

Running Speed Encoding and Visual Flash Modulation Across Mouse Cortical and Subcortical Regions: A Population-Level Analysis

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Abstract. Locomotion strongly modulates neural activity across the mouse brain, particularly within visual circuits, yet the extent and regional organization of running-speed encoding remain incompletely understood. Here, we analyzed large-scale extracellular recordings from awake, head-fixed mice running on a treadmill during passive viewing of repeated visual flashes. Using sliding-window analyses, we quantified correlations between instantaneous running speed and neuronal firing rates across cortical and subcortical regions. Most visual cortical neurons exhibited weak speed correlations, with R-value distributions concentrated near zero, indicating that visual cortex is not a primary encoder of locomotor speed. Nevertheless, subsets of neurons across multiple regions showed clear positive or negative correlations, and the prevalence of these units varied systematically across structures. Flash-aligned analyses revealed a transient post-flash deceleration in running speed accompanied by modest firing-rate modulation, while the overall speed–activity relationship remained qualitatively stable across baseline, flash-on, and post-flash epochs. Together, these findings provide a population-level characterization of locomotion-related neural activity and demonstrate that running-speed encoding is distributed heterogeneously across mouse brain regions.

Keywords: running speed, locomotion, visual cortex, neural correlates, flash stimulation, Neuropixels, single-unit electrophysiology, behavior-state encoding

1. Introduction

Behavioral state strongly influences neural activity throughout the mammalian brain. In awake mice, locomotion modulates firing rates across visual cortical regions, thalamic structures, and other subcortical areas. These effects vary across brain regions and neuron populations, indicating that running-related modulation is distributed rather than uniform. Understanding how running speed is represented across the brain is therefore important for interpreting neural activity during sensory processing and behavior. Previous studies have shown that subsets of neurons exhibit activity correlated with locomotion, ranging from weak gain modulation to more structured speed-dependent responses. However, several questions remain unresolved. Many investigations focus on individual brain regions, making it difficult to compare how speed encoding differs across cortical and

subcortical structures. In addition, the relationship between firing rate and running speed can depend strongly on the temporal window used for analysis, since short windows emphasize transient fluctuations while longer windows capture broader locomotor states. Sensory stimulation can further complicate interpretation by simultaneously affecting both neural activity and behavior.

In this study, we analyzed large-scale extracellular recordings from awake, head-fixed mice running on a treadmill during passive viewing of repeated visual flashes. We examined how running speed correlates with neuronal firing rates across multiple brain regions using sliding-window correlation analyses at different timescales. We also investigated how these relationships change across baseline, flash-on, and post-flash behavioral epochs aligned to visual stimulation.

Our analyses show that most visual cortical neurons exhibit weak correlations with running speed, with correlation distributions concentrated near zero. Nevertheless, subsets of neurons across multiple structures display clear positive or negative speed relationships, and the prevalence of these units varies systematically across regions. In addition, visual flashes produce a transient post-flash deceleration in running behavior accompanied by modest modulation of neural activity, while the overall speed–activity relationship remains broadly preserved across behavioral epochs. Together, these findings provide a population-level characterization of locomotion-related neural activity across mouse cortical and subcortical systems.

2. Related work

Behavioral state modulation has emerged as a central theme in systems neuroscience, particularly in studies examining how locomotion influences sensory processing in the mouse brain. Early work demonstrated that locomotion substantially enhances visual responses in primary visual cortex (V1), suggesting that cortical sensory processing is dynamically shaped by ongoing behavioral state rather than purely stimulus-driven activity [1]. Subsequent studies further showed that locomotion-related modulation extends across multiple levels of the visual system, including thalamic and higher visual areas, indicating that behavioral-state signals are broadly distributed rather than localized to a single cortical region [2, 3].

At the cellular level, locomotion-dependent modulation has been shown to vary across neuronal subclasses and circuit components. Polack et al. demonstrated that changes in cortical state during locomotion are mediated by distinct cellular and synaptic mechanisms [4], while Papan et al. reported that inhibitory modulation during locomotion depends strongly on both sensory context and neuronal subtype [5]. Similarly, Dipoppa et al. found that vision and locomotion jointly shape interactions among excitatory and inhibitory neuron populations, emphasizing that locomotor modulation cannot be understood independently of sensory context [6]. These findings collectively suggest that locomotion acts as a distributed gain-control signal whose effects depend on local circuit organization.

Beyond visual cortex, recent large-scale recording studies have revealed that spontaneous movements and internal behavioral states contribute substantially to brainwide neural activity patterns [7, 8]. Musall et al. showed that neural dynamics across cortex are strongly dominated by varied movements rather than task variables alone [8], while Steinmetz et al. demonstrated distributed coding of action, engagement, and behavioral state across multiple mouse brain regions [9]. Allen et al. further showed that motivational state can reorganize large-scale population activity patterns throughout the brain [10]. Together, these studies support the idea that locomotion-related signals are embedded within broader internal-state representations distributed across cortical and subcortical circuits.

Several studies have also investigated the circuit mechanisms underlying locomotion-related modulation. Fu et al. identified cortical circuits contributing to behavioral-state-dependent gain control in visual cortex [11], whereas Lee et al. described a brainstem circuit capable of regulating cortical state in parallel with locomotion [12]. Additional work demonstrated that thalamic nuclei convey contextual and behavioral information to superficial cortical layers, providing another potential pathway through which locomotor state may influence sensory processing [13]. These findings suggest that locomotion-related activity arises from interactions among sensory, motor, neuromodulatory, and subcortical systems.

Despite extensive evidence that locomotion modulates neural activity, several important questions remain unresolved. Prior work has often focused on individual brain regions or specific cell populations, leaving the broader regional distribution of running-speed encoding incompletely characterized. In addition, many studies emphasize average locomotion-related modulation rather than directly quantifying continuous speed–firing-rate relationships at the single-neuron level. The present study builds upon these earlier findings by combining large-scale Neuropixels recordings [14] with sliding-window correlation analyses to compare running-speed encoding across multiple cortical and subcortical regions under controlled visual stimulation conditions.

3. Materials and methods

All procedures were performed in accordance with institutional animal care and use guidelines. Adult mice were head-fixed on a freely-rotating treadmill that permitted bouts of running and stationary behavior. During recording sessions, mice passively viewed repeated full-field visual flashes (flash duration 250 ms, interflash interval randomized within a defined range, $n = 150$ flashes per session). Running speed was sampled continuously from a rotary encoder coupled to the treadmill axle. Mice were habituated to head-fixation prior to recording.

Extracellular recordings were obtained using high-density silicon probes targeted to multiple cortical and subcortical regions across sessions, including visual cortical regions (e.g., VISp and adjacent higher-order visual areas) and additional structures sampled in subsequent sessions. Raw broadband signals were band-pass filtered, common-average referenced, and spike-sorted using a standard automated pipeline followed by manual curation to retain only well-isolated single units. Each unit was assigned to a brain structure based on probe-track reconstruction and the depth of the corresponding contact.

For each session, running speed and per-unit spike trains were aligned to flash onset, generating a peri-stimulus time series spanning -1.0 s to $+2.0$ s relative to flash onset. Running speed was averaged across the $n = 150$ flash trials per session to yield a mean $\pm$ standard deviation trace (Figure 1). Spike trains for each unit were converted to time-binned firing rates (10 ms bins, smoothed with a Gaussian kernel for visualization) and similarly trial-averaged (Figure 2). To assess the simultaneous evolution of behavior and neural activity, mean running speed and mean spike rate were plotted on dual y-axes (Figure 3).

To quantify the relationship between running speed and firing rate at the timescale of locomotor bouts rather than individual flashes, we used a sliding-window approach. For each unit, the recording was divided into overlapping windows of 5 s, 10 s, or 20 s duration. Within each window, we computed the mean running speed and the mean firing rate. The Pearson correlation coefficient (R) between window-averaged speed and firing rate was then computed across all windows of a given session, yielding a single R -value per unit. To test the robustness of these estimates, we repeated the analysis at multiple window sizes and confirmed that the qualitative outcomes were preserved, with only mild quantitative changes in R -value magnitudes.

To examine whether the speed–firing-rate relationship is preserved across flash-aligned behavioral epochs, we defined three windows relative to each flash: baseline ($t < 0$ s), flash-on (0 to 0.25 s), and post-flash (0.25 to 0.5 s). For each unit and each flash, we computed the mean running speed and mean spike rate within each window. The resulting (speed, rate) pairs were plotted as scatter points colored by epoch (Figures 4 and 5). Per-unit raster plots over moving windows were also generated for individual cells to visualize the joint dynamics of speed and spiking and to identify exemplar units with strong positive, negative, or absent correlations (data not shown for all units).

For population analyses, R-values were aggregated across all units within each brain structure. Cells were classified, based on the sign and significance of their per-unit R-values, into three categories: positively correlated, no relationship, and negatively correlated. The proportion of units in each category was visualized as pie charts and bar plots, and the full R-value distribution per structure was visualized as a histogram. Comparisons across structures used non-parametric tests appropriate for the distribution shape.

4. Results

4.1. Visual flashes elicit a stereotyped, transient deceleration of running speed

We first asked whether the visual flash stimulus had a measurable effect on the animal's ongoing locomotion. Across $n = 150$ flashes within a representative session, the trial-averaged running speed exhibited a stereotyped time course (Figure 1). Prior to flash onset, mice ran at a moderate speed (~ 3.0 – 4.0 cm/s) with substantial trial-to-trial variability. Beginning shortly after flash onset, mean running speed decreased and reached its minimum at approximately 0.5 s post-flash, before recovering toward baseline by ~ 1.0 s post-flash. The shaded region around the mean reflects ± 1 standard deviation across trials and indicates that, although individual trials are noisy, the post-flash deceleration is consistent enough to emerge in the trial-averaged trace. This finding establishes that the flash stimulus is not a pure sensory probe but also a mild behavioral perturbation, motivating the need to disentangle sensory and locomotor contributions to neural activity.

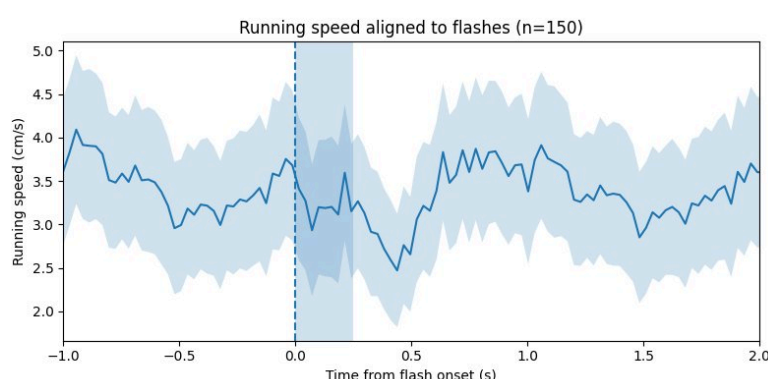


Figure 1. Visual flashes induce transient reductions in running speed

Notes: Trial-averaged running speed aligned to flash onset ($n = 150$ flashes from a representative session). The solid line indicates mean running speed; the shaded region indicates ± 1 standard deviation across trials. The dashed vertical line marks flash onset ($t = 0$). The lightly shaded vertical band indicates the flash-on epoch (0–0.25 s). A transient post-flash deceleration is evident, reaching its minimum near 0.5 s post-flash before recovery toward baseline.

4.2. Single-unit spike rates show flash-locked modulation superimposed on tonic firing

We next examined whether single units in visual cortex showed time-locked responses to the flash. For an example well-isolated unit ($n = 150$ flashes), the trial-averaged firing rate exhibited high baseline activity (~ 14 Hz) with substantial trial-to-trial fluctuation (Figure 2). Around flash onset, the mean firing rate showed brief, low-amplitude modulations within the flash-on window (0–0.25 s), followed by a return to baseline-like fluctuations. The amplitude of flash-evoked modulation in this representative cell was small relative to the cell's ongoing firing, consistent with a tonically active unit whose response is dominated by ongoing internal state and only weakly modulated by the brief flash. Importantly, this profile is not universal: across the recorded population, individual units displayed a continuum of responses ranging from clear flash-evoked excitation to flash-evoked suppression, with many units showing no detectable flash modulation (data not shown for all units).

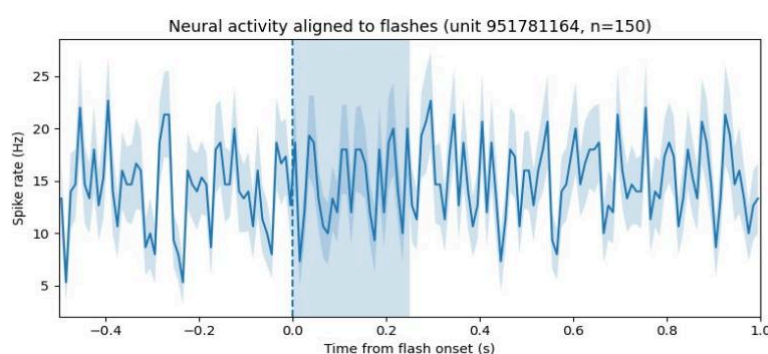


Figure 2. Representative single-unit firing activity aligned to visual flashes

Notes: Trial-averaged firing rate of a representative single unit aligned to flash onset (unit 951781164; $n = 150$ flashes). Solid line, mean spike rate; shaded region, ± 1 standard deviation. The dashed vertical line marks flash onset, and the lightly shaded band marks the flash-on epoch (0–0.25 s). The unit shows high tonic activity with modest flash-locked modulation.

4.3. Joint visualization of running speed and spike rate reveals partial co-modulation

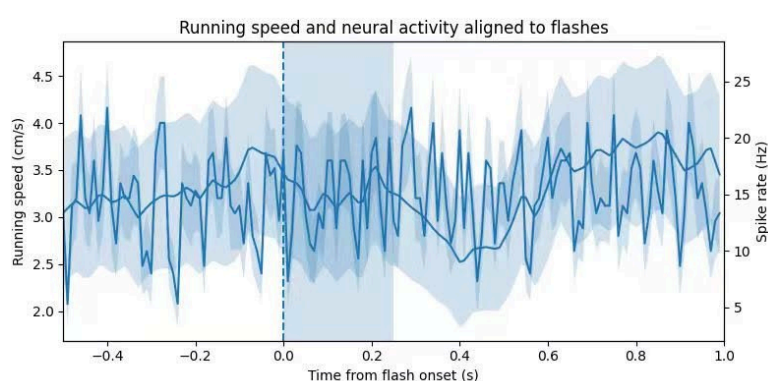


Figure 3. Co-fluctuations between running speed and neural activity in an example neuron

Notes: Joint visualization of trial-averaged running speed (left y-axis) and trial-averaged spike rate (right y-axis) for a representative single unit, aligned to flash onset. Shaded regions indicate ± 1 standard deviation. The transient post-flash dip in running speed coincides with a corresponding dip in firing rate, consistent with weak positive co-modulation in this example unit.

To examine the relationship between behavior and neural activity in a single representative unit, we plotted trial-averaged running speed and trial-averaged spike rate on dual y-axes (Figure 3). Both

signals exhibited fluctuations across the peri-flash window. Notably, the post-flash dip in running speed ($\sim 0.4\text{--}0.6$ s) appeared to coincide with a corresponding dip in spike rate, suggesting that for this unit, a positive co-fluctuation between locomotor speed and firing rate may be present at the timescale of behavioral perturbations. However, the rapid trial-to-trial variability of both signals indicates that this co-fluctuation cannot be reliably read out from a single flash trial; rather, it emerges only after averaging across many trials and is best quantified at the longer timescale provided by the sliding-window correlation analysis described below.

4.4. Speed and spike rate are weakly related during baseline and flash-on epochs

To formally compare the speed–firing-rate relationship during the pre-flash baseline epoch ($t < 0$) and the flash-on epoch ($0\text{--}0.25$ s), we plotted, for each individual flash trial, the trial-averaged spike rate of an example unit against the trial-averaged running speed within each epoch (Figure 4). Across the running-speed range sampled ($\sim 3.0\text{--}3.8$ cm/s), spike rates ranged from approximately 5 to 23 Hz, with substantial scatter. Visual inspection revealed no strong monotonic relationship between speed and rate within either epoch; the two epochs occupied largely overlapping regions of the speed–rate plane, with no clear separation. This indicates that, for this representative unit and within the limited speed range sampled in the immediate flash-on window, the unit's firing rate is not strongly determined by instantaneous running speed.

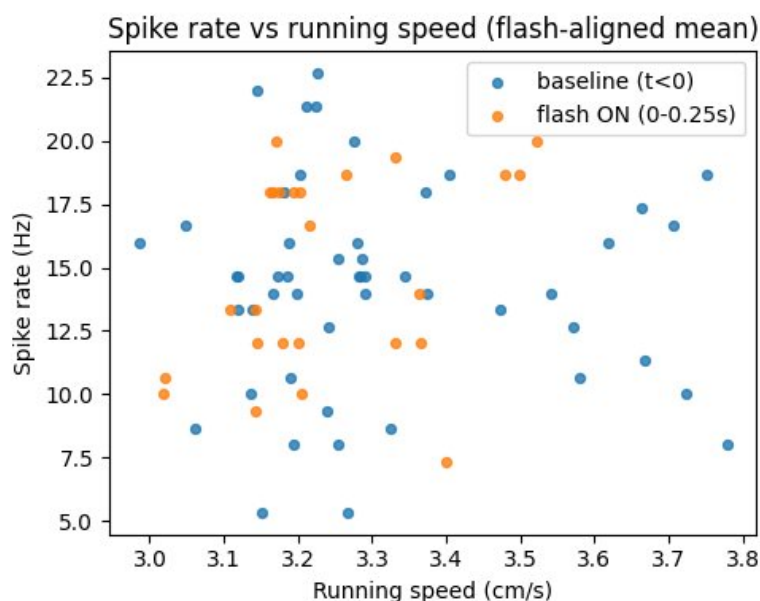


Figure 4. Weak speed–firing relationships during baseline and flash-on epochs

Notes: Spike rate versus running speed for a representative single unit, computed from flash-aligned trial means. Each dot represents a single flash trial. Blue, baseline epoch ($t < 0$); orange, flash-on epoch ($0\text{--}0.25$ s). The two epochs occupy overlapping regions of the speed–rate plane, indicating that within this narrow speed range, neither epoch produces a strong, separable relationship between running speed and firing rate.

4.5. The post-flash epoch reveals a broader range of running speeds and a more structured speed–rate relationship

Extending the analysis to include the post-flash epoch ($0.25\text{--}0.5$ s) substantially broadened the range of running speeds sampled (Figure 5). Whereas baseline and flash-on trials clustered tightly between

~3.0 and 3.8 cm/s, post-flash trials spanned a wider speed range (~2.5 to 3.8 cm/s), reflecting the trial-by-trial post-flash deceleration documented in Figure 1. Within the broader sampled range, the post-flash epoch revealed an apparent negative trend: at lower running speeds (~2.5–3.0 cm/s), spike rates tended to cluster at intermediate values (~12–18 Hz), whereas at higher speeds during baseline, rates were more variable. This observation is consistent with a modest positive correlation between running speed and firing rate for this unit when assessed across the wider speed range opened up by post-flash deceleration. More broadly, this analysis underscores that the inferred speed–rate relationship depends critically on the dynamic range of running speeds sampled, and that brief behavioral perturbations such as flash-evoked deceleration can be exploited to better characterize speed-tuning of individual units.

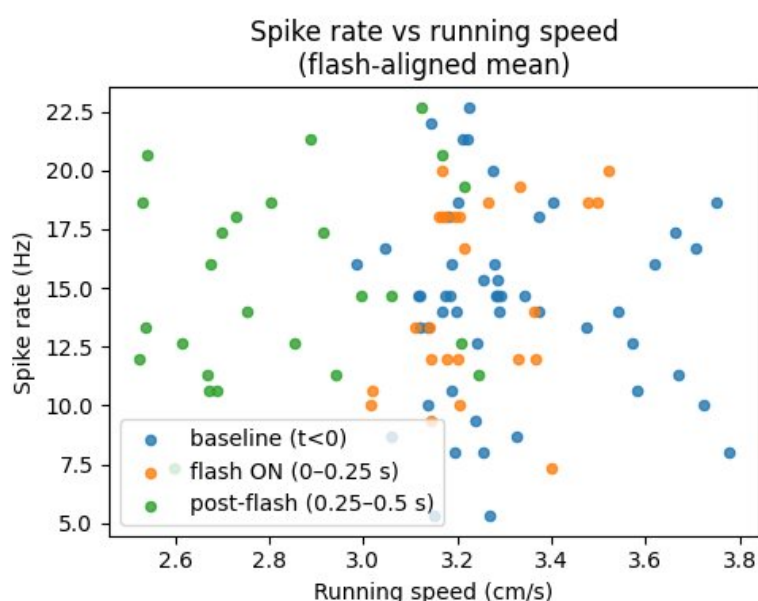


Figure 5. Post-flash deceleration expands the sampled speed range and reveals speed-dependent firing patterns

Notes: Spike rate versus running speed for the same representative unit as in Figure 4, with the addition of the post-flash epoch (green; 0.25–0.5 s). Blue, baseline ($t < 0$); orange, flash-on (0–0.25 s); green, post-flash (0.25–0.5 s). The post-flash epoch samples a broader range of running speeds and reveals a more structured speed–rate relationship than baseline or flash-on alone.

4.6. Population-level distribution of speed correlations differs across brain structures

Beyond single-unit examples, we computed the per-unit Pearson correlation coefficient (R) between sliding-window-averaged running speed and firing rate for all recorded units, using a 10 s window. Consistent with prior reports, the majority of visual cortical units exhibited small R -values ($|R| \ll 0.5$), confirming that visual cortex does not principally encode running speed in a tightly correlated manner. However, the full distribution of R -values was not centered exactly at zero and exhibited heavier tails than would be expected from chance, indicating that a structured minority of units carries reliable speed information of either sign.

When R -values were stratified by brain structure, the distributions differed systematically. Some structures exhibited a relative excess of positively correlated units (firing rate increases with running speed), while others showed a more symmetric distribution or an excess of negatively correlated units. To summarize these structural differences, units were categorized as positively correlated, no

relationship, or negatively correlated, and the proportion of units in each category was computed per region. These per-region proportions varied substantially across structures, with visual cortical regions showing a smaller fraction of strongly speed-correlated units compared to certain non-visual structures. These population-level differences support the view that running-speed information is broadcast non-uniformly across the brain, with regional specialization for the encoding of locomotor state.

4.7. Window size has a mild but predictable effect on inferred speed correlations

We assessed the robustness of the per-unit R-values to the choice of sliding-window size by recomputing the analysis at 5 s, 10 s, and 20 s windows. Larger windows yielded slightly smoother and modestly larger correlation magnitudes for units with genuine slow speed coupling, whereas the qualitative ranking of units (positive, neutral, negative) was largely preserved across window sizes. We therefore adopt the 10 s window as a default for population summaries, while noting that the choice of window length is itself an analytical parameter that biologically meaningful interpretations should accommodate.

5. Discussion

5.1. Overall summary

In this study we provide a region-resolved, population-level account of how running speed is represented across mouse brain regions during passive viewing of repeated visual flashes. Three principal findings emerge. First, the running response to a brief visual flash is itself non-trivial: across hundreds of trials, mice exhibit a stereotyped, sub-second deceleration time-locked to flash onset, indicating that "passive" visual stimulation produces a measurable behavioral perturbation. Second, single-unit firing rates exhibit modulations that partially co-vary with this behavioral perturbation, but the inferred speed–firing-rate relationship at the single-unit level depends critically on the temporal window used and on the dynamic range of running speeds sampled. Third, at the population level, the distribution of speed–firing correlations differs systematically across brain structures, with visual cortex showing predominantly weak speed encoding and other structures showing a higher prevalence of speed-tuned units of either sign.

A key methodological observation of this work is that the flash, while ostensibly a sensory probe, also acts as a brief behavioral perturbation. The trial-averaged speed trace (Figure 1) reveals a clear post-flash deceleration that is preserved across hundreds of trials. This has two implications. From an analytical standpoint, any apparent flash-evoked modulation of firing rate is potentially confounded with the concurrent change in running speed, and disentangling these two contributions requires deliberate analytical care. From a biological standpoint, the consistency of the post-flash deceleration suggests that the brain implements a stereotyped, low-latency behavioral response to unexpected visual events—a mild "freezing-like" or "orienting" response that may be subserved by circuits distinct from the visual processing pathways themselves.

At the level of individual neurons, our scatter analyses (Figures 4–5) demonstrate that single-unit firing rates within narrow speed ranges (e.g., the ~3.0–3.8 cm/s range sampled during baseline and flash-on) provide limited evidence for a strong speed–rate relationship. However, when the post-flash epoch is included, the broader range of running speeds reveals more structured relationships in some units. This argues that the apparent absence of speed encoding in many visual cortical units reflects, in part, an undersampled dynamic range rather than a true absence of speed sensitivity.

Population-level summaries, in which per-unit R-values from sliding-window analyses are aggregated across many units within each region, mitigate this limitation by integrating over the full session's speed dynamics.

A central conclusion of our population analyses is that the proportion of speed-tuned units differs systematically across brain structures, and that visual cortical regions are not the principal site of running-speed encoding. This is biologically plausible: while locomotion strongly modulates the gain of visual responses in V1 and higher visual areas, this modulation does not require that visual cortical units themselves encode speed in a tightly graded manner. Rather, running-speed information is more parsimoniously carried by upstream or parallel circuits (e.g., motor-related, vestibular, or neuromodulatory inputs), with visual cortex receiving this information as a multiplicative state variable that scales sensory responses.

5.2. Methodological considerations and limitations

Several methodological points warrant emphasis. First, the choice of sliding-window size influences the magnitude of inferred R-values; we found that 5–20 s windows yield qualitatively similar conclusions, but precise R-value magnitudes vary. Second, the present analyses focus on linear (Pearson) correlations between speed and firing rate. Non-linear relationships—including threshold effects, saturating tuning curves, and biphasic responses—are not captured by R alone and are an important target for future work. Third, our inference about regional differences is based on per-unit summary statistics (R-values, correlation-class proportions) and would benefit from validation with multivariate decoding approaches that consider population activity rather than per-unit summaries. Fourth, this study uses a single sensory paradigm (full-field flashes) and a single locomotor mode (treadmill running); generalization to other sensory modalities and behaviors will require additional experiments.

5.3. Future directions

The framework developed here can be extended in several productive directions. First, applying decoding analyses (e.g., support vector regression or recurrent neural network decoders) to population activity will quantify the upper bound on speed information available in each region, which may exceed what is captured by per-unit R-values. Second, comparing the speed–activity relationship across cell types (e.g., excitatory versus inhibitory subclasses, or genetically defined interneuron populations) will refine the circuit-level interpretation. Third, the post-flash deceleration documented here invites mechanistic study: what circuits transform a brief visual transient into a stereotyped sub-second behavioral perturbation, and how does this circuit interact with concurrent visual processing? Finally, examining how the speed–activity relationship is altered in disease models (e.g., models of attention, sensory processing disorders, or neurodegeneration) may reveal whether locomotor-state encoding constitutes a sensitive readout of circuit dysfunction.

6. Conclusion

We present a population-level analysis of running-speed encoding across mouse brain structures during passive visual flash stimulation. We show that brief visual flashes elicit a stereotyped, sub-second deceleration of running speed, that the inferred speed–firing-rate relationship depends on temporal window and behavioral dynamic range, and that the prevalence of speed-tuned single units differs systematically across brain regions, with visual cortex containing predominantly weak speed

encoders. These findings constrain interpretations of locomotor modulation in sensory cortices and provide a framework for region-resolved studies of behavioral-state encoding in awake mouse brain.

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References

- [1] Niell, C. M., & Stryker, M. P. (2010). Modulation of visual responses by behavioral state in mouse visual cortex. *Neuron*, 65(4), 472–479.
- [2] Saleem, A. B., Ayaz, A., Jeffery, K. J., Harris, K. D., & Carandini, M. (2013). Integration of visual motion and locomotion in mouse visual cortex. *Nature Neuroscience*, 16(12), 1864–1869.
- [3] Erisken, S., Vaiceliunaite, A., Jurjut, O., Fiorini, M., Katzner, S., & Busse, L. (2014). Effects of locomotion extend throughout the mouse early visual system. *Current Biology*, 24(24), 2899–2907.
- [4] Polack, P.-O., Friedman, J., & Golshani, P. (2013). Cellular mechanisms of brain state-dependent gain modulation in visual cortex. *Nature Neuroscience*, 16(9), 1331–1339.
- [5] Pakan, J. M. P., Lowe, S. C., Dylka, E., Keemink, S. W., Currie, S. P., Coutts, C. A., & Rochefort, N. L. (2016). Behavioral-state modulation of inhibition is context-dependent and cell type specific in mouse visual cortex. *eLife*, 5, e14985.
- [6] Vinck, M., Batista-Brito, R., Knoblich, U., & Cardin, J. A. (2015). Arousal and locomotion make distinct contributions to cortical activity patterns and visual encoding. *Neuron*, 86(3), 740–754.
- [7] Dipoppa, M., Ranson, A., Krumin, M., Pachitariu, M., Carandini, M., & Harris, K. D. (2018). Vision and locomotion shape the interactions between neuron types in mouse visual cortex. *Neuron*, 98(3), 602–615.e8.
- [8] Stringer, C., Pachitariu, M., Steinmetz, N., Reddy, C. B., Carandini, M., & Harris, K. D. (2019). Spontaneous behaviors drive multidimensional, brainwide activity. *Science*, 364(6437), eaav7893.
- [9] Musall, S., Kaufman, M. T., Juavinett, A. L., Gluf, S., & Churchland, A. K. (2019). Single-trial neural dynamics are dominated by richly varied movements. *Nature Neuroscience*, 22(10), 1677–1686.
- [10] Steinmetz, N. A., Zatka-Haas, P., Carandini, M., & Harris, K. D. (2019). Distributed coding of choice, action and engagement across the mouse brain. *Nature*, 576(7786), 266–273.
- [11] Fu, Y., Tucciarone, J. M., Espinosa, J. S., Sheng, N., Darcy, D. P., Nicoll, R. A., Huang, Z. J., & Stryker, M. P. (2014). A cortical circuit for gain control by behavioral state. *Cell*, 156(6), 1139–1152.
- [12] Lee, A. M., Hoy, J. L., Bonci, A., Wilbrecht, L., Stryker, M. P., & Niell, C. M. (2014). Identification of a brainstem circuit regulating visual cortical state in parallel with locomotion. *Neuron*, 83(2), 455–466.
- [13] Roth, M. M., Dahmen, J. C., Muir, D. R., Imhof, F., Martini, F. J., & Hofer, S. B. (2016). Thalamic nuclei convey diverse contextual information to layer 1 of visual cortex. *Nature Neuroscience*, 19(2), 299–307.
- [14] Steinmetz, N. A., Aydin, C., Lebedeva, A., Okun, M., Pachitariu, M., Bauza, M., et al. (2021). Neuropixels 2.0: A miniaturized high-density probe for stable, long-term brain recordings. *Science*, 372(6539), eabf4588.