Context-dependent modulations of sensory adaptation and pupil-linked arousal as substrates of flexible decision-making

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Abstract

Visual decisions typically require the accumulation of uncertain sensory evidence over time. To be effective in the real world, where evidence is often uncertain and unstable, the dynamics of this accumulation process must be flexible. Here, we examined sources of this flexibility by leveraging simultaneous psychophysics, electrophysiology, and pupillometry in non-human primates performing a visual decision-making task. We found that the rate of change of recent stimulus statistics (i.e., context stability) affected both the degree of sensory adaptation in single neurons encoding relevant sensory evidence and the dynamics of pupil diameter. These changes in evidence encoding and pupil-linked arousal depended on whether or not the monkeys tended to use flexible evidence accumulation during a given session, indicating a relationship between sensory adaptation, arousal, and evidence-integration behavior. Collectively, these findings demonstrate that context stability can affect both "bottom-up" evidence encoding in cortex and "top-down" arousal-related modulations that work together to support flexible decision-making behavior.

Introduction

Decision-making in uncertain and unstable environments requires flexible processing of sensory information (Glaze, Kable, & Gold, 2015; Murphy, Wilming, Hernandez-Bocanegra, Prat-Ortega, & Donner, 2021). One feature of this flexibility involves adaptive, leaky evidence accumulation, where the rate of leak depends on the level of environmental stability. Specifically, when the environment changes more frequently, people tend to accumulate evidence with a stronger leak. However, it remains unknown where and how the brain implements this stability-dependent leak. Here, we examined potential neural mechanisms from two complementary processes: (1) bottom-up, stimulus-dependent adjustments to the dynamics of adaptation in neurons that encode sensory evidence; and (2) top-down, context-dependent modulations by pupil-linked arousal systems.

Methods

Three rhesus macaques (An, Ch, and Mi) performed a modified version of the random-dot motion task in which each motion stimulus underwent a series of changes in direction (called "change-points"). These change-points occurred during a 2400 ms "adapting" epoch at either a low (1 change-point at 1200 ms) or high (5 change-points at 400 ms intervals) frequency, creating two context-stability conditions. As the monkey continued to fixate, the stimulus transitioned into a final, unchanging "testing" stimulus that lasted 100–1200 ms, after which the monkey reported the final motion direction with a saccade. For both low- and high-switch frequency conditions (LSF and HSF, respectively), there was a 50% chance that an additional change-point occurred between the adapting and testing stimulus, rendering a switch in motion direction prior to the behaviorally relevant stimulus equally likely.

While monkeys performed the task, we collected continuous measures of pupil diameter and recorded from single neurons in middle temporal area (MT), known to contribute causally to decisions about motion direction (Hanks, Ditterich, & Shadlen, 2006). All stimulus attributes were tailored to the tuning of the isolated MT neuron (e.g., the motion switched between preferred and anti-preferred, or "null", directions) to maximize potential effects of the adapting stimulus on stimulus encoding and integration (Van Wezel & Britten, 2002).

Results

Monkeys can perform context-stability-dependent evidence accumulation

The stability (e.g., switch rate) of the adapting stimulus affected how the testing stimulus, which remained unchanged between HSF and LSF conditions, was integrated. Both within (Figure 1A) and across (Figure 1B) sessions, monkeys were less sensitive to evidence as a function of viewing time at HSF relative to LSF, which is consistent with a normative, adaptive leak that depends on context stability.

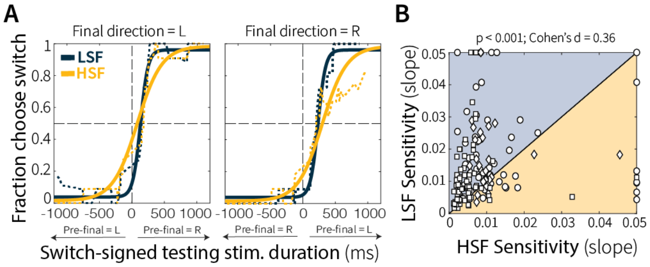

Figure 1: (A) Behavioral data (dotted) and psychometric fits (solid) for a representative session. LSF (blue) and HSF (orange) conditions were fit separately. Shallower slope fits imply leakier evidence accumulation and decreased perceptual sensitivity. (B) Comparison of slope fits for LSF and HSF conditions across sessions (An = 53 sessions, circles; Ch = 35, diamonds; Mi = 76, squares). On average, all three monkeys used leakier evidence accumulation at HSF, as predicted by normative models.

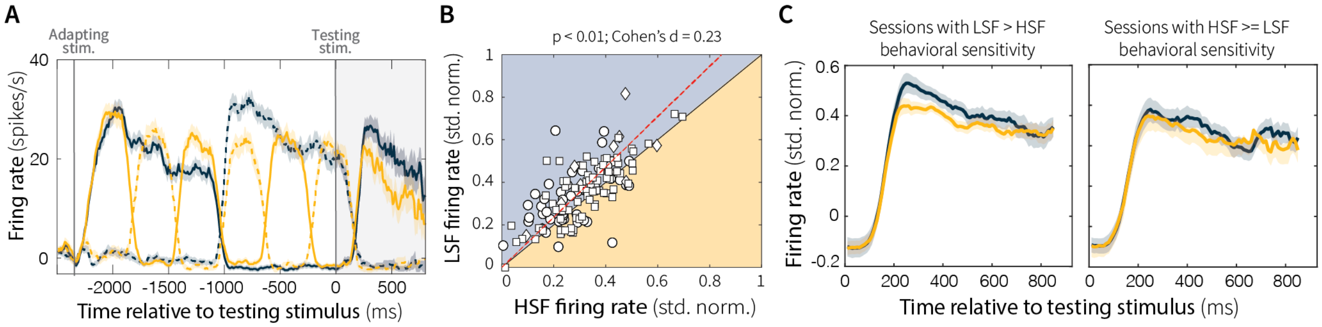

Figure 2: (A) Baseline-subtracted MT responses from a representative neuron. Solid and dashed lines indicate responses to motion in the unit's preferred and anti-preferred direction, respectively, relative to the testing stimulus. (B) Summary of average neural activity (baseline subtracted and normalized) during the testing stimulus for LSF and HSF conditions (red dashed line is a linear fit). (C) Mean±SEM MT activity for sessions in which the monkeys were more sensitive to evidence at LSF (left, n=123 units) vs. HSF (right, n=35).

Increased sensory adaptation relates to differences in evidence-accumulation behavior

For individual MT neurons, there was a marked reduction in responses to the testing stimulus at HSF relative to LSF (example in Figure 2A, summary in Figure 2B). This decreased responsiveness was not an innate difference between LSF and HSF conditions, given that neural activity was well matched between the two conditions early in the adapting epoch (Figure 2A). Instead, differences in evidence encoding appeared only after ongoing presentations of the stimuli alternating at different rates, suggesting a form of context-dependent sensory adaptation.

Across all recorded cells (An = 57; Ch = 13; Mi = 88), there was also a consistent relationship between the difference in sensory adaptation at LSF versus HSF and the overall firing rate (Figure 2B). The more strongly a neuron responded to preferred motion, the greater the difference in sensory adaptation between conditions. The same was true for neurons with sharper direction tuning, suggesting that MT neurons that more selectively and more strongly encode sensory evidence are more sensitive to its temporal statistics and stability.

To assess the functional consequence of this context-dependent sensory adaptation, we split sessions based on the monkeys' evidence-accumulation behavior (Figure 2C). For sessions in which the monkeys were less sensitive to the testing stimulus (i.e., performed leakier evidence accumulation) at HSF relative to LSF (points falling above the unity line in Figure 1B) there was more neural adaptation at HSF relative to LSF. Conversely, for days in which the monkeys were equally sensitive/leaky across switch frequency conditions or less sensitive/leakier at LSF (e.g., points falling below the unity line in Figure 1B), differences in sensory adaptation were diminished. This result is consistent with the idea that adaptation-driven differences in evidence encoding in MT underlie differences in evidence-accumulation behavior, perhaps implementing a form of context-dependent leakiness.

Pupil diameter is affected by context stability and correlates with evidence-accumulation behavior

Pupil diameter also depended on stimulus switch rate. These effects tended to increase gradually over the course of each trial, perhaps reflecting learned expectations about stimulus statistics that could be leveraged for decisions about the subsequent testing stimulus (Figure 3A).

Moreover, we found that the average stability-related differences in pupil diameter during the testing stimulus correlated with differences in the monkey's behavioral sensitivity (Figure 3B). As such, sessions with larger context-dependent differences in behavioral sensitivity tended also to have larger context-dependent differences in pupil diameter. These results imply that pupil-linked arousal systems may also play a role in flexible adjustments of the evidence-accumulation process.

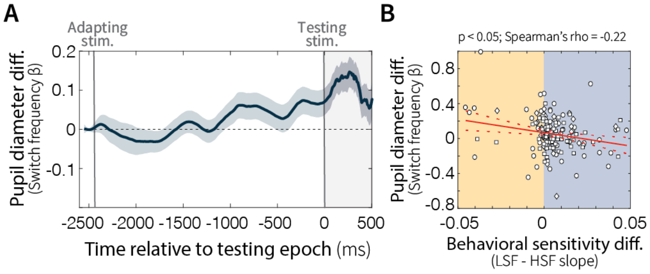

Figure 3: (A) Mean±SEM beta coefficients from linear regressions predicting pupil diameter using switch frequency condition, after controlling for baseline pupil diameter, eye position (microsaccades), and trial number (block effects). B) Correlation between the average difference in pupil diameter and difference in behavioral sensitivity for each session. Red line is a linear fit plus 95% confidence intervals.

Acknowledgments

Funding sources: R01 EY015260 and R01 MH127566 (J.I.G) & NSFGRFP DGE-1845298 (K.D.M). The authors thank Jean Zweigle for expert animal care.

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