Annual Review of Neuroscience

Ecological Visual Processing in the Mouse

Cristopher M. Niell,[1,*] Michael Beyeler,[2,*] Michael J. Goard,[3,*] and Spencer LaVere Smith[4,*]

[1]Institute of Neuroscience and Department of Biology, University of Oregon, Eugene, Oregon, USA; email: cniell@uoregon.edu

[2]Departments of Computer Science and Psychological & Brain Sciences, University of California, Santa Barbara, California, USA; email: mbeyeler@ucsb.edu

[3]Departments of Psychological & Brain Sciences and Molecular, Cellular, and Developmental Biology, University of California, Santa Barbara, California, USA; email: michaelgoard@ucsb.edu

[4]Department of Electrical & Computer Engineering, University of California, Santa Barbara, California, USA; email: sls@ucsb.edu

Annu. Rev. Neurosci. 2026. 49:189–209

First published as a Review in Advance on March 20, 2026

The *Annual Review of Neuroscience* is online at neuro.annualreviews.org

https://doi.org/10.1146/annurev-neuro-112723-040446

*These authors contributed equally to this article

Keywords

visual cortex, superior colliculus, motion processing, active sensing, scene analysis, navigation

Abstract

Visual systems evolved to extract behaviorally relevant information while animals move through and interact with their world. Such ecological vision differs fundamentally from standard laboratory paradigms in many key aspects, making this a much harder problem for the brain to solve, and for the neuroscientist to study. However, emerging technologies and experimental approaches have enabled investigation of visual computations under these ecological conditions. These approaches are particularly powerful in the mouse, combining well-developed genetic tools, high-throughput recordings, and quantifiable ethological tasks. Here we review computations that are engaged in ecological contexts, including active sensing, motion processing, scene analysis, distance estimation, and spatial perception. We delineate experimental approaches that engage these computations and synthesize current understanding of their neural implementations based on mouse research. These studies reveal how ecological vision engages distinct processing strategies and novel neural circuitry, while highlighting the vast territory that remains unexplored in understanding real-world visual computation.

Contents

1. INTRODUCTION

Vision is fundamentally an active modality that enables interaction with the world. Yet much vision research has focused on passive viewing paradigms or discrimination of simple stimuli. This provides a powerful approach to study the processing of specific features such as orientation selectivity and object identity, as well as revealing general principles of neural circuit computation (Niell & Scanziani 2021). However, it leaves vast territories of visual function unexplored, particularly those computations engaged when animals actively navigate and interact with their environments.

The ecological approach to vision, articulated in the classic work of J.J. Gibson (1979), recognizes that visual systems evolved not for abstract scene reconstruction but for guiding behavior in complex environments. Here we emphasize three key principles that distinguish ecological vision from standard lab paradigms for vision. First, natural visual input consists of rich, dynamic information from complex 3D scenes rather than impoverished laboratory stimuli. Second, vision operates through active exploration, with animals continuously moving their eyes, heads, and bodies to sample their environment. Third, visual processing is inherently coupled to specific behavioral needs, extracting task-relevant information rather than (or in addition to) building general-purpose representations. Here we review the computational challenges that the visual system must solve to function in this context (**Figure 1**), enabling successful interaction with natural environments.

The mouse provides an excellent model system for investigating ecological vision because it must achieve many of the fundamental behavioral goals shared across species, such as navigating complex environments, detecting predators, and identifying food sources. In fact, these aspects of natural vision, and the associated challenges, are more likely what the mouse visual system evolved for than the standard lab paradigms that are often used in the mouse. Combined with powerful genetic tools for circuit dissection (Huberman & Niell 2011, Luo et al. 2008) and amenability to both virtual reality paradigms (Harvey et al. 2009, Saleem et al. 2018) and freely moving behavioral studies (Skyberg & Niell 2024), the mouse enables detailed mechanistic investigation of visual computations in naturalistic contexts.

In this review we focus on the broad computational challenges inherent in ecological vision and discuss the neural circuit mechanisms implementing these computations where known. We do not focus on specific visually guided behaviors, which have been reviewed elsewhere (Branco & Redgrave 2020, Saleem & Busse 2023, Skyberg & Niell 2024, Zhao et al. 2023), although we do examine how behavioral demands provide experimental access and reveal distinct computational strategies. Notably, our understanding of neural circuits for ecological vision remains far more

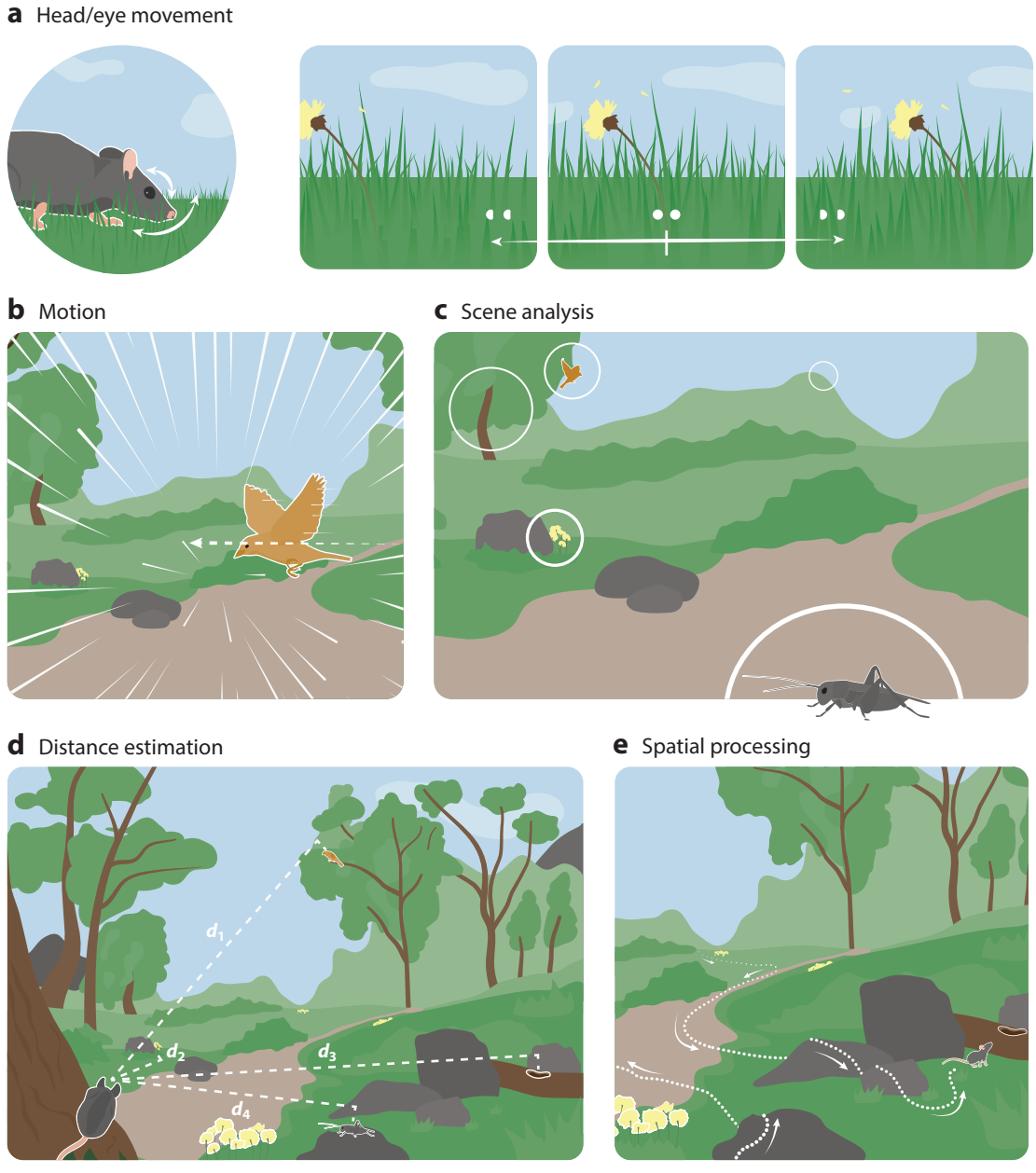

Figure 1

Overview of computational challenges in ecological vision reviewed here. (*a*) Head and eye movements allow active sensing and shape visual input through stabilization and gaze shifts. (*b*) Multiple forms of motion processing are required, including optic flow induced by locomotion and object motion. (*c*) Complex scene analysis to identify object and landmarks involves challenges such as texture and occlusion. (*d*) Estimation of distance to points in the scene is enabled by a range of binocular and monocular cues. (*e*) Spatial processing enables navigation through the environment. Figure adapted from images created by Gil Costa.

MODEL ALIGNMENT UNDER ECOLOGICAL OBJECTIVES

In fitting quantitative models to neural coding, the target objective matters. In current models, mouse cortex aligns better with shallower, lower-resolution, self-supervised (contrastive) models, while the primate ventral stream aligns with deeper, category-supervised pipelines (Nayebi et al. 2023). Cross-species evaluation improves with sparse-positive alignment metrics that capture species-specific inductive biases rather than neuron-wise matching (Conwell et al. 2024). Consistent with this view, Xu et al. (2023) showed that a multimodal V1 model in freely moving mice exhibits mixed selectivity to visual and self-motion variables—an early integration signature expected under ecology-first objectives. Looking ahead, foundation models trained on large, multimouse, multimodal datasets can capture broad regularities and generalize across stimuli and animals, supporting tasks from neural prediction to cell type inference (Wang et al. 2025). Objectives emphasizing stability under self-motion, affordance detection, and rapid threat/opportunity routing likely shape mouse codes as much as anatomy, yielding concrete hypotheses (e.g., low-rank flow decomposition, prediction-error parsing) and sharper task suites to bridge mouse and primate vision.

limited than for classical visual processing, and so we emphasize new approaches and important directions for future inquiry.

2. MOUSE VISION FROM AN ECOLOGICAL PERSPECTIVE

We first provide an overview of mouse vision, in terms of visual system organization, visual environment, and experimental tools, to provide context for its use in studying ecological vision. These factors are also likely to serve as important constraints in computational models of visual processing in the mouse (see the sidebar titled Model Alignment Under Ecological Objectives).

The mouse visual system shares many aspects of the general mammalian organization, including that of primates. This includes the major cell types of the retina, pathways from retina to thalamus to cortex, the layered structure of cortex, and the presence of a number of higher visual areas (HVAs) beyond primary visual cortex (V1) (Busse 2018, Glickfeld & Olsen 2017, Hübener 2003, Huberman & Niell 2011, Seabrook et al. 2017). Mice also share the pathway from retina to superior colliculus (SC), and in fact this pathway dwarfs that of primates, with the majority of retinal ganglion cells (RGCs) projecting to SC, in contrast to a small fraction projecting in the primate. In this sense, mice represent an evolutionary intermediate between nonmammalian vertebrates such as fish, birds, and reptiles, where the optic tectum (homolog of SC) dominates, and primates, where the cortical pathway dominates (Knudsen 2020).

An important constraint on mouse vision is their small eyes and correspondingly low spatial resolution, roughly 100-fold lower than primate peak acuity. This difference is compounded by the fact that mice lack a fovea that could create a region of enhanced acuity. It also makes the mouse retina more uniform than that of primates, although recent evidence supports a region of increased density of one RGC type (Bleckert et al. 2014), suggested to be evolutionarily related to primate midget ganglion cells (Hahn et al. 2023), in the central lower visual field. This region, which has been termed the focea or functional focus, has increased cortical representation (van Beest et al. 2021) and may represent a behaviorally relevant specialization (Holmgren et al. 2021). The mouse retina is rod dominated, with only a small fraction, roughly 3%, of cones (Jeon et al. 1998). These cones express opsins centered on green and ultraviolet (UV), with many cones coexpressing both opsins, and UV opsins concentrated in the upper visual field (Applebury et al. 2000). Furthermore, their eyes are on the sides of the head, resulting in a large lateral field of view but limited binocular overlap of approximately 40°. The combination of lateral eyes, low spatial resolution, and a

rod-dominated retina makes mouse vision overall most analogous to peripheral vision in primates. The small eye size eliminates the need for accommodation, maintaining focus across their visual range (Balkema & Pinto 1982). As discussed below, mice make a range of eye movements, including both vestibulo-ocular reflex (VOR) and optokinetic reflex (OKR) stabilization and rapid saccades, with a typical range of up to 20° (Ambrad Giovannetti & Rancz 2024).

The visual statistics of the mouse's natural environment differ dramatically from typical laboratory stimuli or even standard natural scene databases collected from human eye height. Recent studies have provided quantitative assessment of the static scene statistics from the mouse's perspective. This has revealed differences in spectral wavelength distributions matched to the cone densities (Qiu et al. 2021), and the statistics of the scene are also reflected in variations in spatial receptive fields across the retina (Gupta et al. 2023). Less is known about the dynamic properties of the visual scene. Video from freely walking humans has shown how self-movement patterns dramatically alter scene dynamics, in ways that can be both a confound and informative about the visual scene (Matthis et al. 2022). Mice experience a ground-level view characterized by rapid self-motion through cluttered environments, creating dynamic optic flow patterns fundamentally different from the static images or even natural movies (generally popular culture movies, from a human viewpoint) often used in experiments.

While their spatial resolution is relatively low compared to many mammals, mice are able to adeptly use their vision for diverse behavioral goals. These goals include detecting and avoiding overhead threats (Yilmaz & Meister 2013), capturing prey through visually guided pursuit (Hoy et al. 2016), estimating distance to guide movement (Boone et al. 2021, Parker et al. 2022a), navigating to safety (Campagner et al. 2023, Morris et al. 1982), and recognizing conspecifics for social interactions (Greer et al. 2025). These natural behaviors demonstrate sophisticated visual capabilities that may be surprising given the apparent difficulty mice have with some simple laboratory discrimination tasks.

Indeed, the notion that mice have supposedly poor vision is perpetuated by experimental paradigms that may not engage their natural visual capabilities. While mice take extended time to learn, and often employ alternate strategies for, two-alternative forced-choice discriminations of seemingly distinct stimuli (Ashwood et al. 2022, Busse et al. 2011, Luongo et al. 2023), especially under head-fixed conditions, they readily master complex visual tasks that better match their ecological needs. In fact, many ecologically relevant behaviors require no training whatsoever: Prey capture, predator avoidance, and gap jumping emerge spontaneously in the appropriate behavioral context. Furthermore, it is apparent that mice can use many visual features that take effort to train. For example, mice may take weeks to learn to discriminate a horizontal versus vertical stimulus (Wekselblatt et al. 2016), but they readily jump onto horizontal surfaces (Parker et al. 2022a) and do not jump onto vertical ones (i.e., walls). This apparent paradox—that mice are challenged in performing standard primate-centric tasks but naturally perform a number of ethological tasks using the same information—suggests the challenge lies not in visual discrimination but in mapping arbitrary visual features to learned behavioral responses and finding ways to reinforce those mappings in training paradigms. This also limits the ability to use trained tasks to assay what a mouse can see, as mice may very well be able to see a feature, but they simply do not learn to associate it with an arbitrary action and reward.

In addition to the genetic tools that helped establish the mouse as a model for studying vision (Huberman & Niell 2011, Luo et al. 2008), there are also a range of recent experimental approaches that have been developed to better engage ecological vision while maintaining experimental accessibility and control. Notably, these approaches must concurrently solve the challenges of measuring neural activity during naturalistic interaction with the environment, and either measuring or controlling the visual input in such conditions. Freely moving paradigms

with head-mounted recording devices allow unrestrained interactions with the environment (Newman et al. 2025), while head-mounted cameras enable eye tracking and reconstruction of retinal input (Meyer et al. 2018, Parker et al. 2022b). Neural recording capabilities during free movement are limited compared to head fixation, though advances in high-density silicon probes (Steinmetz et al. 2021) and miniaturized two-photon microscopes (Zong et al. 2022) help narrow the gap. On the other hand, in head-fixed conditions, virtual reality systems provide precise stimulus control and enable extensive neural recordings and manipulations, though they sacrifice real-world physical interactions. Intermediate approaches, such as air-lifted platforms (Kislin et al. 2014) and rotating imaging systems (Voigts & Harnett 2020), have the potential to combine benefits of both paradigms. These complementary experimental approaches, together with computational methods to quantify continuous behavior and relate it to neural activity (Datta et al. 2019, Mathis & Mathis 2025, Pereira et al. 2020), provide the tools necessary to investigate how visual computations operate under ecological conditions.

3. ECOLOGICAL VISUAL COMPUTATIONS

3.1. Active Sensing and Head/Eye Movements

Active sensing enables animals to strategically acquire visual information through coordinated movements of their sensory apparatus. While animals must move to achieve behavioral goals, they can also reposition their head and eye to gather information. In primates, including humans, targeted saccades direct gaze toward task-relevant features, demonstrating active visual sampling strategies (Hayhoe & Ballard 2005, Yarbus 1967).

3.1.1. Head and eye movements during behavior. Recent advances using miniature head-mounted cameras have revealed the complexity of mouse eye movements during natural behavior. Mice and rats employ compensatory mechanisms to stabilize their visual field during locomotion (Meyer et al. 2020, Michaiel et al. 2020, Wallace et al. 2013), but due to the lateral positioning and angular orientation of their eyes, these compensatory movements differ markedly from those of primates. For instance, when tilting the head downward, mice move their eyes upward and backward while simultaneously rotating around the pupil axis (cyclotorsion). However, compensatory movements have limited range, particularly along the horizontal axis, necessitating rapid reset saccades—the quick phase of the VOR. Together, this creates a saccade-and-fixate pattern seen across the animal kingdom (Land 1999), resulting in rapid shifts of the visual input when the eye saccades, interspersed between periods of stabilized visual input when the head and eyes move in opposite directions (compensatory/fixation). These saccades occur frequently during both free exploration and targeted behaviors (Meyer et al. 2020, Michaiel et al. 2020) but do not appear to target specific points such as prey (Michaiel et al. 2020). During prey capture, mice do position prey targets in the focea (described above), which also corresponds to the region of low optic flow (Holmgren et al. 2021), though whether this reflects active visual targeting or is primarily a consequence of aiming the head toward prey to facilitate capture is unclear. It remains possible that concurrent head- and eye-orienting movements could serve as a rapid targeting mechanism, as seen in primates (Bizzi et al. 1972).

Notably, this also means that eye movements are tightly coupled to head movements, raising important caveats about the study of eye movements in head-fixed preparations. In fact, saccades in head-fixed mice have been shown to correspond to attempts to move the head, rather than independent movements of the eyes themselves, based on measurements of the force applied to the head restraint during saccades (Meyer et al. 2020, Zahler et al. 2021).

These movement patterns have subsequent implications for the nature of the visual input. Given their low spatial resolution and relatively large retinal specializations, mice may not

require precise eye positioning for target acquisition, as in primate saccades that bring relevant stimuli to the fovea. Thus, rather than information acquisition, that is, collecting new visual input, mouse eye movements may be best considered as primarily serving for information formatting, that is, putting the retinal input into a form that is useful for neural processing. Without compensatory mechanisms, every head or body movement would sweep images across the retina, creating a challenging image-processing problem. Instead, the VOR and OKR create a biological "steadycam," segmenting visual experience into stable epochs separated by saccadic transitions, with the abrupt shift of saccades providing a discrete time point for arrival of new visual input and subsequent processing. Stabilizing movements also maintain alignment between retinal specializations and environmental features, such as the vertical gradient of cone sensitivity (Qiu et al. 2021) and receptive field structure relative to the horizon (Gupta et al. 2023).

3.1.2. Neural processing in head and eye movements. The pattern of head and eye movements also has significant consequences for the neural processing of visual input. As noted above, rather than parsing a continuous visual scene, the brain must analyze short sequences of stabilized input interspersed by abrupt gaze shifts. Additionally, it must stitch together the different views of the world that result from the jumps in gaze direction.

The impact of the saccade-and-fixate pattern on processing in V1 was recently studied by combining head-mounted eye tracking with chronic electrophysiology (Parker et al. 2023). This revealed that each gaze shift results in a temporal sequence of activity across the population, from neurons responding immediately after the saccade to neurons responding primarily during the subsequent fixation. This sequence also corresponded to spatial frequency tuning, with the earliest neurons encoding low spatial frequency and later neurons encoding high spatial frequency, consistent with a coarse-to-fine computational principle of visual processing, proposed from human psychophysics and supported by recordings in head-fixed monkeys and mice (Boi et al. 2017, Bredfeldt & Ringach 2002, Hegdé 2008, Skyberg et al. 2022). Notably, the formatting of visual input by the saccade-and-fixate movement pattern means that the coarse-to-fine computation is engaged by the arrival of new visual information with each gaze shift. Strikingly, a similar pattern following saccades was observed in freely gazing monkeys viewing natural scenes (Parker et al. 2023), suggesting that despite the differences in mouse and primate vision, aspects of ecological visual processing are shared.

Another important computational challenge is conveying information about eye movements to the rest of the visual system. A recent study demonstrated that the pulvinar conveys a signal from SC to visual cortex, tuned to the direction of eye movement during a saccade (Miura & Scanziani 2022). In V1 neurons, this information was integrated with standard direction selectivity randomly—there was no clear alignment between the tuning for direction of movement of the visual scene and movement of the eyes. While this may appear to confound processing, this could also serve to disambiguate the two sources of motion by orthogonalizing the representation at the population level. Intriguingly, information about eye movements is conveyed even during REM sleep, since head direction tuning in thalamus updates with eye movements, as predicted if the animal was shifting its gaze while dreaming (Senzai & Scanziani 2022), based on drive from SC (Senzai & Scanziani 2024), suggesting that active sensing circuitry is engaged even in dreams.

Head and eye movements are also a component of other behavioral and active sensing goals, for example, orienting to targets such as prey, or moving to generate motion parallax, which is discussed in following sections. However, the many roles of head and eye movements also raise the challenge of determining the motivation and impact of specific movements. For example, in the context of prey capture, does the mouse turn its head to look at the cricket, to chase the cricket, or both?

3.2. Motion Processing in Ecological Vision

Natural behavior places continuous demands on motion computation: Moving animals must stabilize retinal input, infer self-motion in six degrees of freedom, segregate object motion from self-generated flow, estimate time to collision, and convert these estimates into behavioral output. In mice, these computations draw on retinal direction-selective tiling, vestibular and proprioceptive signals, corollary discharge, and state-dependent gain that converge across subcortical and cortical circuits (Niell & Scanziani 2021, Saleem & Busse 2023, Skyberg & Niell 2024). We organize this section around three computations: optic flow, self- versus object motion, and looming/time to collision.

3.2.1. Optic-flow estimation and self-motion readout. Locomotion transforms local retinal motion into global flow whose translational and rotational components specify heading, speed, and ground-plane geometry. In the mouse retina, direction-selective RGCs aligned to the body axes tile visual space, providing a basis for parsing optic flow (Sabbah et al. 2017). Accessory optic and cerebellar pathways use these signals for gaze stabilization, while cortex contributes multisensory integration and higher-order readout. In V1, deep-layer neurons combine visual motion with vestibular input consistent with self-motion estimation (Vélez-Fort et al. 2018). Dorsal HVAs show selectivity for translational and rotational flow and a relative specialization for motion over texture (Rasmussen et al. 2021, Yu et al. 2022). Retinotopic asymmetries, including lower visual field bias, indicate encoding tuned to a ground-dwelling niche (Sit & Goard 2020).

Retrosplenial cortex (RSC) anchors heading to visual landmarks and integrates self-motion signals, though optic-flow tuning in RSC remains limited (Keshavarzi et al. 2022). In contrast, dorsal HVAs (RL/AL/AM) show robust translational/rotational optic-flow selectivity and likely provide motion-derived inputs to association cortices (Rasmussen et al. 2021, Sit & Goard 2020). At the algorithmic level, posterior parietal cortex (PPC) adaptively integrates self-motion with behavioral goals (Alexander et al. 2022, Lian et al. 2023). Converging evidence and theory further suggest that RSC and PPC may employ conjunctive (mixed-selectivity) codes linking motion, heading, and landmarks (Alexander et al. 2023, Beyeler et al. 2019, Pouget & Sejnowski 1997).

Together, these results outline a computation that assembles 2D direction-tuned inputs into a 3D self-motion estimate and routes it to navigation circuits. An open question is how full 3D flow (i.e., pitch, roll, yaw, and linear translations) is reconstructed from 2D retinal tiling and aligned to body axes across development and experience. This self-motion estimate then supplies the prediction needed for the next computation: subtracting expected reafference to reveal independently moving objects.

3.2.2. Flow parsing: segregating self- and object motion. To determine whether observed motion arises from self-movement or external objects, the core computation is prediction and subtraction: Estimate the reafferent motion (sensory input resulting from one's own movement) and subtract it to expose externally caused motion. In mouse V1, mismatch neurons report local deviations between expected and observed motion, consistent with corollary discharge reaching early visual cortex and driving prediction-error signals (Jordan & Keller 2020, Keller et al. 2012, Zmarz & Keller 2016). Downstream, PPC can integrate these residual signals with goals and actions, yielding mixed selectivity codes that support flexible visuomotor behavior (Alexander et al. 2022, Goard et al. 2016, Pho et al. 2018). A potential confound is that locomotion also modulates V1 responses through state-dependent gain control mediated by inhibitory circuitry, often described as a VIP to SST to PV disinhibitory motif (Dipoppa et al. 2018, Fu et al. 2014, Niell & Stryker 2010). However, this mechanism is largely global, scaling responses broadly with behavioral state, whereas mismatch responses are stimulus specific and spatially local, appearing

only where visual input violates the movement-based prediction. Consistent with this distinction, locomotion-induced gain changes alone do not account for mismatch responses (Vasilevskaya et al. 2023), supporting the interpretation that mismatch activity reflects a computation beyond global state gain, namely a local comparison between predicted and actual motion (flow parsing). Key unknowns include where and when efference-copy signals enter the visual hierarchy and how mismatch tuning adapts as environmental statistics change. This parsing computation also supplies motion-defined segmentation cues for complex scene analysis.

3.2.3. Looming and collision avoidance. Detection of incoming objects, whether an approaching obstacle or a looming predator, is a key ecological demand. Imminent collision can be read out from the rate of image expansion. Retinal small-field OFF pathways and W3-like RGCs feed SC, which drives rapid freeze/flight via dorsal periaqueductal gray circuits (Evans et al. 2018, Shang et al. 2018, Yilmaz & Meister 2013). Layer-specific SC activity distinguishes self- from object-generated loom, and looming gain is strongly state dependent (Relota et al. 2025, Zucca et al. 2025). These findings support looming as a dedicated, thresholded computation whose sensitivity is tuned by arousal and ongoing behavior. Open questions include how these threat channels are gated during intentional approach (e.g., hunting) and the extent to which cortical inputs modulate sensitivity to image expansion beyond SC.

3.3. Complex Scene Analysis

Once we start relaxing restrictions on visual stimuli, away from simple parameterized stimuli, and toward an ecological context with richer stimuli that span more degrees of freedom, the brain is faced with an array of complexity that must be reckoned with to support robust adaptive behavior. The natural world is filled with textures, objects, and other agents that must be segmented and represented in neuronal activity to guide behavior. These processes are extraordinarily robust to changes in low-level appearance, e.g., lighting or occlusions. Moreover, they must be robust to out-of-distribution stimuli the mouse has never seen before, in environments it did not evolve within, such as modern houses or subway stations. We know this robustness must exist, because we observe that mouse behavior itself is highly robust. Whether in a forest, a prairie, a house, or a sterile laboratory environment, mice exhibit stereotypically robust behavior, the likes of which our best human-made systems can not yet replicate with any amount of energy consumption, let alone the 1-W power envelope that mouse brains operate within.

Texture is a fundamental component of visual perception (Victor et al. 2017). Distinguishing textures requires a sensitivity to spatial frequency, which can be mapped with simple grating stimuli. V1 and HVAs can be precisely delineated by retinotopy, and these cortical areas vary in their mean population responses as a function of the spatiotemporal characteristics of stimuli presented (Andermann et al. 2011, Glickfeld & Olsen 2017, Marshel et al. 2011, Smith et al. 2017, Wang & Burkhalter 2007). Studies with Gabor filter–based models of visual neuron turning indicate that there is a trade-off between encoding texture or form stimuli and motion stimuli (Glickfeld et al. 2013, Saleem et al. 2013, Yu et al. 2022), and this could account for some diversity in preferences among HVAs. Neurons whose activity is well-correlated to texture parameters are enriched in mouse HVAs (Yu et al. 2022), supporting a role in scene analysis.

HVAs are critical for visually driven behavior in mice (Goldbach et al. 2021), and while there are differences between primates and rodents in trained behavior (Luongo et al. 2023), in both species, texture stimuli have been used to discern functional differences among visual areas (Bolaños et al. 2024, Freeman et al. 2013, Okazawa et al. 2015, Victor et al. 2017, Yu et al. 2022, Ziemba et al. 2016). In large-scale studies, mouse area LM appears to exhibit neural dynamics that correlate with texture stimulus parameters with high fidelity (Bolaños et al. 2024, Yu et al. 2022), and the

activity of neurons in HVAs correlates with categories of stimuli after learning (Goltstein et al. 2021).

Segmentation can follow quickly from texture, as edges and borders help break a visual stimulus up into components (Schnabel et al. 2018). Mice can readily discriminate monochrome naturalistic scenery images presented on video displays (Yu et al. 2018), yet more subtle manipulations of visual stimuli, such as removing or rescaling components of an image, are not reliably detected (S.L. Smith, unpublished data, available upon request). Thus, it seems as though mice experience perceptions of visual stimuli with moderate semantic detail, yet this is sufficient to support behavior in their ecological niche.

In real-world situations, object transformations, noise, occlusions, and other perturbations often occur, and perception must be robust to these perturbations. In artificial neural networks, this can be facilitated by recurrent circuitry, rather than pure feedforward networks, and relatedly, primates show processing delays that could be consistent with biological implementations of similar recurrent mechanisms (Tang et al. 2018). Recent data from mice are also consistent with this idea (Shin et al. 2025). Rodents can recognize shaped objects despite transformations (Froudarakis et al. 2020, Zoccolan et al. 2009). Mice can recognize motion in the presence of noise (Marques et al. 2018, Stirman et al. 2016), and perform visual tasks with complex stimuli [including stimuli with constant luminance but contrast or textural changes (Khastkhodaei et al. 2016)], despite occlusions, fog, and other visual perturbations (Schneider et al. 2025; **https://robustforaging.github.io/**). Thus, mice have extensive capabilities for parsing complex scenes to guide behavior. Elucidating the neural circuitry that enables this analysis of complex natural scenes can reveal novel mechanisms for robust extraction of behaviorally relevant information. Ecologically, mice can use these capabilities to visually sense the world around them, their place in it, and how they can interact with it.

3.4. Distance Estimation

Knowledge of object distance is crucial both for direct interaction with objects in the environment, such as reaching or prey capture, and for spatial navigation through environments containing obstacles and landmarks. Despite possessing limited binocular overlap (~40°) and low visual acuity, mice behaviorally demonstrate highly capable distance estimation using multiple visual strategies.

Evidence for depth perception emerged early in research in mouse vision based on the visual cliff test (Walk & Gibson 1961), wherein animals (including humans) will avoid walking across a transparent floor that covers a drop-off. An early study assayed five mouse strains on the visual cliff, showing that strains with intact vision avoid the cliff while a strain with retinal degeneration did not (Fox 1965). A modern variant of this task was developed in which a mouse climbs down a pole toward platforms at different depths below the transparent floor, allowing estimation of the decision point and better control of the visual cues (Boone et al. 2021). An alternative approach to study ecological distance estimation is based on the animal's ability to jump across gaps of different distances, as assayed in Mongolian gerbils (Ellard et al. 1984) and more recently in mice (Parker et al. 2022a).

Most studies of distance estimation in the mouse have focused on binocular vision based on disparity, the difference in the retinal image between the two eyes. This emphasis likely stems from the fact that disparity can be precisely controlled in head-fixed experiments and computational principles are well-understood in primates (Qian 1997). Although the region of binocular overlap in mice is smaller than in primates, due to their lateral eye position, it does subtend a substantial portion of the visual field, approximately 40° (Gordon & Stryker 1996). Head-fixed mice can discriminate depth from stereoscopic images separately to the two eyes in

trained decision tasks (Samonds et al. 2019, Boone et al. 2021). Neural recordings have revealed the coding of binocular information in the mouse cortex, including disparity tuning and the matching of information between the two eyes (Cang et al. 2023; Fu et al. 2023; La Chioma et al. 2019, 2020; Scholl et al. 2013). Intriguingly, disparity tuning varies across visual areas and retinotopic locations (La Chioma et al. 2019), potentially reflecting ecological relevance.

However, real-world depth perception extends far beyond stereopsis. Indeed, a significant proportion of humans lack functional stereo vision, often undiagnosed, yet navigate successfully using other cues (Chopin et al. 2019). These additional monocular depth signals—including motion parallax, occlusion, size constancy, and perspective—critically depend on either natural scene statistics or active movement, making them less accessible in traditional laboratory paradigms but an essential part of ecological vision.

However, the neural mechanisms underlying monocular depth perception remain relatively unexplored. Recent studies have begun to address one such cue, motion parallax—the distance-dependent shift in the retinal image resulting from self-movement, where objects that are far away appear to move less than objects that are close up (Kim et al. 2016). Behavioral evidence for the use of motion parallax in mice comes from gap-jumping experiments (Parker et al. 2022a), where it was shown that mice can perform accurately when one eye is closed (monocular occlusion), demonstrating that they do not need binocular vision in this context. Furthermore, before jumping, mice performed vertical head-bob movements that could generate the appropriate motion parallax cues, and these movements were performed more often under monocular conditions where motion parallax information is needed (Parker et al. 2022a).

The first study of motion parallax encoding in the mouse was recently performed in head-fixed mice, where motion of a virtual reality stimulus dependent on locomotion was used to emulate the effects of motion parallax. This revealed neurons in V1 tuned to different distances, as defined by motion parallax selectivity, at each location of retinotopic space, effectively generating a map of 3D space (He et al. 2024). The circuit basis by which information about self- and retinal movement is combined to calculate effective depth remains to be investigated.

Given the multiple cues beyond stereopsis that can be used to estimate distance in natural contexts, there are likely a range of underlying circuit mechanisms that remain to be discovered. Furthermore, distance information must be transmitted to downstream areas to be used for behavior, such as generating the appropriate force to jump across a gap. In particular, distance estimation is used to create a spatial representation of the surroundings for use in navigation, which is discussed further below.

3.5. Visual Contributions to Spatial Perception

One key task for which mice share a reliance on vision is perceiving the structure of the local spatial environment. For mice, survival very much depends on being able to sense obstacles and affordances in order to guide motor plans, navigation, and escape behaviors. The mouse visual system, despite its low resolution, is well-suited to accurately localizing distal features, invisible to their other senses, and using this input to generate egocentric and allocentric internal models of the local spatial environment. Here, we review how mice use their visual system for spatial perception.

3.5.1. Using retinotopic input for egocentric spatial perception. After entering a room and briefly scanning the visual environment, we create an internal model of the spatial structure of the environment, allowing us to accurately estimate the bearing and distance of objects, walls, or other salient features even with our eyes closed. Although this capability is seemingly effortless, transforming retinotopic visual input into a 3D spatial model requires sophisticated neural

computations. One component of this transformation is the accurate perception of the distance of features of the environment, discussed earlier in this review. A second critical component is our ability to transform the location of features from an eye-centered (retinotopic) coordinate system to a head-centered (egocentric) coordinate system. This egocentric representation is a common coordinate space that enables motor planning and action, as well as serving as the basis for allocentric representations (Bicanski & Burgess 2020, Martins et al. 2024).

The operating assumption is that visual information entering the mammalian visual system is encoded in a retinotopic coordinate system, based on the pattern of light landing on the retina, but that this information is converted into an egocentric coordinate system somewhere along the cortical hierarchy. Physiology studies in primates found that neurons in the parietal cortex exhibit responses to retinotopic visual stimuli, but that the responses are highly modulated by the gaze direction, called a gain field (Andersen & Mountcastle 1983; Andersen et al. 1985, 1990). This discovery prompted several groups to develop coordinate transformation models (Pouget & Sejnowski 1994, Salinas & Thier 2000, Zipser & Andersen 1988) in which retinotopically organized inputs are combined with gaze direction inputs to generate neurons with gain field responses. These neurons can in turn be used as a basis set for encoding visual objects in egocentric coordinates. However, it should be noted that while V1 neurons primarily encode visual input in retinotopic coordinates, their responses are also modulated by gaze direction (Morris & Krekelberg 2019, Trotter & Celebrini 1999), so the distinction between retinotopic and egocentric coding across areas appears to be graded rather than absolute.

Despite decades of work on this problem in primates, we still have only a rudimentary understanding of how retinotopic input is converted into an egocentric representation at the circuit level. Given the powerful tools we have for mapping, measuring, and manipulating neural circuitry in the mouse, this could be a powerful model system for studying this important transformation. Similar to those of primates, mouse V1 neurons have primarily retinotopic receptive fields, though their responses can be modulated by eye position in a manner consistent with gain fields (Parker et al. 2022b). On the other hand, neurons in mouse association regions such as PPC and RSC exhibit egocentric coding of environmental boundaries (Alexander et al. 2020, van Wijngaarden et al. 2020) and salient objects or features (Alexander et al. 2022, Wilber et al. 2014). Using new technical approaches, researchers are starting to examine the nature of inputs coding gaze position to the visual cortex (King et al. 2023, Miura & Scanziani 2022, Parker et al. 2022b), including in freely moving animals. Future studies will hopefully reveal the circuit-level mechanisms underlying the transformation in response properties, and help confirm or improve existing coordinate transformation models (Pouget & Sejnowski 1997, Zipser & Andersen 1988).

3.5.2. Using visual inputs to orient and map environments. In order to generate an allocentric model of the environment, animals need to know both where things are relative to their body and which direction they are facing in an allocentric reference frame. Influential models of spatial transformations (Bicanski & Burgess 2018, Byrne et al. 2007) have proposed that neurons can combine egocentric signals (e.g., "there is a wall on my left side") with orientation signals ("I am facing north") to generate allocentric representations ("there is a wall due west of me"). As discussed in the previous section, visual input is crucial for generating egocentric representations, but it also plays a key role in allowing animals to orient themselves relative to their environment. Early work on head direction cells, neurons that are active only in particular head orientations within an environment (Taube 2007, Taube et al. 1990a), found that coding of head direction relies on vestibular input (Yoder & Taube 2009, 2014). However, the researchers also found that rodents use vision to align head direction cell activity to specific cues in the environment (Taube et al. 1990b, Yoder & Taube 2014). For example, if a visual cue card is moved with an environment, the

head direction cells will coherently rotate their preferred tuning (Taube et al. 1990b). Intuitively, this makes sense—if a person were to walk around a familiar location blindfolded, their sense of orientation might drift from their actual orientation, but raising the blindfold would allow them to rapidly correct any error. Consistent with this, recent studies have shown that sighted mice placed in the dark show impaired head direction tuning (Asumbisa et al. 2022), although blind mice are still able to orient using stereo olfaction in the absence of visual input (Asumbisa et al. 2022, 2025). Mice without either vision or olfaction continued to show head direction tuning, consistent with ring attractor models of the head direction system (Peyrache et al. 2015, Skaggs et al. 1995, Zhang 1996), but the encoded head direction was untethered to the external environment (Asumbisa et al. 2022).

Recent work has examined how visual input is used to anchor the head direction system to visual landmarks for accurate orienting. The primary hub of the head direction system, the anterior thalamic nucleus (ATN), does not receive direct visual input. However, two reciprocally connected regions, the postsubiculum and RSC, have both head direction tuning and strong visual input. Moreover, lesions to either of these regions impair stable anchoring of head direction to the external environment (Clark et al. 2010). In RSC, researchers have used symmetrical environments to investigate neural responses, finding that subsets of neurons appear to encode visual landmarks, while other neurons encode head direction alone (Jacob et al. 2016, Sit & Goard 2023, Zhang et al. 2022). These neurons are thought to register head direction tuning to visual cues and allow for the recovery of accurate orienting after periods of darkness (Bicanski & Burgess 2016, Page & Jeffery 2018, Sit & Goard 2023). However, stable head direction tuning also has a mnemonic component. For example, when a visual cue is rotated around an animal, the ATN head direction representation continues to rotate even in the dark (Ajabi et al. 2023). Further work is necessary to determine how visual input acts with other senses and short-term memory to produce stable head direction signals.

Allocentric coding in the hippocampal formation and entorhinal cortex has traditionally been viewed as a sensory modality–independent cognitive map of position (O'Keefe & Nadel 1978). However, a number of studies in primates have found spatial view cells—neurons that fire in response to viewing particular remote locations in allocentric space (Killian et al. 2012, Piza et al. 2024, Rolls et al. 1997). Although there is no strong evidence for allocentric spatial view cells in mice, recent studies have found that the hippocampus can be strongly driven by naturalistic visual scenes, even during passive viewing (Purandare & Mehta 2023). This suggests that in rich environments, visual activity may modulate or drive allocentric responses in mice, though there may be fundamental differences between species based on how they explore visual space (Martinez-Trujillo 2025). Studying visual processing during active navigation will be critical for determining how vision is leveraged for spatial perception.

4. CONCLUSION

The field of visual neuroscience is beginning a shift toward ecological vision, along with its experimental and conceptual challenges. As reviewed here, researchers are developing new behavioral paradigms, mapping computations to specific brain regions, and characterizing neural coding that emerges specifically in naturalistic contexts. These studies reveal computational strategies—from active sensing to flexible coordinate transformations—that are often not engaged in traditional laboratory vision paradigms. As Gibson (1979, p. 303) remarked, "The standard approach to vision begins with the eye fixed and exposed to a momentary pattern of stimuli.... The ecological approach to visual perception works from the opposite end. It begins with the flowing array of the observer who walks from one vista to another, moves around an object of interest, and can

approach it." Modern experimental approaches are making this ecological approach feasible, coupled with precise and large-scale measurements of neural activity.

Moving forward, the mouse model offers powerful opportunities to apply circuit-level analysis to ecological vision. The powerful genetic circuit dissection approaches that revealed mechanisms of features such as orientation selectivity, direction selectivity, and surround suppression in simplified contexts can now be directed toward understanding how these circuits operate during natural behavior. Cell type–specific recordings, connectivity mapping, and targeted perturbations have the potential to reveal how distinct neuronal populations contribute to ecological computations. However, a critical challenge lies in bridging knowledge of basic feature encoding with function in complex environments. To what extent do tuning properties measured with conventional approaches predict responses during ecological behaviors? What components of naturalistic visual stimuli are robustly represented in neural activity to guide ethological behavior? Which brain areas and circuits are critical for creating these robust neural dynamics that guide behavior? These questions highlight the need for investigation of neural dynamics during naturalistic visual stimuli and ethological behavior. By studying vision as it evolved to function—processing dynamic, behaviorally relevant information during active exploration—we may gain insight into overlooked, yet fundamental, aspects of neural circuit organization and computation in the visual system.

FUTURE ISSUES

1. What are the relative contributions of cortical and subcortical processing in the mouse, and how are these coordinated?
2. Are there novel circuit motifs that are engaged during ecological vision, or is similar circuitry as that engaged by simpler stimuli (such as for orientation selectivity) repurposed?
3. Can visual processing during ecological vision be predicted from known aspects of vision from reductionist studies?
4. How does the visual system analyze scenes in a robust manner despite the complexity of ecological contexts such as variable illumination and occlusion?
5. How will findings in the mouse translate to primates and particularly humans? Will ecological processing be more generalizable across species, since these are fundamental challenges all animals face rather than specializations for a specific niche?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported by National Institutes of Health grant R01NS121919 (C.M.N., M.B., M.J.G., S.L.S.).

LITERATURE CITED

Ajabi Z, Keinath AT, Wei X-X, Brandon MP. 2023. Population dynamics of head-direction neurons during drift and reorientation. *Nature* 615(7954):892–99

Alexander AS, Carstensen LC, Hinman JR, Raudies F, Chapman GW, Hasselmo ME. 2020. Egocentric boundary vector tuning of the retrosplenial cortex. *Sci. Adv.* 6(8):eaaz2322
Alexander AS, Place R, Starrett MJ, Chrastil ER, Nitz DA. 2023. Rethinking retrosplenial cortex: perspectives and predictions. *Neuron* 111(2):150–75
Alexander AS, Tung JC, Chapman GW, Conner AM, Shelley LE, et al. 2022. Adaptive integration of self-motion and goals in posterior parietal cortex. *Cell Rep.* 38(10):110504
Ambrad Giovannetti E, Rancz E. 2024. Behind mouse eyes: the function and control of eye movements in mice. *Neurosci. Biobehav. Rev.* 161:105671
Andermann ML, Kerlin AM, Roumis DK, Glickfeld LL, Reid RC. 2011. Functional specialization of mouse higher visual cortical areas. *Neuron* 72(6):1025–39
Andersen RA, Bracewell RM, Barash S, Gnadt JW, Fogassi L. 1990. Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* 10(4):1176–96
Andersen RA, Essick GK, Siegel RM. 1985. Encoding of spatial location by posterior parietal neurons. *Science* 230(4724):456–58
Andersen RA, Mountcastle VB. 1983. The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 3(3):532–48
Applebury ML, Antoch MP, Baxter LC, Chun LL, Falk JD, et al. 2000. The murine cone photoreceptor: A single cone type expresses both S and M opsins with retinal spatial patterning. *Neuron* 27(3):513–23
Ashwood ZC, Roy NA, Stone IR, The International Brain Laboratory, Urai AE, et al. 2022. Mice alternate between discrete strategies during perceptual decision-making. *Nat. Neurosci.* 25(2):201–12
Asumbisa K, Peyrache A, Trenholm S. 2022. Flexible cue anchoring strategies enable stable head direction coding in both sighted and blind animals. *Nat. Commun.* 13(1):5483
Asumbisa K, Peyrache A, Trenholm S. 2025. Stereo olfaction underlies stable coding of head direction in blind mice. *Nat. Commun.* 16(1):3545
Balkema GW Jr., Pinto LH. 1982. Electrophysiology of retinal ganglion cells in the mouse: a study of a normally pigmented mouse and a congenic hypopigmentation mutant, pearl. *J. Neurophysiol.* 48(4):968–80
Beyeler M, Rounds EL, Carlson KD, Dutt N, Krichmar JL. 2019. Neural correlates of sparse coding and dimensionality reduction. *PLOS Comput. Biol.* 15(6):e1006908
Bicanski A, Burgess N. 2016. Environmental anchoring of head direction in a computational model of retrosplenial cortex. *J. Neurosci.* 36(46):11601–18
Bicanski A, Burgess N. 2018. A neural-level model of spatial memory and imagery. *eLife* 7:e33752
Bicanski A, Burgess N. 2020. Neuronal vector coding in spatial cognition. *Nat. Rev. Neurosci.* 21(9):453–70
Bizzi E, Kalil RE, Morasso P. 1972. Two modes of active eye-head coordination in monkeys. *Brain Res.* 40(1):45–48
Bleckert A, Schwartz GW, Turner MH, Rieke F, Wong ROL. 2014. Visual space is represented by nonmatching topographies of distinct mouse retinal ganglion cell types. *Curr. Biol.* 24(3):310–15
Boi M, Poletti M, Victor JD, Rucci M. 2017. Consequences of the oculomotor cycle for the dynamics of perception. *Curr. Biol.* 27(9):1268–77
Bolaños F, Orlandi JG, Aoki R, Jagadeesh AV, Gardner JL, Benucci A. 2024. Efficient coding of natural images in the mouse visual cortex. *Nat. Commun.* 15(1):2466
Boone HC, Samonds JM, Crouse EC, Barr C, Priebe NJ, McGee AW. 2021. Natural binocular depth discrimination behavior in mice explained by visual cortical activity. *Curr. Biol.* 31(10):2191–98.e3
Branco T, Redgrave P. 2020. The neural basis of escape behavior in vertebrates. *Annu. Rev. Neurosci.* 43:417–39
Bredfeldt CE, Ringach DL. 2002. Dynamics of spatial frequency tuning in macaque V1. *J. Neurosci.* 22(5):1976–84
Busse L. 2018. The mouse visual system and visual perception. In *Handbook of Object Novelty Recognition*, ed. A Ennaceur, MA de Souza Silva. Elsevier
Busse L, Ayaz A, Dhruv NT, Katzner S, Saleem AB, et al. 2011. The detection of visual contrast in the behaving mouse. *J. Neurosci.* 31(31):11351–61
Byrne P, Becker S, Burgess N. 2007. Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychol. Rev.* 114(2):340–75

Campagner D, Vale R, Tan YL, Iordanidou P, Pavón Arocas O, et al. 2023. A cortico-collicular circuit for orienting to shelter during escape. *Nature* 613(7942):111–19
Cang J, Fu J, Tanabe S. 2023. Neural circuits for binocular vision: ocular dominance, interocular matching, and disparity selectivity. *Front. Neural Circuits* 17:1084027
Chopin A, Bavelier D, Levi DM. 2019. The prevalence and diagnosis of "stereoblindness" in adults less than 60 years of age: a best evidence synthesis. *Ophthalmic Physiol. Opt.* 39(2):66–85
Clark BJ, Bassett JP, Wang SS, Taube JS. 2010. Impaired head direction cell representation in the anterodorsal thalamus after lesions of the retrosplenial cortex. *J. Neurosci.* 30(15):5289–302
Conwell C, Prince JS, Kay KN, Alvarez GA, Konkle T. 2024. A large-scale examination of inductive biases shaping high-level visual representation in brains and machines. *Nat. Commun.* 15(1):9383
Datta SR, Anderson DJ, Branson K, Perona P, Leifer A. 2019. Computational neuroethology: a call to action. *Neuron* 104(1):11–24
Dipoppa M, Ranson A, Krumin M, Pachitariu M, Carandini M, Harris KD. 2018. Vision and locomotion shape the interactions between neuron types in mouse visual cortex. *Neuron* 98(3):602–15.e8
Ellard CG, Goodale MA, Timney B. 1984. Distance estimation in the Mongolian gerbil: the role of dynamic depth cues. *Behav. Brain Res.* 14(1):29–39
Evans DA, Stempel AV, Vale R, Ruehle S, Lefler Y, Branco T. 2018. A synaptic threshold mechanism for computing escape decisions. *Nature* 558(7711):590–94
Fox MW. 1965. The visual cliff test for the study of visual depth perception in the mouse. *Anim. Behav.* 13(2):232–33
Freeman J, Ziemba CM, Heeger DJ, Simoncelli EP, Movshon JA. 2013. A functional and perceptual signature of the second visual area in primates. *Nat. Neurosci.* 16(7):974–81
Froudarakis E, Cohen U, Diamantaki M, Walker EY, Reimer J, et al. 2020. Object manifold geometry across the mouse cortical visual hierarchy. Preprint, bioRxiv. **https://www.biorxiv.org/content/10.1101/2020.08.20.258798v1**
Fu J, Tanabe S, Cang J. 2023. Widespread and multifaceted binocular integration in the mouse primary visual cortex. *J. Neurosci.* 43(38):6495–507
Fu Y, Tucciarone JM, Espinosa JS, Sheng N, Darcy DP, et al. 2014. A cortical circuit for gain control by behavioral state. *Cell* 156(6):1139–52
Gibson JJ. 1979. *The Ecological Approach To Visual Perception*. Psychology Press
Glickfeld LL, Andermann ML, Bonin V, Reid RC. 2013. Cortico-cortical projections in mouse visual cortex are functionally target specific. *Nat. Neurosci.* 16(2):219–26
Glickfeld LL, Olsen SR. 2017. Higher-order areas of the mouse visual cortex. *Annu. Rev. Vis. Sci.* 3:251–73
Goard MJ, Pho GN, Woodson J, Sur M. 2016. Distinct roles of visual, parietal, and frontal motor cortices in memory-guided sensorimotor decisions. *eLife* 5:e13764
Goldbach HC, Akitake B, Leedy CE, Histed MH. 2021. Performance in even a simple perceptual task depends on mouse secondary visual areas. *eLife* 10:e62156
Goltstein PM, Reinert S, Bonhoeffer T, Hübener M. 2021. Mouse visual cortex areas represent perceptual and semantic features of learned visual categories. *Nat. Neurosci.* 24(10):1441–51
Gordon JA, Stryker MP. 1996. Experience-dependent plasticity of binocular responses in the primary visual cortex of the mouse. *J. Neurosci.* 16(10):3274–86
Greer D, Lei T, Kryshtal A, Jessen ZF, Schwartz GW. 2025. Visual identification of conspecifics shapes social behavior in mice. *Curr. Biol.* 35(2):287–99.e4
Gupta D, Młynarski W, Sumser A, Symonova O, Svatoň J, Joesch M. 2023. Panoramic visual statistics shape retina-wide organization of receptive fields. *Nat. Neurosci.* 26(4):606–14
Hahn J, Monavarfeshani A, Qiao M, Kao AH, Kölsch Y, et al. 2023. Evolution of neuronal cell classes and types in the vertebrate retina. *Nature* 624(7991):415–24
Harvey CD, Collman F, Dombeck DA, Tank DW. 2009. Intracellular dynamics of hippocampal place cells during virtual navigation. *Nature* 461(7266):941–46
Hayhoe M, Ballard D. 2005. Eye movements in natural behavior. *Trends Cogn. Sci.* 9(4):188–94
He Y, Nieto AC, Blot A, Znamenskiy P. 2024. A depth map of visual space in the primary visual cortex. Preprint, bioRxiv. **https://www.biorxiv.org/content/10.1101/2024.09.27.615442v1**

Hegdé J. 2008. Time course of visual perception: coarse-to-fine processing and beyond. *Prog. Neurobiol.* 84(4):405–39
Holmgren CD, Stahr P, Wallace DJ, Voit K-M, Matheson EJ, et al. 2021. Visual pursuit behavior in mice maintains the pursued prey on the retinal region with least optic flow. *eLife* 10:e70838
Hoy JL, Yavorska I, Wehr M, Niell CM. 2016. Vision drives accurate approach behavior during prey capture in laboratory mice. *Curr. Biol.* 26(22):3046–52
Hübener M. 2003. Mouse visual cortex. *Curr. Opin. Neurobiol.* 13(4):413–20
Huberman AD, Niell CM. 2011. What can mice tell us about how vision works? *Trends Neurosci.* 34(9):464–73
Jacob P-Y, Casali G, Spieser L, Page H, Overington D, Jeffery K. 2016. An independent, landmark-dominated head-direction signal in dysgranular retrosplenial cortex. *Nat. Neurosci.* 20(2):173–75
Jeon C-J, Strettoi E, Masland RH. 1998. The major cell populations of the mouse retina. *J. Neurosci.* 18(21):8936–46
Jordan R, Keller GB. 2020. Opposing influence of top-down and bottom-up input on excitatory layer 2/3 neurons in mouse primary visual cortex. *Neuron* 108(6):1194–206.e5
Keller GB, Bonhoeffer T, Hübener M. 2012. Sensorimotor mismatch signals in primary visual cortex of the behaving mouse. *Neuron* 74(5):809–15
Keshavarzi S, Bracey EF, Faville RA, Campagner D, Tyson AL, et al. 2022. Multisensory coding of angular head velocity in the retrosplenial cortex. *Neuron* 110(3):532–43.e9
Khastkhodaei Z, Jurjut O, Katzner S, Busse L. 2016. Mice can use second-order, contrast-modulated stimuli to guide visual perception. *J. Neurosci.* 36(16):4457–69
Killian NJ, Jutras MJ, Buffalo EA. 2012. A map of visual space in the primate entorhinal cortex. *Nature* 491(7426):761–64
Kim HR, Angelaki DE, DeAngelis GC. 2016. The neural basis of depth perception from motion parallax. *Philos. Trans. R. Soc. B* 371(1697):20150256
King CW, Ledochowitsch P, Buice MA, de Vries SEJ. 2023. Saccade-responsive visual cortical neurons do not exhibit distinct visual response properties. *eNeuro* 10(9):ENEURO.0051-23.2023
Kislin M, Mugantseva E, Molotkov D, Kulesskaya N, Khirug S, et al. 2014. Flat-floored air-lifted platform: a new method for combining behavior with microscopy or electrophysiology on awake freely moving rodents. *J. Vis. Exp.* (88):e51869
Knudsen EI. 2020. Evolution of neural processing for visual perception in vertebrates. *J. Comp. Neurol.* 528(17):2888–901
La Chioma A, Bonhoeffer T, Hübener M. 2019. Area-specific mapping of binocular disparity across mouse visual cortex. *Curr. Biol.* 29(17):2954–60.e5
La Chioma A, Bonhoeffer T, Hübener M. 2020. Disparity sensitivity and binocular integration in mouse visual cortex areas. *J. Neurosci.* 40(46):8883–99
Land MF. 1999. Motion and vision: why animals move their eyes. *J. Comp. Physiol. A* 185(4):341–52
Lian Y, Williams S, Alexander AS, Hasselmo ME, Burkitt AN. 2023. Learning the vector coding of egocentric boundary cells from visual data. *J. Neurosci.* 43(28):5180–90
Luo L, Callaway EM, Svoboda K. 2008. Genetic dissection of neural circuits. *Neuron* 57(5):634–60
Luongo FJ, Liu L, Ho CLA, Hesse JK, Wekselblatt JB, et al. 2023. Mice and primates use distinct strategies for visual segmentation. *eLife* 12:e74394
Marques T, Summers MT, Fioreze G, Fridman M, Dias RF, et al. 2018. A role for mouse primary visual cortex in motion perception. *Curr. Biol.* 28(11):1703–13.e6
Marshel JH, Garrett ME, Nauhaus I, Callaway EM. 2011. Functional specialization of seven mouse visual cortical areas. *Neuron* 72(6):1040–54
Martinez-Trujillo J. 2025. Why do primates have view cells instead of place cells? *Trends Cogn. Sci.* 29(3):226–29
Martins DM, Manda JM, Goard MJ, Parker PRL. 2024. Building egocentric models of local space from retinal input. *Curr. Biol.* 34(23):R1185–202
Mathis MW, Mathis A. 2025. Joint modelling of brain and behaviour dynamics with artificial intelligence. *Nat. Rev. Neurosci.* 27:87–100
Matthis JS, Muller KS, Bonnen KL, Hayhoe MM. 2022. Retinal optic flow during natural locomotion. *PLOS Comput. Biol.* 18(2):e1009575

Meyer AF, O'Keefe J, Poort J. 2020. Two distinct types of eye-head coupling in freely moving mice. *Curr. Biol.* 30(11):2116–30.e6

Meyer AF, Poort J, O'Keefe J, Sahani M, Linden JF. 2018. A head-mounted camera system integrates detailed behavioral monitoring with multichannel electrophysiology in freely moving mice. *Neuron* 100(1):46–60.e7

Michaiel AM, Abe ET, Niell CM. 2020. Dynamics of gaze control during prey capture in freely moving mice. *eLife* 9:e57458

Miura SK, Scanziani M. 2022. Distinguishing externally from saccade-induced motion in visual cortex. *Nature* 610(7930):135–42

Morris AP, Krekelberg B. 2019. A stable visual world in primate primary visual cortex. *Curr. Biol.* 29(9):1471–80.e6

Morris RG, Garrud P, Rawlins JN, O'Keefe J. 1982. Place navigation impaired in rats with hippocampal lesions. *Nature* 297(5868):681–83

Nayebi A, Kong NCL, Zhuang C, Gardner JL, Norcia AM, Yamins DLK. 2023. Mouse visual cortex as a limited resource system that self-learns an ecologically-general representation. *PLOS Comput. Biol.* 19(10):e1011506

Newman JP, Zhang J, Cuevas-López A, Miller NJ, Honda T, et al. 2025. ONIX: a unified open-source platform for multimodal neural recording and perturbation during naturalistic behavior. *Nat. Methods* 22(1):187–92

Niell CM, Scanziani M. 2021. How cortical circuits implement cortical computations: mouse visual cortex as a model. *Annu. Rev. Neurosci.* 44:517–46

Niell CM, Stryker MP. 2010. Modulation of visual responses by behavioral state in mouse visual cortex. *Neuron* 65(4):472–79

Okazawa G, Tajima S, Komatsu H. 2015. Image statistics underlying natural texture selectivity of neurons in macaque V4. *PNAS* 112(4):E351–60

O'Keefe J, Nadel L. 1978. *The Hippocampus as a Cognitive Map*. Oxford University Press

Page HJI, Jeffery KJ. 2018. Landmark-based updating of the head direction system by retrosplenial cortex: a computational model. *Front. Cell. Neurosci.* 12:377383

Parker PRL, Abe ETT, Beatie NT, Leonard ESP, Martins DM, et al. 2022a. Distance estimation from monocular cues in an ethological visuomotor task. *eLife* 11:e74708

Parker PRL, Abe ETT, Leonard ESP, Martins DM, Niell CM. 2022b. Joint coding of visual input and eye/head position in V1 of freely moving mice. *Neuron* 110(23):3897–906.e5

Parker PRL, Martins DM, Leonard ESP, Casey NM, Sharp SL, et al. 2023. A dynamic sequence of visual processing initiated by gaze shifts. *Nat. Neurosci.* 26(12):2192–202

Pereira TD, Shaevitz JW, Murthy M. 2020. Quantifying behavior to understand the brain. *Nat. Neurosci.* 23(12):1537–49

Peyrache A, Lacroix MM, Petersen PC, Buzsáki G. 2015. Internally organized mechanisms of the head direction sense. *Nat. Neurosci.* 18(4):569–75

Pho GN, Goard MJ, Woodson J, Crawford B, Sur M. 2018. Task-dependent representations of stimulus and choice in mouse parietal cortex. *Nat. Commun.* 9(1):2596

Piza DB, Corrigan BW, Gulli RA, Do Carmo S, Cuello AC, et al. 2024. Primacy of vision shapes behavioral strategies and neural substrates of spatial navigation in marmoset hippocampus. *Nat. Commun.* 15(1):4053

Pouget A, Sejnowski TJ. 1994. A neural model of the cortical representation of egocentric distance. *Cereb. Cortex* 4(3):314–29

Pouget A, Sejnowski TJ. 1997. Spatial transformations in the parietal cortex using basis functions. *J. Cogn. Neurosci.* 9(2):222–37

Purandare C, Mehta M. 2023. Mega-scale movie-fields in the mouse visuo-hippocampal network. Preprint, *eLife* 12:RP85069. **https://elifesciences.org/articles/85069**

Qian N. 1997. Binocular disparity and the perception of depth. *Neuron* 18(3):359–68

Qiu Y, Zhao Z, Klindt D, Kautzky M, Szatko KP, et al. 2021. Natural environment statistics in the upper and lower visual field are reflected in mouse retinal specializations. *Curr. Biol.* 31(15):3233–47.e6

Rasmussen RN, Matsumoto A, Arvin S, Yonehara K. 2021. Binocular integration of retinal motion information underlies optic flow processing by the cortex. *Curr. Biol.* 31(6):1165–74.e6

Relota XJ, Ford A, Savier EL. 2025. Behavioral modulation and molecular definition of wide-field vertical cells in the mouse superior colliculus. *J. Neurosci.* 45(16):e1816242025
Rolls ET, Robertson RG, Georges-François P. 1997. Spatial view cells in the primate hippocampus. *Eur. J. Neurosci.* 9(8):1789–94
Sabbah S, Gemmer JA, Bhatia-Lin A, Manoff G, Castro G, et al. 2017. A retinal code for motion along the gravitational and body axes. *Nature* 546(7659):492–97
Saleem AB, Ayaz A, Jeffery KJ, Harris KD, Carandini M. 2013. Integration of visual motion and locomotion in mouse visual cortex. *Nat. Neurosci.* 16(12):1864–69
Saleem AB, Busse L. 2023. Interactions between rodent visual and spatial systems during navigation. *Nat. Rev. Neurosci.* 24(8):487–501
Saleem AB, Diamanti EM, Fournier J, Harris KD, Carandini M. 2018. Coherent encoding of subjective spatial position in visual cortex and hippocampus. *Nature* 562(7725):124–27
Salinas E, Thier P. 2000. Gain modulation: a major computational principle of the central nervous system. *Neuron* 27(1):15–21
Samonds JM, Choi V, Priebe NJ. 2019. Mice discriminate stereoscopic surfaces without fixating in depth. *J. Neurosci.* 39(41):8024–37
Schnabel UH, Bossens C, Lorteije JAM, Self MW, Op de Beeck H, Roelfsema PR. 2018. Figure-ground perception in the awake mouse and neuronal activity elicited by figure-ground stimuli in primary visual cortex. *Sci. Rep.* 8(1):17800
Schneider M, Canzano J, Peng J, Hou Y, Smith SL, Beyeler M. 2025. Mouse versus AI: a neuroethological benchmark for visual robustness and neural alignment. Preprint, arXiv:2509.14446 [q-bio.NC]
Scholl B, Burge J, Priebe NJ. 2013. Binocular integration and disparity selectivity in mouse primary visual cortex. *J. Neurophysiol.* 109(12):3013–24
Seabrook TA, Burbridge TJ, Crair MC, Huberman AD. 2017. Architecture, function, and assembly of the mouse visual system. *Annu. Rev. Neurosci.* 40:499–538
Senzai Y, Scanziani M. 2022. A cognitive process occurring during sleep is revealed by rapid eye movements. *Science* 377(6609):999–1004
Senzai Y, Scanziani M. 2024. The brain simulates actions and their consequences during REM sleep. Preprint, bioRxiv. **https://www.biorxiv.org/content/10.1101/2024.08.13.607810v1**
Shang C, Chen Z, Liu A, Li Y, Zhang J, et al. 2018. Divergent midbrain circuits orchestrate escape and freezing responses to looming stimuli in mice. *Nat. Commun.* 9(1):1232
Shin H, Ogando MB, Abdeladim L, Durand S, Belski H, et al. 2025. Recurrent pattern completion drives the neocortical representation of sensory inference. *Nat. Neurosci.* 28:2319–29
Sit KK, Goard MJ. 2020. Distributed and retinotopically asymmetric processing of coherent motion in mouse visual cortex. *Nat. Commun.* 11(1):3565
Sit KK, Goard MJ. 2023. Coregistration of heading to visual cues in retrosplenial cortex. *Nat. Commun.* 14(1):1992
Skaggs WE, Knierim JJ, Kudrimoti HS, McNaughton BL. 1995. A model of the neural basis of the rat's sense of direction. *Adv. Neural Inf. Process. Syst.* 7:173–80
Skyberg R, Niell CM. 2024. Natural visual behavior and active sensing in the mouse. *Curr. Opin. Neurobiol.* 86:102882
Skyberg R, Tanabe S, Chen H, Cang J. 2022. Coarse-to-fine processing drives the efficient coding of natural scenes in mouse visual cortex. *Cell Rep.* 38(13):110606
Smith IT, Townsend LB, Huh R, Zhu H, Smith SL. 2017. Stream-dependent development of higher visual cortical areas. *Nat. Neurosci.* 20(2):200–8
Steinmetz NA, Aydin C, Lebedeva A, Okun M, Pachitariu M, et al. 2021. Neuropixels 2.0: a miniaturized high-density probe for stable, long-term brain recordings. *Science* 372(6539):eabf4588
Stirman J, Townsend LB, Smith S. 2016. A touchscreen based global motion perception task for mice. *Vis. Res.* 127:74–83
Tang H, Schrimpf M, Lotter W, Moerman C, Paredes A, et al. 2018. Recurrent computations for visual pattern completion. *PNAS* 115(35):8835–40
Taube JS. 2007. The head direction signal: origins and sensory-motor integration. *Annu. Rev. Neurosci.* 30:181–207

Taube JS, Muller RU, Ranck JB. 1990a. Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J. Neurosci.* 10(2):420–35
Taube JS, Muller RU, Ranck JB. 1990b. Head-direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations. *J. Neurosci.* 10(2):436–47
Trotter Y, Celebrini S. 1999. Gaze direction controls response gain in primary visual-cortex neurons. *Nature* 398(6724):239–42
van Beest EH, Mukherjee S, Kirchberger L, Schnabel UH, van der Togt C, et al. 2021. Mouse visual cortex contains a region of enhanced spatial resolution. *Nat. Commun.* 12(1):4029
van Wijngaarden JB, Babl SS, Ito HT. 2020. Entorhinal-retrosplenial circuits for allocentric-egocentric transformation of boundary coding. *eLife* 9:e59816
Vasilevskaya A, Widmer FC, Keller GB, Jordan R. 2023. Locomotion-induced gain of visual responses cannot explain visuomotor mismatch responses in layer 2/3 of primary visual cortex. *Cell Rep.* 42(3):112096
Vélez-Fort M, Bracey EF, Keshavarzi S, Rousseau CV, Cossell L, et al. 2018. A circuit for integration of head- and visual-motion signals in layer 6 of mouse primary visual cortex. *Neuron* 98(1):179–91.e6
Victor JD, Conte MM, Chubb CF. 2017. Textures as probes of visual processing. *Annu. Rev. Vis. Sci.* 3:275–96
Voigts J, Harnett MT. 2020. Somatic and dendritic encoding of spatial variables in retrosplenial cortex differs during 2D navigation. *Neuron* 105(2):237–45.e4
Walk RD, Gibson EJ. 1961. A comparative and analytical study of visual depth perception. *Psychol. Monogr.* 75(15):1–44
Wallace DJ, Greenberg DS, Sawinski J, Rulla S, Notaro G, Kerr JND. 2013. Rats maintain an overhead binocular field at the expense of constant fusion. *Nature* 498(7452):65–69
Wang EY, Fahey PG, Ding Z, Papadopoulos S, Ponder K, et al. 2025. Foundation model of neural activity predicts response to new stimulus types. *Nature* 640(8058):470–77
Wang Q, Burkhalter A. 2007. Area map of mouse visual cortex. *J. Comp. Neurol.* 502(3):339–57
Wekselblatt JB, Flister ED, Piscopo DM, Niell CM. 2016. Large-scale imaging of cortical dynamics during sensory perception and behavior. *J. Neurophysiol.* 115(6):2852–66
Wilber AA, Clark BJ, Forster TC, Tatsuno M, McNaughton BL. 2014. Interaction of egocentric and world-centered reference frames in the rat posterior parietal cortex. *J. Neurosci.* 34(16):5431–46
Xu A, Hou Y, Niell CM, Beyeler M. 2023. Multimodal deep learning model unveils behavioral dynamics of V1 activity in freely moving mice. *Adv. Neural Inf. Process. Syst.* 36:15341–57
Yarbus AL. 1967. *Eye Movements and Vision*. Springer
Yilmaz M, Meister M. 2013. Rapid innate defensive responses of mice to looming visual stimuli. *Curr. Biol.* 23(20):2011–15
Yoder RM, Taube JS. 2009. Head direction cell activity in mice: Robust directional signal depends on intact otolith organs. *J. Neurosci.* 29(4):1061–76
Yoder RM, Taube JS. 2014. The vestibular contribution to the head direction signal and navigation. *Front. Integr. Neurosci.* 8:71638
Yu Y, Hira R, Stirman JN, Yu W, Smith IT, Smith SL. 2018. Mice use robust and common strategies to discriminate natural scenes. *Sci. Rep.* 8(1):1379
Yu Y, Stirman JN, Dorsett CR, Smith SL. 2022. Selective representations of texture and motion in mouse higher visual areas. *Curr. Biol.* 32(13):2810–20.e5
Zahler SH, Taylor DE, Wong JY, Adams JM, Feinberg EH. 2021. Superior colliculus drives stimulus-evoked directionally biased saccades and attempted head movements in head-fixed mice. *eLife* 10:e73081
Zhang K. 1996. Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: a theory. *J. Neurosci.* 16(6):2112–26
Zhang N, Grieves RM, Jeffery KJ. 2022. Environment symmetry drives a multidirectional code in rat retrosplenial cortex. *J. Neurosci.* 42(49):9227–41
Zhao Z-D, Zhang L, Xiang X, Kim D, Li H, et al. 2023. Neurocircuitry of predatory hunting. *Neurosci. Bull.* 39(5):817–31
Ziemba CM, Freeman J, Movshon JA, Simoncelli EP. 2016. Selectivity and tolerance for visual texture in macaque V2. *PNAS* 113(22):E3140–49
Zipser D, Andersen RA. 1988. A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* 331(6158):679–84

Zmarz P, Keller GB. 2016. Mismatch receptive fields in mouse visual cortex. *Neuron* 92(4):766–72
Zoccolan D, Oertelt N, DiCarlo JJ, Cox DD. 2009. A rodent model for the study of invariant visual object recognition. *PNAS* 106(21):8748–53
Zong W, Obenhaus HA, Skytøen ER, Eneqvist H, de Jong NL, et al. 2022. Large-scale two-photon calcium imaging in freely moving mice. *Cell* 185(7):1240–56.e30
Zucca S, Schulz A, Gonçalves PJ, Macke JH, Saleem AB, Solomon SG. 2025. Visual loom caused by self-movement or object-movement elicits distinct responses in mouse superior colliculus. *Curr. Biol.* 35(17):4241–50.e4