Pupil dilations reflect surprisal during rapid auditory belief updating

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Abstract

Pupil responses indicate modulations of belief updating by the locus coeruleus noradrenaline arousal system during explicit decision-making. In the present study we show that pupil dilation is sensitive to ongoing surprisal during rapid, online auditory perception. A group of 22 participants indicated the final direction of auditory motion sequences with random length and directional change points in a two-alternative forced choice task design. The ongoing pupil traces were aggregated in "low" and "high" surprisal conditions derived from Bayesian model predictions. This resulted in a positive relationship between high surprisal and pupil size from 571 – 1249 ms after sound onset. We conclude a mediatory role of the arousal system for implicit belief updating during ongoing perception.

Keywords: Pupillometry, Surprisal, Bayesian Inference, Perceptual Inference, Perceptual Decision-Making, Spatial Hearing

Introduction

The pupil is, next to changes in light or focal distance, sensitive to cognitive processes (Mathot, 2018). One phenomenon that has been the center of increased focus over the last decade is dilation of the pupil as a response to tasks associated with the updating of beliefs (Nassar et al., 2012; Preuschoff et al., 2011). Task-evoked pupil dilations are seen as a proxy for activity in the locus coeruleus (LC) noradrenaline (NA) arousal system (Lawson et al., 2021). The release of NA modulates processes of belief updating by increasing sensitivity to novel, salient information and suppressing existing beliefs (Lawson et al., 2021; Mather et al., 2016), likely as a response to prediction errors (Preuschoff et al., 2011). While, from a computational perspective, the exact role of pupil-linked LC-NA arousal is still up for debate, its modulation is shown in a variety of decision-making and estimation tasks (Filipowicz et al., 2020; Krishnamurthy et al., 2017; O'Reilly et al., 2013; Preuschoff et al., 2011) requiring belief updating under uncertainty. Notably, evidence for this pupil-linked modulation comes primarily from tasks featuring conscious decision-making best described as statistical learning (Razmi & Nassar, 2022). Like statistical learning, perception can be well described by Bayesian-like probabilistic inference (Aggelopoulos, 2015). This common computational framework suggests a shared underlying neurophysiological mechanism, a notion that has been frequently implied (Krishnamurthy et al., 2017; Lawson et al., 2021) but rarely tested. In the present study we devised an implicit, online, low-level auditory perception task to investigate whether ongoing surprisal evokes a task-evoked pupil response indicative of LC-NA arousal.

Methods

Participants. We collected data from 22 participants between 22 and 33 years old (12 female, M = 24.45 years, SD = 3.25 years). All participants reported to be right-handed, healthy, with normal hearing and normal or corrected-to-normal vision.

Task. Participants were tasked with inferring and tracking the current motion direction during 200 auditory sequences of random length with directional change points (Fig. 1). Each momentary evidence of motion direction (↑↓) was defined through two consecutive spatialized sounds ( ). Per motion direction, the spatial change was drawn from a normal distribution on every sound. Participants indicated the final motion direction in a two-alternative forced choice design.

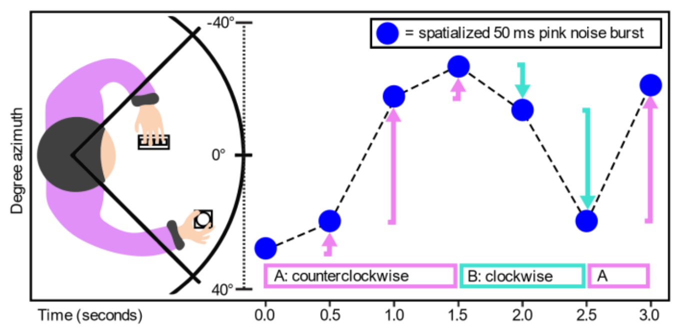

Figure 1: Setup and exemplary sequence.

Observer model. An ideal Bayesian observer model was fitted to the behavioral responses to compute momentary estimations of surprisal for every sound of every trial. The observer is assumed to learn the generative process for sequence presentation and estimate relevant parameters (prior on direction p = 0.5, change point hazard rate H = 0.2, mean of spatial change sampling distribution, variance of sampling distribution, sensory noise). Surprisal values were split along the median in "low" and "high".

Stimuli. Pink noise bursts of 50 ms were presented via in-ear headphones at a stimulus onset asynchrony (SOA) of 500 ms. To achieve stimulus spatialization, we filtered the stimuli with individually measured head-related transfer functions (HRTFs).

Pupil data. We recorded pupil dilations during the task using an eye tracker (EyeLink 1000 Plus; SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. Pupil data was first cleaned of blinks, gaps and recording artifacts, then z-scored and lowpass filtered at 4 Hz using a zero-phase, low-pass finite impulse response (FIR) filter. Pupil traces were baselined from -1500–0 ms before onset of defining stimulus (Fig. 2).

Results and discussion

A “low” and a “high” surprisal condition were constructed by aggregating all sections of a pupil trace within a sequence (excluding first and last motion) where a defining “low” or “high” stimulus (onset: 0 ms, Fig. 2) was preceded by two “low” stimuli (dashed vertical lines, Fig. 2) to form a mutual baseline. The average pupil traces continually show smaller evoked positive peaks at the rate of stimulus presentation in both conditions. Further, the “high” condition shows a positive deflection relative to the overall downwards trend elicited by the two preceding low-surprisal stimuli. We interpret the overall decay of pupil dilation as a result of several consecutive low surprisal stimuli in the chosen sections as a result of an overall demanding experimental paradigm, likely evoking rather high relative baseline uncertainty. Each pupil trace’s temporal derivative was averaged per participant and condition. A cluster-based permutation analysis (dependent samples *t*-test, FieldTrip version 20231220) over the duration of 0-2500 ms after onset of defining stimulus revealed a significant difference ($p < 0.05$) from 571 – 1249 ms. This cluster is generally in line with the expected delay of about a 1 second of the psychosensory pupil response (Mathot, 2018). While seemingly on the earlier side, arousal-related effects as early as 400 ms (Gingras et al., 2015) are documented in literature and peaks to salient auditory stimuli are expected at about 900 ms (Hoeks & Levelt, 1993). The presented pupil traces show a sensitivity to ongoing surprisal, elicited from an auditory low-level implicit perceptual discrimination task. Under the premise of pupil dilations reflecting involvement of the LC-NA arousal system, which is a simplified view at least (Grujic et al., 2024), this supports the notion of an arousal-modulated perceptual belief updating mechanism similar to those found in statistical learning (Lawson et al., 2021).

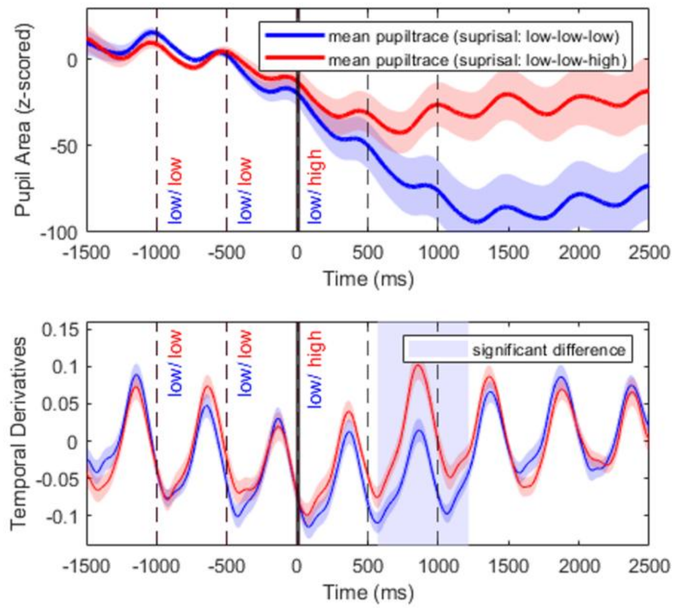

Figure 2: Pupil traces and derivatives per condition.

The presented study employs a pure perceptual discrimination task with a rapid temporal presentation of stimuli to eliminate higher cognitive processing and focus on single stimuli as much as possible. While this forces continuous integration of stimuli and online belief updating, it also pushes the temporal resolution (SOA = 500 ms) into faster territory, where pupil traces cease to be directly interpretable due to the relatively sluggish pupil response (~1 second; Mathot, 2018). To circumvent this limitation, we plan to extract each stimulus’s unique contribution to the pupil trace via deconvolution, enabling a continuous regression analysis of the relationship with surprisal.

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