Pupil-linked arousal tracks belief updating in a dynamic auditory environment

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Abstract

Bayesian theory prescribes that highly surprising outcomes should prompt rapid belief updating. Here we developed a novel passive belief updating protocol, suitable for humans and potentially mice. We observed multiple pupil-based signatures of belief updating: (i) pupil response magnitude was enhanced for stimuli that were unexpected given the recent history, and (ii) the relationship between pupil response magnitude and Bayesian change-point probability (surprise), derived from a normative belief updating model, reflected the participant's belief about the volatility of the environment. We conclude that phasic arousal supports belief updating when encountering unexpected incoming information.

Keywords: Oddball, change point, pupil, arousal, prediction error, Bayesian modeling.

Introduction

Most of our decisions are guided by predictions—for instance, opting for a bike over a bus based on expected travel time and weather. Unexpected changes, such as roadworks causing delays, can invalidate these predictions. According to normative Bayesian theory, highly surprising outcomes should prompt rapid belief updating, incorporating new information to improve future decisions (Glaze et al., 2015; Yu & Dayan, 2005). Influential computational models suggest that the locus coeruleus plays a key role in tracking unexpected changes and facilitating belief updating (Dayan & Yu, 2006; Jordan, 2023; Sales et al., 2019). Critical experimental data to constrain these theories is however scarce due to the difficulty to assay and perturb those systems, especially in awake animals. Hence, we set out to develop a passive belief updating protocol, bypassing the need of active reports, allowing us to efficiently and precisely study this fundamental building block of cognition.

Methods

Human participants (N=20) were exposed to a novel belief updating protocol, based on a passive oddball design (standard, 90%; oddball, 10%) using high- and low-frequency tones (2kHz and 1kHz; tone duration, 0.5s; inter-tone-interval, 1s; total of 3600 stimuli per participant) (Fig. 1A). Critically, we introduced (i) two states, defined by their opposite mapping between the frequencies and probabilities of the two tones, and (ii) a 5% chance ("hazard rate") of a state change after every tone presentation (Fig. 1B). This ensured that both tones appeared equally often within a block, and that oddball status was dependent on the local state (Fig. 1C). We also considered a visual variant, which was identical except the two stimuli were now clockwise and counter-clockwise oriented Gabor patches (Fig. 1A). Throughout, we measured pupil size at constant luminance as a marker of ascending arousal, including noradrenergic activity (de Gee et al., 2017; Joshi & Gold, 2020). We used a Bayesian belief updating model (Glaze et al., 2015) (Fig. 1D) to describe the accumulation of samples (stimuli) that carry information (in the form of log-likelihood ratios) about the two possible states and to compute sample-by-sample change-point probability, a common measure of surprise (Murphy et al., 2021).

Results

Pupil response magnitude was larger for state-dependent oddballs vs standards in the auditory domain (Fig. 1E, top) but not in the visual domain (Fig. 1E, bottom). Specifically, there was a significant interaction between the effects of tone identity and state on the tone-evoked pupil response (difference of differences compared against 0 with a Wilcoxon test): $p<0.001$. With a "many standards control" experiment we ruled out the alternative hypothesis that enhanced pupil responses to local oddballs were merely due to (bottom-up) stimulus-specific adaptation. We next generated a sequence of sample-by-sample change-point probabilities that an ideal observer would exhibit, by feeding the observed log-likelihood ratios into the belief updating model (Methods) using a "subjective hazard rate" that matched the generative one: P(state change)=0.05. Tone-evoked pupil responses linearly reflected change-point probability (Fig. 1G). We then computed the same relationship between pupil response magnitude and change-point probability for different subjective hazard rates (Fig. 1H). We found that this correlation peaked for a subjective hazard rate that matched the generative one and was significantly higher than hazard rates >= 0.25.

Discussion

The observed state-dependent differences in pupil response magnitude to the same auditory stimulus led us to the conclusion that after state changes participants update their belief about which tone to expect next. So far, participant's beliefs about the volatility of the environment (subjective hazard rate) were estimated through their choice behavior in active change point detection tasks (Glaze et al., 2015; Murphy et al., 2021). Strikingly, here we achieved the same using pupillometry in a passive protocol, which is suitable for human and mouse observers. In ongoing work, we aim to characterize the involvement of specific neuromodulatory systems in belief updating, using multi-fiber photometry in primary auditory areas in mice and brainstem fMRI (7T) in humans. Our results will provide the much-needed empirical data to close the gap between computational theory of belief updating and its underlying biological mechanisms.

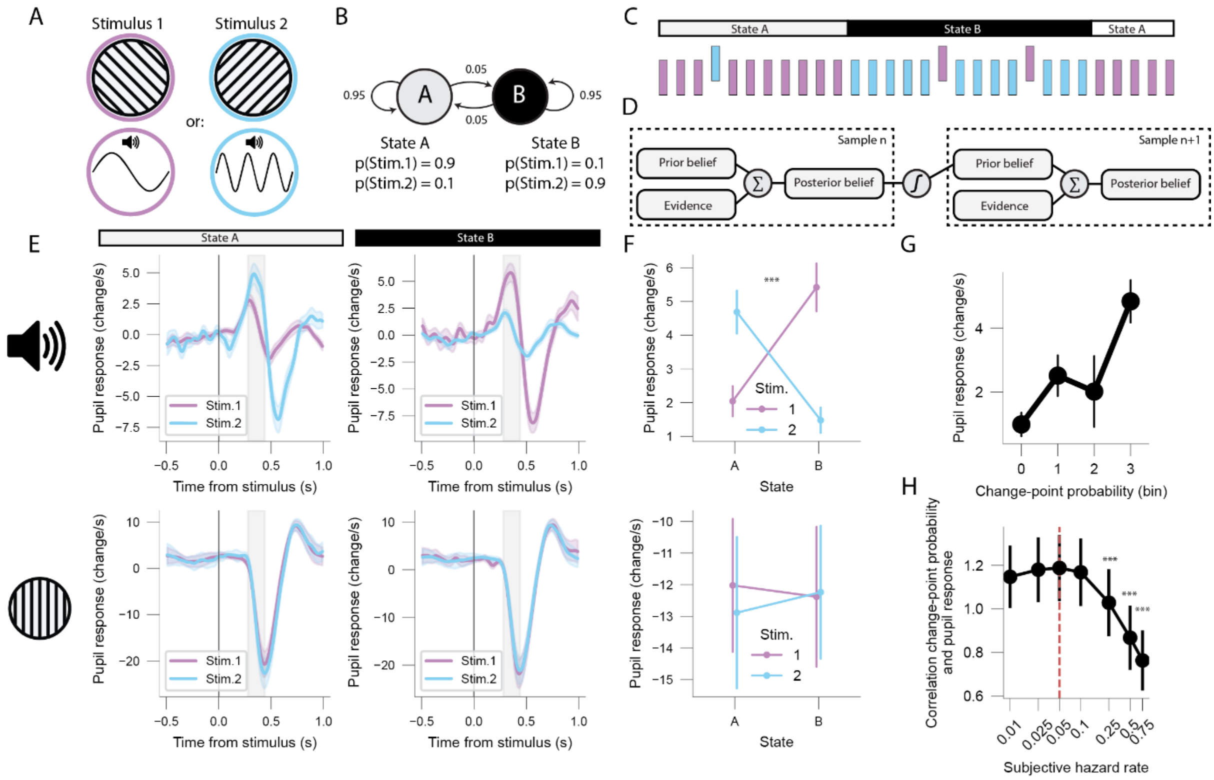

Figure 1. (A) Stimuli. **(B)** The probability of state change ("hazard rate") was 0.05 after every tone presentation. **(C)** Example sequence of states and stimuli. **(D)** Schematic illustration of the Bayesian belief updating model (Methods). **(E)** Pupil response (first derivative) time-locked to each stimulus, separately for states and stimuli, and separately for the auditory and visual domain. Grey window, interval for computing stimuli-wise pupil response magnitudes. **(F)** Pupil response magnitude interaction between stimulus and state identity. **(G)** In the auditory domain, relationship between pupil response magnitude and change-point probability (4 bins). **(H)** As G, but for sample-by-sample correlation, and separately for different subjective hazard rates (see main text). Red line, generative hazard rate. Panels E-H: shading or error bars, S.E.M. across participants (N=20).

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