayes factors for the difference between each transition condition and the corresponding no-transition control condition, with the varying thickness indicating different evidence levels (BF₁₀ > 1, 3, and 10). (B) Average normalized pupil size over time in no-transition control conditions. These conditions led to similar pupil size changes (pupil sizes extended from -1 sec to 0 sec before the trial onset were used for baseline correction). This finding suggests that PDRs to the violation of regularities (REG10-RAND10 and REG10a-REG10b) but not to the emergence of regularities (RAND10-REG10) are not a side effect of baseline pupil size differences between RAND10 and REG10. Shaded areas indicate the between-participant SEMs.

significant difference [Hit rates: p = .31, 95% CI = (-.1, .3), d_z = .31; False alarm rates: p = .2, 95% CI = (-.04, .01), d_z = .41]. Bayes factor analyses moderately favoured the null hypothesis (Hit rates: BF₁₀ = .361; False alarm rates: BF₁₀ = .483).

3.2. Analysis of PDRs

We statistically compared transition conditions with corresponding no-transition control conditions. The emergence of auditory regularities in RAND10-REG10 trials did not induce PDRs. By contrast, the violation of auditory regularities in REG10-RAND10 trials did elicit PDRs (Fig. 5A). We observed that the pupil responds to regularity violations at around 620 msec. Specifically, $BF_{10} > 1$ is observed at 620 msec ($BF_{10} = 1.32$) and $BF_{10} > 3$ at 680 msec ($BF_{10} = 3.58$). After that, the pupil diameter increases steeply until 1500 msec, with a magnitude of approximately .25, gradually dropping.

Similarly, REG10a-REG10b, the violation of auditory regularities and the emergence of new regularities, elicited PDRs (Fig. 5A). Similar to REG10-RAND10, PDRs in REG10a-REG10b deviated from REG10, the baseline. BF₁₀ value exceeds 1 at 620 msec (BF₁₀ = 1.25) and 3 at 680 msec (BF₁₀ = 3.24).

Both Bayesian and frequentist statistical tests indicate that the evidence for differing pupil sizes gradually decreases for REG10a-REG10b but not for REG10-RAND10. This trend is visible at 2750 msec (REG10a-REG10b: $BF_{10} = 1.30$, p = .128; REG10-RAND10: $BF_{10} = 3.74$, p = .032) and continues by the end of the trial (REG10a-REG10b: $BF_{10} = .83$, p = .247; REG10-RAND10: $BF_{10} = 3.58$, p = .034). The direct comparison did not show a statistically significant effect (mean statistical values 2–3 sec post-transition: $BF_{10} = .43$, p = .22, $d_z = .35$). We will elaborate on this point in the discussion.

Regularity violations (REG10-RAND10, REG10a-REG10b) but not their emergence (RAND10-REG10) evoked PDRs (see Section 2 for a comparison with Zhao et al., 2019). Additional statistical analyses using significant clusters (p < .05) and orthogonal polynomials (see Figures S3 and S7) further confirmed these findings.

To create the stimuli for the REG10a-REG10b condition, we randomly sampled REG10a and REG10b patterns. This random sampling operation introduced varying degrees of dissimilarities between these patterns. As the dissimilarity between the two patterns increases, the magnitude of PDR could also increase because the degree of violations will be greater. As an exploratory analysis, we quantified the dissimilarity between REG10a and REG10b using edit distance methods (Navarro, 2001; Wagner & Fischer, 1974; Yu et al., 2016). We observed using linear-mixed effect models that the degree of dissimilarity between REG10a and REG10b could positively influence the magnitudes of PDRs ($\beta \approx .05$, $R^2 \approx .37$) but had little or no impact on their temporal properties (see Section S8).

3.3. Analysis of sustained pupil sizes

To examine whether pattern type affects sustained pupil sizes, we compared pupil sizes in REG10 and RAND10. Fig. 5B shows no considerable difference between REG10 and RAND10, suggesting that PDRs to the violation of regularities (REG10-RAND10 and REG10a-REG10b) but not to the emergence of regularities (RAND10-REG10) are not a side effect of



Fig. 6— PDRs and gap detection performance. Note. Mean pupil dilation responses (PDRs) and gap detection performance. (A) Represents the mean pupil responses of participants, averaged over the time range of .6—3 sec and sorted according to values shown for REG10-RAND10. Most participants' pupil size increased due to the violation of regularities. On the other hand, the emergence of regularities led to a reduction in pupil size. (B) Shows the correlation between mean pupil responses in regularity violation conditions (REG10-RAND10, REG10a-REG10b). Pupil sizes following two types of regularity violations showed a high and reliable correlation. The data were split according to the median sensitivity to examine if performance (as a proxy of the attentional state of participants) affects this relationship. Participants with high d' seemed to show a slightly low correlation between regularity violation conditions. This finding suggests that participants' attentional state does not impact this relationship.

baseline pupil size differences between RAND10 and REG10 (See Figure S11 for the sustained pupil responses prior to baseline correction²).

3.4. Effect of gap detection performance on pupil size

Most participants' pupil sizes increased due to regularity violations. Specifically, as a descriptive statistic, 18 out of 22 participants in the REG10a-REG10b and 17 in the REG10-RAND10 conditions demonstrated a pupil size increase (Fig. 6A). Conversely, although the emergence of regularities predominantly led to a reduction in pupil size (N = 16), the magnitude of this decrease was smaller than the increase in pupil size observed in response to regularity violations.

Pupil sizes following two types of regularity violations showed a high and reliable correlation [r = .62, BF₁₀ = 21.81, p = .002, 95% CI = (.27, .82); Fig. 6B]. To investigate whether participants' gap detection performance (as a proxy of their attentional state) affects this relationship, we controlled performance variables (d', hit rate, and false alarm rates) by partial correlation. We observed only a minor change [r = .64, BF₁₀ = 29, p = .002, 95% CI = (.27, .82)]. Further, to investigate if this correlation is affected by participants' performances, we split participants into two groups based on the median sensitivity (d' = 3.33) and computed correlations separately: the results were similar across groups [low d': r = .75, BF₁₀ = 8.44, p = .007, 95% CI = (.27, .93); high d': r = .6, BF₁₀ = 2.14, p = .048, 95% CI = (.01, .88); difference: z = -.54, p = .586, BF₁₀ = .33; Fig. 6B].

Participants' performance, as estimated by d', was not associated with pupil size [Pupil baselines: r = .16, BF₁₀ = .330, p = .49, 95% CI = (-.29, .54), mean PDRs: r = .09, BF₁₀ = .287, p = .678, 95% CI = (-.34, .50)]. Hit and false positive rates led to similar results. We extended these results with RTs of participants; results were not strong (pupil baselines: r = .33, BF₁₀ = .75, p = .135, 95% CI = [-.11, .66]; PDRs: r = -.3, BF₁₀ = .64, p = .17, 95% CI = [-.64, .14]). Overall, these results suggest that the irrelevant task performance did not affect PDRs but may affect pupil baselines (RTs but not d).

3.5. Pupil event rate analysis

To determine the effect of transitions between patterns on pupil responses, we determined micro-dilations and microconstriction events and computed their rates over time.

Pupil event rate analysis conducted using 75 and 300 msec thresholds for the minimum gaps between successive detections yielded comparable results with the literature (see Section S4 for a comparison with Zhao et al., 2019 and Section S5 for number and size of these events). Fig. 7A shows that

² As recommended by an anonymous reviewer.



Fig. 7– Pupil event rate analyses. Note. Pupil dilation and constriction rates computed using a running average with a 500 msec window. (A) Dilation rates for REG10-RAND10 and REG10a-REG10b increased due to transitions. On the other hand, the transition from RAND10 to REG10 did not lead to an increase in pupil dilation rate. (B) Pupil constriction rates mirrored dilation rates. Coloured horizontal lines indicate regions where $BF_{10} > 1$, 3, and 10 (represented by varying thickness levels) between each transition condition and the no-transition control. These lines are positioned above and below the graphs corresponding to the 75 msec and 300 msec thresholds, respectively. Shaded areas represent the between-participant SEMs.

dilation rates for REG10-RAND10 and REG10a-REG10b became apparent after the transition. The transition from RAND10 to REG10 did not lead to an increase in pupil dilation rate. Fig. 7A and B shows that pupil constriction rates mirrored dilation rates.

Our results diverged from the reported baseline event rates in the literature (Zhao et al., 2019; see Section S4). After reanalysing their publicly available data, we determined that the event rates should be approximately .75 Hz and .35 Hz for 75 msec and 300 msec, respectively, and not 3 Hz and 1.4 Hz. S. Zhao generously confirmed these revised estimates (S. Zhao, personal communication, June 12, 2023).

3.6. Information content analysis

So far, we have shown that transitions between regular patterns affect pupil responses. While the violations of regularities predominantly evoke PDRs (Figs. 5 and 6), their emergence may lead to small pupil constrictions (Fig. 6). We now describe our results on the relationship between information content changes and PDRs.

We evaluated the predictability of tones within a trial using the IDYOM model, serving as a framework for estimating the relationship between information content changes and PDRs. In the following sections, we examine: (a) information content changes due to transitions, (b) the results of our models relating these changes to pupil size and micro-events, and (c) the relationship between irrelevant task performance and model parameters. 3.6.1. Effects of transitions on information content The IDYOM model suggests that the statistical conditions for detecting the violation (REG10-RAND10, REG10a-REG10b) and the immediate emergence (RAND10-REG10) of regularities differed in response to these transitions. We observed a gradual reduction in information content for RAND10-REG10 just after the transition (Fig. 8A), thereby indicating the opportunity for a slow and progressive model update. By contrast, IDYOM reported an abrupt increase in information content for REG10-RAND10 and REG10a-REG10b, indicating unexpected uncertainties that may lead to a model reset.

The subsequent statistical characteristics of REG10-RAND10 and REG10a-REG10b then gradually differed. The average information content for REG10a-REG10b reduced after approximately 15 tones (750 msec), reaching a baseline after 20 tones (1000 msec), suggesting that the IDYOM model had learnt the new regular patterns (REG10b). On the other hand, the average information content for REG10-RAND10 was stable until the end of the epoch, consistent with the sustained expected uncertainty in RAND10 patterns.

Information content increases after the transition covaried with PDRs (compare Fig. 5A with Fig. 8A). However, sustained and elevated information content changes did not seem to have a substantial impact on them (see REG10-RAND10 after the transition in Fig. 5A; compare REG10 and RAND10 in Fig. 5B after the sound onset). These observations suggest that PDRs may be more closely related to changes in information content than to its absolute values.



Fig. 8— Information content analyses. Note. Information content calculated by the IDYOM model for all trials that one of the participants observed during the experiment. (A) The average baseline corrected information content values. Zero represents transition times to the following pattern. The information content for the violation (REG10-RAND10, REG10a-REG10b) and the emergence (RAND10-REG10) of regularities differed in response to transitions. The RAND10-REG10 condition presented a gradual reduction in information content, suggesting a gradual reduction of uncertainties as a sign of model update. On the other hand, the REG10-RAND10 and REG10a-REG10b conditions indicated an abrupt increase in information content, suggesting instant increase of uncertainties as a sign of model reset. Note that, for RAND10-REG10, transition times are shifted one cycle (10 tones, .5 sec), given that the first ten tones in REG10 are indistinguishable from random sequences of tones. For baseline correction, the mean of the 1-sec interval before the transition (from -1 sec to 0) was computed and subtracted from each trial. (B) Information content changes after the transition. (C) Information content changes for the whole trial. Note that transitions were jittered in the experiment; however, for visualisation, we selected trials with a transition at 4 sec. The shaded area represents SEM.

We estimated information content changes to illuminate uncertainties (Fig. 8B). Information content in REG10-RAND10 and REG10a-REG10b suddenly increased after the transition, whereas those in RAND10-REG10 reduced. We used information content changes from the whole trial as the basis of regressors for modelling pupil magnitudes and events (see examples in Fig. 8C).

3.6.2. Pupil size model results

We built 10 models with varying complexities to estimate the relationship between information content changes and pupil size. We compared these models using BICs and R^2 scores. Some models yielded negative R^2 scores for a few participants (3 participants in total). We dropped the data of these

participants from the dataset so we could compare the models. Dropping these participants did not result in a considerable change in mean PDRs, and did not affect the order of BICs.

The most complicated model, IC \pm fit \pm * received the best score (see Table 1; BIC = 6794 and R² = .57). We discuss IC \pm fit \pm * in the main text (see other models in Section S9). Fig. 9 shows PRFs estimated for IC \pm fit \pm *.

Fig. 10 shows predictions of the IC \pm fit \pm *. The model could capture the asymmetry between transition conditions; however, there were some nontrivial differences between actual and predicted pupil responses. The model substantially underestimated the magnitude of PDRs after regularity violations (REG10-RAND10, REG10a-REG10b) and could not

| | Table | e 1 Pupil | l response | function | parameters | for pupil | l size mod | lels. |
|--|-------|-----------|------------|----------|------------|-----------|------------|-------|
|--|-------|-----------|------------|----------|------------|-----------|------------|-------|

| Models | IC | | IC+ | | IC- | IC- | | R ² | BIC |
|----------------------|------------------|------|------------------|------|------------------|------|------|----------------|--------|
| | t _{max} | n | t _{max} | n | t _{max} | n | | | |
| IClit | .93 sec | 10.1 | _ | - | _ | _ | _ | .14 | 14,440 |
| ICfit | 1.35 sec | 1.41 | - | _ | - | _ | _ | .27 | 12,556 |
| IC \pm lit | - | - | .93 sec | 10.1 | .93 sec | 10.1 | _ | .3 | 12,415 |
| IC \pm fit | - | - | 1.96 sec | 2.19 | 1.96 sec | 2.19 | _ | .52 | 8100 |
| IC \pm fit \pm | - | - | 1.68 sec | 2.76 | 1.71 sec | 1.71 | - | .54 | 7356 |
| IClit* | .93 sec | 10.1 | - | - | - | - | 8 | .15 | 14,257 |
| ICfit* | 1.06 sec | 1.14 | - | _ | - | _ | 8.5 | .33 | 11,567 |
| IC \pm lit* | - | - | .93 sec | 10.1 | .93 sec | 10.1 | 4.09 | .32 | 12,292 |
| IC \pm fit* | - | - | 1.95 sec | 1.73 | 1.95 sec | 1.73 | 8.02 | .54 | 7499 |
| IC \pm fit \pm * | - | - | 1.78 | 2.88 | 1.89 sec | 1.46 | 5.72 | .57 | 6794 |

Note. Average pupil response function (PRF) parameters for pupil size models. Italic indicates free parameters; $IC \pm fit$ and $IC \pm fit^*$ use the same PRF for generating IC + and IC-. Bold shows the top two models.



Fig. 9— Pupil response functions of the pupil size model. Note. Pupil response functions. (A) Literature-based PRF (Pupil Response Function). (B) The distribution of PRF parameters that maximize the R² of participants (Red dots: PRF parameters for positive information changes; blue dots: negative changes). (C) PRFs of participants for positive information content changes and (D) negative information content changes. Participant-specific PRFs are represented by different colours. Thick lines show average PRF parameters.

predict the rapid decreases in PDRs after peaks (see REG10-RAND10 in Fig. 10A).

Coefficients of pupil size model. We assessed the fixed effect coefficients of the IC \pm fit \pm * to estimate the relationship between information content changes and pupil responses (see coefficients of other models in Figure S10). Positive information content changes affected the magnitude of pupil responses positively [Fig. 10C; IC+: B = .024, SEM = .0056, BF₁₀ = 60.82, *p* < .001, 95% CI = (.01, .04)] and negative information content changes negatively (a reduction in the absolute value of negative information changes corresponds to an increase in IC-), but the resulting statistical relationship was weak [Fig. 10D; IC-: B = .0138, SEM = .0056, BF₁₀ = 2.31, *p* = .027, 95% CI = (.0, .03)]. The effect of negative information content (M = .0102, SEM = .0019, BF₁₀ = 298, *p* < .001, 95% CI = (.01, .01)].

Pupil baselines negatively affected PDRs [Fig. 10E; B = -.2709, SEM = .0394, BF₁₀ > 1000, p < .001, 95% CI = (-.36, -.19)]. The model suggests a pupil drift [Fig. 10F; B = .0019, SEM = .0005, BF₁₀ = 13.3, p = .003, 95% CI = (.0, .0)], indicating that time within a trial is associated with pupil magnitude increase, but no consistent change across blocks [Fig. 10G; B = .0231, SEM = .0166, BF₁₀ = .526, p = .1907, 95% CI = (-.01, .06)]. The intercept was strong across participants [Fig. 10H; B = -.1299, SEM = .0351, BF₁₀ = 20, p = .002, 95% CI = (-.21, -.05)].

Irrelevant task performance and model parameters. We examined the possible impact of performance variables for the irrelevant task on the parameters of the pupil size model. We did not observe any notable correlation between performance variables and the coefficients of information content changes (see Fig. 10I; BF_{10} values < .4 and ps > .45). These numbers, combined with our earlier results, suggest that the irrelevant task performance does not directly influence PDRs.

We observed a strong correlation between RTs and pupil baseline coefficients [Fig. 10I; r = .498, $BF_{10} = 3.56$, p = .018, %95 CI = (.1, .76)]. Since low RT and high d' are considered as a proxy of effort, the relationship between pupil baseline coefficients and d' was consistent with this relationship (r = -.378) but the statistical tests were inconclusive [$BF_{10} = 1.088$, p = .083, %95 CI = (-.69, .05)]. These observations agree with our earlier results, suggesting a relationship with increasing effort (see RTs) and pupil baselines (see Section 3.4).

Pupil drift coefficients were related to d' [see Fig. 10I; r = .466, BF₁₀ = 2.49, p = .029, %95 CI = (.05, .74)]; however, for RTs, the statistical tests were inconclusive [r = -.284, BF₁₀ = .57, p = .2, %95 CI = (-.63, .16)]. These results may indicate that participants who performed well in the gap detection task exhibited increasing PDRs within a trial.

Further, we investigated whether performance was associated with PRFs (t_{max} or n). For example, participants with a good performance in the irrelevant task might have rapid or shorter PDRs. Interestingly, no consistent relationship was found with t_{max} or n (ps > .3 and $BF_{10} < .4$) except the weak relationship of RTs with the n of the PRF convolved with positive information content changes (r = .45, p = .03, $BF_{10} = 2.1$).

Overall, pupil responses are associated with positive information content in the anticipated direction. The best model, IC \pm fit \pm *, suggest a strong relationship between positive information content and pupil size (BF₁₀ = 60.32). However, the relationship of pupil responses with negative information content is weak (BF₁₀ = 2.31). It is possible that, although negative information content leads to a reduction in pupil size (i.e., pupil constriction), this relationship is too small to be detected using the smoothed, slowly varying, pupil size (Hoeks & Levelt, 1993).

Therefore, we now turn our focus to the pupil event model to clarify this relationship. The aim of this model is to assess the relationship between information content changes and micro-dilation and constriction rates.

3.6.3. Pupil event model results

We followed the same model selection procedure as in the previous. ICfit, the model that did not differentiate the type of information content changes and did not estimate the effect of trial onset, received the best score for both dilation (BIC = 2848) and constriction events (BIC = 2572). We discuss this model in the main text (see other models in Section S10). PRFs estimated for micro-dilations and constrictions were different (micro-constrictions: $t_{max} = .96 \text{ sec}$, n = 50.35; micro-dilations: $t_{max} = 1.63 \text{ sec}$, n = 9.24; for t_{max} : BF₁₀ = 56, p < .001; for n: BF₁₀ = 212, p < .001).

Fig. 11 shows predicted and actual event rates with respect to trial onset up to 6 sec. In this figure, the effects of trial onset and transitions can be seen together at 0 sec-2 sec and 3 sec-5 sec, respectively. The model for pupil dilation rates could not predict rate increases after trial onsets (see the first



Fig. 10– Pupil size model predictions and coefficients. Note. Pupil size model results. (A, B) Actual and predicted pupil responses for transitions and the whole sound sequences up to 6 sec. Actual and predicted pupil responses were represented by solid and dashed lines, respectively. (C, D, E, F, G, H) fixed-effect coefficients determined for the pupil size model. (C) Estimated relationship between positive information content changes and PDRs. These types of changes are positively correlated with PDRs, suggesting that information content increases lead to PDRs. (D) Effect of information content reductions on PDRs. Adding information content reductions as a separate channel increased R^2 and reduced BIC but their relationships with PDRs were not consistent across participants (BF₁₀ = 2.31). (E) Pupil baselines, the mean of 1 sec before the sound onset, had a negative relationship with PDRs. (F) Pupil drift, (G) block order, and (H) intercept. Single points correspond to the coefficients of participants. Error bars represent SEMs. Coloured asterisks represent the degree BF₁₀. (I) Gorrelation between performance variables and coefficients of the pupil size model. The relationship between information content changes (IC+ and IC-) and PDRs were not affected by performance variables. On the other hand, pupil baseline and drift coefficients were highly correlated with them.

row of Fig. 11A, first .5 sec); however, it predicted well the second point at which the pupil dilation rate increased (see up to 1s in Fig. 11A) and the pupil dilation rate increase in response to transitions (see the time range between 3 sec and 5 sec in Fig. 11B and C). The model for pupil constriction rates performed similarly: it coarsely predicted constrictions with small dispersions for trial onsets (see the time range between 0 and 1 sec in Fig. 11D–F), for transitions (see Fig. 11E).

Overall, models captured rate patterns based on information content changes. However, they failed to capture the effect of trial onset and slightly underestimated the effect of transitions.

Coefficients of pupil event model. Changes in information content were positively associated with the rate of pupil dilations [Fig. 11G; B = .0866, SEM = .0137, BF₁₀ > 1000, p < .001, 95% CI = (.06, .12)]; However, their relationships with pupil constrictions were not clear [Fig. 11G; B = -.0533, SEM = .0714, BF₁₀ = .283, p = .4743, 95% CI = (-.21, .1)].

There was no consistent impact of pupil baselines on dilation [Fig. 11H; B = -.0075, SEM = .0162, $BF_{10} = .24$, p = .65, 95% CI = (-.04, .03)] and constriction rates [Fig. 11H; B = .0794,

SEM = .0683, BF₁₀ = .4, p = .27, 95% CI = (-.07, .22)]. The time within a trial (i.e., pupil drift) reduced dilation [Fig. 11I; B = -.1474, SEM = .03, BF₁₀ = 275, p < .001, 95% CI = (-.21, -.08)] and constriction rates [Fig. 11I; B = -.2231, SEM = .0193, BF₁₀ > 1000, p < .001, 95% CI = (-.26, -.18)].

There was no consistent change in pupil rates across blocks [Fig. 11J; for constriction: B = .0608, SEM = .0577, BF₁₀ = .357, p = .3151, 95% CI = (-.06, .18); for dilation: B = -.0184, SEM = .0246, BF₁₀ = .284, p = .4726, 95% CI = (-.07, .03)]. Both models suggested intercepts [Fig. 11K; for dilation: B = -2.805, SEM = .019, BF₁₀ > 1000, p < .001, 95% CI = (-2.85, -2.77); for constriction: B = -2.872, SEM = .0241, BF₁₀ > 1000, p < .001, 95% CI = (-2.92, -2.82)].

In line with the pupil size model, performance variables were irrelevant to the impact of information content changes on dilation [RTs: r = .12, BF₁₀ = .302, p = .6, %95 CI = (-.32, .52); d': r = -.065, BF₁₀ = .275, p = .775, %95 CI = (-.47, .37)] and constriction rates [RTs: -.058, BF₁₀ = .273, p = .8, %95 CI = (-.47, .37); d': r = .08, BF₁₀ = .28, p = .72, %95 CI = (-.35, .49)]. There was no notable relationship between pupil baseline coefficients with performance variables (all BF₁₀ < .3 and ps > .75). We also analysed the possible relationship



Fig. 11— Pupil event model predictions. Note. Pupil event model predictions and coefficients. (A, B, C) Dilation rates for the three conditions. (D, E, F) Constriction rates. The actual event rates are shown in grey, and coloured lines show predicted event rates. Shaded areas indicate the between-participant SEMs. (G, H, I, J, K) Fixed-effect coefficients. (G) Estimated relationship between positive and negative information content changes and pupil dilation and constriction rates. There was a strong positive relationship between information content changes and dilation rate. However, the effect of information content changes on constriction rates was not clear. (H) Relationship between pupil baseline and event rates (I) Effect of trial time (i.e., pupil drift). that reduces the number of pupil events. (J) Block order and (K) Intercepts. Error bars represent SEMs.

between performance variables and PRFs; there was no notable and consistent correlation observed (all $BF_{10} < 1.4$ and ps > .06).

4. Discussion

We investigated how changes in patterns of fast-paced tones are associated with pupil dilation and constriction. Consistent with previous research (Zhao et al., 2019), we observed that the emergence of regularities from random patterns did not lead to PDRs. In contrast, the violation of regularities by random patterns evoked PDRs. To generalise the earlier research, we used a novel but conceptually similar condition to induce regularity violations (REG10a-REG10b). We showed that transitions between two regular patterns also evoked PDRs, supporting the idea that it is not the presence of random patterns but the violation of the antecedent regularity that leads to PDRs.

4.1. Information content and PDRs

We estimated information content of the stimulus sequences using the IDYOM model (Pearce, 2005, 2018) and observed a positive relationship between information content and PDRs, supporting earlier results in the literature (Alamia et al., 2019; Krishnamurthy et al., 2017; Nassar et al., 2012; Preuschoff et al., 2011; Filipowicz, Glaze, Kable, & Gold, 2020; Payzan-LeNestour et al., 2013; Zhao et al., 2019). Namely, transitions that led to an information content increase evoked PDRs (i.e., REG10-RAND10 and REG10a-REG10b) and those that led to a reduction did not (i.e., RAND10-REG10).

How does the information content evoke PDRs? The current empirical evidence indicates that changes in information content, but not its absolute level, are associated with PDRs. For example, (a) although information content profiles of REG10-RAND10 and REG10a-REG10b were quite different after the transition (see Fig. 8A), we only observed a statistically weak difference between them in terms of PDRs (see Fig. 4a). In line with this observation, (b) we did not observe a difference between RAND10 and REG10 (in contrast to earlier observations in the literature, see Milne et al., 2021). If the pupil had been sensitive to absolute information content level, there would have been a substantial difference between these conditions.

However, these conditions (RAND10 versus REG10; REG10a-REG10b versus REG10-RAND10, 750 msec after the transition) still showed differences in terms of information content changes. For example, a RAND10 pattern still presents fluctuations of positive and negative information content in contrast to a REG10 pattern (see Fig. 8A, compare REG10-RAND10 and REG10a-REG10b after switching to a new pattern).

Based on these observations, we used changes in information content (Fig. 7A) as a proxy for the uncertainty that participants would perceive during the experiment and investigated their relationships with pupil responses. We developed two types of models to investigate how information content changes relate to PDRs. The first type of model focused on slowly varying pupil size and the magnitude of pupil responses; the second type of model focused on quick changes in pupil size and the micro-dilation and constriction rates.

In our models, we used PRFs either to estimate the effect of information content changes on timing of pupil responses or as a tool for investigating the temporally varying effect of information content changes on pupil event rates. We estimated PRFs based on an optimization procedure for each participant; we leave a fully Bayesian analysis of the parameter uncertainties to future work.

4.2. Pupil size model

We employed a convolutional approach based on linear models (Cai et al., 2023; de Gee et al., 2014; Denison et al., 2020; Hoeks & Levelt, 1993; Wierda et al., 2012) to analyse the link between information content changes and the magnitude of PDRs.

We used a set of models with varying complexities to pinpoint essential model components that explain the relationship between information content changes and pupil responses. The top two models (IC \pm fit \pm * and IC \pm fit \pm) that differentiated the effects of negative and positive information content changes on pupil responses received better BICs and R^2 scores than other models. However, the poor result of IC ± lit and IC ± lit* indicate that differentiation of these signals by itself was not sufficient; models including participantspecific PRFs were consistently better than those using the literature-based PRF, indicating a trend favouring individual variabilities (Denison et al., 2020).

IC \pm fit \pm * was able to capture the increase in pupil size. However, for conditions where a regularity was violated, it underestimated the peak magnitude, and after peaks, it overestimated the pupil response magnitude especially for REG10-RAND10. Nevertheless, the model accurately captured the main asymmetry between transition conditions. Coefficients of the model suggested a relationship in the predicted direction: while positive information content is associated with pupil size increase (i.e., dilation; BF₁₀ = 60.82), negative information content is associated with pupil size reduction (i.e., constriction; BF₁₀ = 2.32). However, note that the latter relationship was weak.

We observed from estimated PRFs of participants that (a) the average peak pupil response to information content (t_{max}) was 1.78 sec in contrast to the literature's suggestion of .93 sec (b) The parameter that controls the width of PDRs (*n*) was around 2.9 in contrast to the literature's suggestion of n = 10.1 (Hoeks & Levelt, 1993). Hoeks and Levelt (1993) had already pointed out that *n* was quite variable between participants ($n = 10.1 \pm 4.1 \sigma$). We believe that this is a fundamental area to be explored in the future.

One limitation of the current model is that its results could not be cross-validated on unseen data, probably due to trialby-trial variability of pupil size. Early research crossvalidated its results with the mean of unseen data (Denison et al., 2020). Since we were interested in the trial-by-trial relationship between information content changes and the time course of pupil size, we focused on trials.

4.3. Pupil event model

The pupil size model focuses on the relatively slow dynamics of pupil responses (Hoeks & Levelt, 1993). However, this may mis-characterize the relationship between pupil responses and fast changes in information content. Based on the inconclusive results of pupil size model for the relationship between negative information content changes and pupil constrictions, we focused on micro-events. Specifically, to identify the conditions that lead to the emergence of microevents, we modelled their rates based on several predictors, including changes in information content.

For pinpointing the essential model components, we followed the same comparison procedure as for the pupil size model. This procedure chose one of the simplest models for pupil events, namely ICfit. In contrast with the model selected for pupil size (i.e., $IC \pm fit \pm *$), this model does not estimate the value of information content changes for individual participants; and does not suggest a differential sensitivity of pupil rates for positive and negative information content changes. Therefore, the result of model selection procedure only allowed us to investigate the cumulative impact of information content changes on event rates.

The event model suggests that information content change is positively associated with the rate of dilations ($BF_{10} > 1000$). This result is similar to the result of the pupil size model, demonstrating that positive changes in information content are positively associated with the magnitude of pupil responses (i.e., dilation). However, the relationship between information content changes and the rate of pupil constrictions is not clear.

Our results, in combination with those of the pupil size model, show that information content increase (i.e., model reset) is positively associated with an increase in the magnitude of slowly varying pupil size and the rate of microdilations. However, there was no reliable relationship between information content reduction (i.e., model update) and the magnitude of pupil size as well as the rate of constrictions. This observation does not fully align with a previous study, which reported that a reduction in information content during a trial led to pupil constriction (Milne et al., 2021). However, the study only found a significant difference with a stimulus of similar complexity to ours after 7 sec, suggesting that the effect of information content reduction on pupil responses may be slow.

Our modelling approach assumes that the same information content will always lead to the same PDRs, positive/ negative information content changes and PDRs are related linearly, and the characteristics of this relationship do not change over time. These properties have been demonstrated to hold in other domains such as for modelling the effect of simple auditory and visual stimuli on PDRs (Hoeks & Levelt, 1993) and were utilized to model pupil responses in earlier studies for various phenomena such as attention and decision-making (Cai et al., 2023; de Gee et al., 2014; Denison et al., 2020; Hoeks & Levelt, 1993; Wierda et al., 2012). The current models captured the coarse dynamics of pupil behaviour in response to changes in information content within sound sequences; however, it is still an open question if these assumptions are appropriate for modelling the impact of continuous, very rapidly changing signals on PDRs.

4.4. Irrelevant task performance and pupil responses

Previous research has not clarified the relationship between irrelevant task performance and PDRs (Zhao et al., 2019). We observed in our study that there was insufficient evidence for any impact of performance variables (RTs and d') on PDRs generated by regularity violations. Further, we tested their possible effects on the coefficients of the IC \pm fit \pm * of pupil size model and the ICfit of pupil event model, demonstrating that there was no direct impact of performance variables on PDRs to changes in information content.

These results overall suggest that the modulation of irrelevant task performance of the relationship between information content and PDRs is small, if not absent. Our replication results are consistent with this notion: although our participants performed slightly less well in the irrelevant task than Zhao et al. (2019)'s participants, the observed PDRs were highly similar.

Does irrelevant task performance affect baseline pupil size? In contrast to earlier observations that the task difficulty increases pupil baselines (van der Wel & Van Steenbergen, 2018), in our first analysis based on average baseline pupil sizes, we could not pinpoint a strong relationship. On the other hand, participants' RTs and their coefficients of pupil baselines in the pupil size model were highly and positively correlated. This observation is in line with previous research reporting that task dynamics, such as task difficulty, affect baseline pupil responses (Relaño-Iborra et al., 2022).

Given that pupil baselines impact the magnitude of PDRs negatively, the irrelevant task performance may disguise possible increases in PDRs, especially when the pupil size is at ceiling. A recent report suggests that the slope, delay and curvature of PDRs along with peak pupil responses (but not mean pupil responses) are affected by pupil baselines (Relaño-Iborra et al., 2022). We did not observe a consistent effect of baselines (in terms of size) on pupil event rates. We propose future research examines the rich effect of baseline pupil responses on the time course of pupil responses as well as the rate of pupil events.

4.5. Pupil response times

We observed a slight pupil response time difference between regularity violation conditions in the analysis using linear regressions for baseline correction. However, we could not validate this result in further analyses. Statistical tests and exploratory analyses suggest that although participants' pupil response times varied, pupils responded to regularity violations -on average-after 600 msec (see Section S6).

To model the temporal relationship between information content changes and micro-events. This model suggests that average peak pupil responses to positive information content changes are at around 1.6 sec. This result does not exactly align with the results of Joshi et al. (2016), who observed that electrical micro-stimulation of the LC leads to maximum evoked pupil size change after approximately 500 msec in primates. Considering that the human brain needs around 150 msec to detect violations of regularities (Barascud et al., 2016), the peak pupil response should still be around 650 msec. These figures do not exactly match with the numbers in the literature, further research is needed to establish the timing of PDRs to changes in environmental statistics.

4.6. Possible neural and neuromodulatory underpinnings

Overall, these results suggest that PDRs are a reliable biomarker of the violation of an already established internal model. In this respect, they resemble the MMN, a specific negative neural response shown in EEG and MEG (Magnetoencephalography) to deviant events that violate a simple, sequential standard tone or abstract rule-based structures (Paavilainen, 2013). Further research inspired by the MMN literature should investigate the conditions that can modulate PDRs associated with model reset.

However, the MMN is not the only neural response that can be associated with PDRs. Relationships between PDRs and various brain signals have previously been investigated. One candidate brain signal is the P300 component in EEG. P300 has been suggested to reflect the response of the LC-NE system to the outcome of internal decision-making to significant events (Nieuwenhuis et al., 2005), context updating in response to critical changes in the environment (Donchin & Coles, 1998), and other cognitive processes (Verleger, 2020). Studies explored the relationship between P300 (also referred to as P3) and its subcomponents (P3a and P3b) with pupil-related measures. For example, Murphy et al. (2011) investigated the relationship of baseline and PDRs with P300 in an active auditory oddball task and documented that baseline pupil size has a U-shaped relationship with P300; however, PDRs were only correlated with P300s that were elicited in later trials. Using an active auditory oddball task, Hong et al. (2014) observed a negative relationship between baseline pupil size and P3, but P3 was not associated with PDRs. Lu et al. (2023) only recently observed a positive relationship between PDRs and P300 in a gamified version of an n-back task.

In all these studies (Lu et al., 2023; Murphy et al., 2011; Hong et al., 2014), participants were instructed to do tasks that required active tracking of environmental statistics, which could modulate the arousal system (Zhao et al., 2019). In the present study, by contrast, participants were not instructed to make decisions based on environmental statistics. Instead, they were instructed to find task-irrelevant gaps. Considering the modulatory effect of behavioural requirements (Zhao et al., 2019) and motor responses (Privitera et al., 2010) on the arousal system and PDRs, a remaining question is how various event related potentials in EEG and MEG, including P300, are associated with PDRs and whether behavioural requirements modulate this association.

The literature consistently showed the relationship between PDRs and phasic activity of the LC-NE system (de Gee et al., 2017; Joshi et al., 2016; Murphy et al., 2014; Reimer et al., 2016; Strauch et al., 2022). However, it is important to note that a wide range of neural pathways can influence pupil dynamics (Joshi et al., 2016; Joshi & Gold, 2020; Strauch et al., 2022), and these pathways are also engaged in various perceptual and cognitive processes. This suggests other members of the arousal network that might modulate pupil responses to changes in environmental statistics. One brain area that needs to be considered is the basal forebrain-ACh system (Larsen & Waters, 2018; Lloyd et al., 2023; Strauch et al., 2022). Like the LC, the basal forebrain has extensive projections in the brain and regulates learning and attention by prioritizing bottom-up sensory processing using ACh as a medium (Bentley et al., 2011; Yu & Dayan, 2005). Therefore, the neurotransmitter ACh may mediate expected uncertainties and evoke pupil constrictions through antagonistic interaction with NE that has been associated with pupil dilations (Yu, 2012). However, recent observations report that ACh has a dilatory effect on pupils of moving (Mridha et al., 2021; Nelson & Mooney, 2016) as well as idle mice (Reimer et al., 2016). Also, a recent report indicates that the basal forebrain-ACh activation measured via fMRI accompanies pupil dilations in resting humans (Lloyd et al., 2023). Further research is necessary to elucidate the effects of brain regions along with the associated neuromodulators on pupil size and how environmental statistics lead to the observed effects.

Our condition in which regularities emerge from random patterns (RAND10-REG10) can be interpreted based on the observation that the basal forebrain-ACh activation leads to an increase in pupil size. Since emerging regularities are learnable, this condition must allow gradual model update and reduction of expected uncertainties. Given the suggested relationship between ACh and expected uncertainties (Bouret & Sara, 2005; Dayan & Yu, 2003; Marshall et al., 2016; Nassar et al., 2012; Yu & Dayan, 2005), emerging regularities should covary with the reduction of ACh (Milne et al., 2021; Reimer et al., 2016), possibly leading to a reduction of ACh-driven pupil dilation in the light of recent observations in the literature (Larsen & Waters, 2018; Lloyd et al., 2023; Mridha et al., 2021; Nelson & Mooney, 2016; Reimer et al., 2016; Strauch et al., 2022).

4.7. Limitations and future studies

In our experiment, we included RAND10-REG10 as an instance of emergence of regularities. However, this transition is rather stark, and it would be interesting to present semideterministic (rather than fully deterministic) patterns after random patterns that involve tones breaking the predictable structure. An anonymous reviewer suggested the possibility of manipulating the rate of evidence for a regularity, for example, by changing a tone at each repeat and keeping it at the same place until the new regularity is established. Thereby, the relationship of gradual model update and pupil responses can be better understood.

We used changes in information content as a proxy for the degree of environmental changes that update or reset internal models. However, the brain might be using other heuristics to determine when to reset internal models, and these heuristics do not always accompany information content increases. For example, Zhao et al. (2019) observed that pupils respond to transitions from random patterns to very simple regular patterns that consist of 1 or 2 repeating tones (i.e., RAND10-REG1 and RAND10-REG2). Since these simple regular patterns become immediately predictable, the IDYOM model would produce abrupt negative changes in information content. The current models assume a continuous and linear mapping between information content changes and PDRs, and so cannot explain this observation. Future studies should extend our results to clarify further the link between pupil responses and internal model changes.

Given the spontaneous nature of PDRs to information content that leads to model reset, future studies should investigate PDRs associated with the reset of models built for different modalities, such as vision or tactile, or the properties of models built in conjunction with other models. Through this approach, the relationship between different types of internal models and their relationships with the arousal system can be better understood.

5. Conclusion

Many studies suggest that phasic LC-NE activation relates to PDRs (de Gee et al., 2017; Joshi & Gold, 2020; Murphy et al., 2014; Reimer et al., 2016); thereby, the PDR is considered a biomarker of the NE and arousal response. Our results directly supported earlier research (Zhao et al., 2019) that PDRs are associated with internal model reset as a response to abrupt violations of predictive relationships (i.e., unexpected uncertainties). The size and rate of PDRs appear to reveal the sensitivity of the LC-NE system to environmental changes, even when these changes are not behaviourally relevant, which is consistent with its role as a neural reset signal.

Open practices

The study in this article has earned Open Data, Open Materials and Preregistered badges for transparent practices. The data, materials and preregistered studies are available at: https:// osf.io/KPW57.

CRediT authorship contribution statement

Hamit Basgol: Writing – original draft, Visualization, Software, Investigation, Formal analysis. Peter Dayan: Writing – review & editing, Supervision, Funding acquisition. Volker H. Franz: Writing – review & editing, Supervision, Funding acquisition.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2024.10.023.

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