

Distinct Functional Circuits in the Superior Colliculus and Their Connection to Behavior

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Keywords

superior colliculus, sensorimotor transformation, innate behavior, cell types, circuits, evolution, ecology

Abstract

The superior colliculus is a conserved midbrain structure that converts sensory input into motor output to guide orienting, defensive, and appetitive behaviors. Once regarded as a reflexive sensorimotor relay, it is now recognized as a set of anatomically and functionally distinct circuits defined by cell type, laminar position, projection target, and spatial domain. These circuits form parallel pathways that transform sensory representations into specific motor commands and are dynamically modulated by cortical, subcortical, and state-dependent inputs, providing a structural basis for the flexible adaptation of innate behavioral responses to changing environments, contexts, and brain states. Drawing primarily on work in mice, and using selected findings from primates, birds, and other vertebrates for comparison, we argue that the superior colliculus is organized by three principles: laminar organization, topographic alignment of sensory and motor maps, and modular specialization of cell types and pathways. Together, these principles allow a conserved midbrain structure to generate context-appropriate orienting, approach, and avoidance behaviors across vertebrate species.

1. INTRODUCTION

Across vertebrates, survival depends on the rapid transformation of sensory information into motor commands that support orienting, approach, or defensive actions (Tinbergen 1951). The superior colliculus (referred to here as simply “colliculus”) is a highly conserved midbrain structure that plays a central role in this transformation: integrating and converting sensory inputs into spatially organized motor outputs (Branco & Redgrave 2020, Cooper & McPeck 2021, Dean et al. 1989, Hoy & Farrow 2025, Sparks 1986). Although the basic laminar and topographic organization of the colliculus is well established, molecular and circuit-level studies in mice have revealed a finer subdivision into cell type-specific modules with distinct projection targets and behavioral correlates. These findings challenge the traditional view of the colliculus as a unitary sensorimotor relay, suggesting a modular architecture that implements multiple parallel transformations from sensation to action. This review first describes the architectural principles that define the rodent colliculus, with a particular focus on cell types and functional modules in mice. We then use selected findings from primates, birds, and other vertebrates to evaluate which of these principles are conserved and which appear specialized.

2. ANATOMICAL BLUEPRINT

The organization of the colliculus can be understood through three complementary principles: laminar organization across depth, topographic alignment of sensory and motor maps, and regional specialization across the visual field (**Figure 1**).

2.1. Laminar Organization

Across depth, the colliculus is arranged into alternating layers of cell bodies and fibers that form parallel strata, each with distinct connectivity and function (May 2006, Yang et al. 2025). Although often divided into superficial and deep regions, the structure can be more precisely described as containing multiple layers: seven, in the case of mice, that extend from the surface to the periaqueductal gray (PAG) (**Figure 1**). The superficial layers receive direct retinal input and are specialized for visual processing (Angaut & Repérant 1976, Ellis et al. 2016, Graybiel 1975, Hunt & Webster 1975, Lund et al. 1980, Petry et al. 1989, Pollack & Hickey 1979, Remy & Güntürkün 1991, Robles et al. 2013, Zhang & Hoffmann 1993). Deeper layers integrate visual, auditory, and somatosensory information from the cortex, thalamus, hypothalamus, and brainstem (Benavidez et al. 2021, Drager & Hubel 1976). These layers give rise to two major descending pathways: a crossed output that mediates orienting movements and an uncrossed output associated with defensive behaviors (Dean et al. 1989, Isa et al. 2020, Sahibzada et al. 1986).

2.2. Topographic Organization and Regional Specialization

Within each layer, the colliculus preserves the spatial relationships of sensory inputs in the form of aligned topographic maps. Retinal afferents establish a precise retinotopic projection in the superficial layers (Drager & Hubel 1975, 1976; Molotkov et al. 2023; Mrcsic-Flogel et al. 2005; Sibille et al. 2022). In species with minimal binocular overlap, such as rodents, nearly all retinal axons project contralaterally, whereas species with greater binocular vision show additional ipsilateral projections that create eye-specific domains (Graybiel 1975, Isa et al. 2020, Tigges & Tigges 1981, Wässle & Illing 1980). Across species, the anterior–posterior axis represents azimuth (nasal–temporal visual field), whereas the medial–lateral axis represents elevation (upper–lower visual field). Deeper layers contain additional representations of auditory and somatosensory space that are coregistered with the visual map (Drager & Hubel 1975, 1976; Finlay et al. 1978;

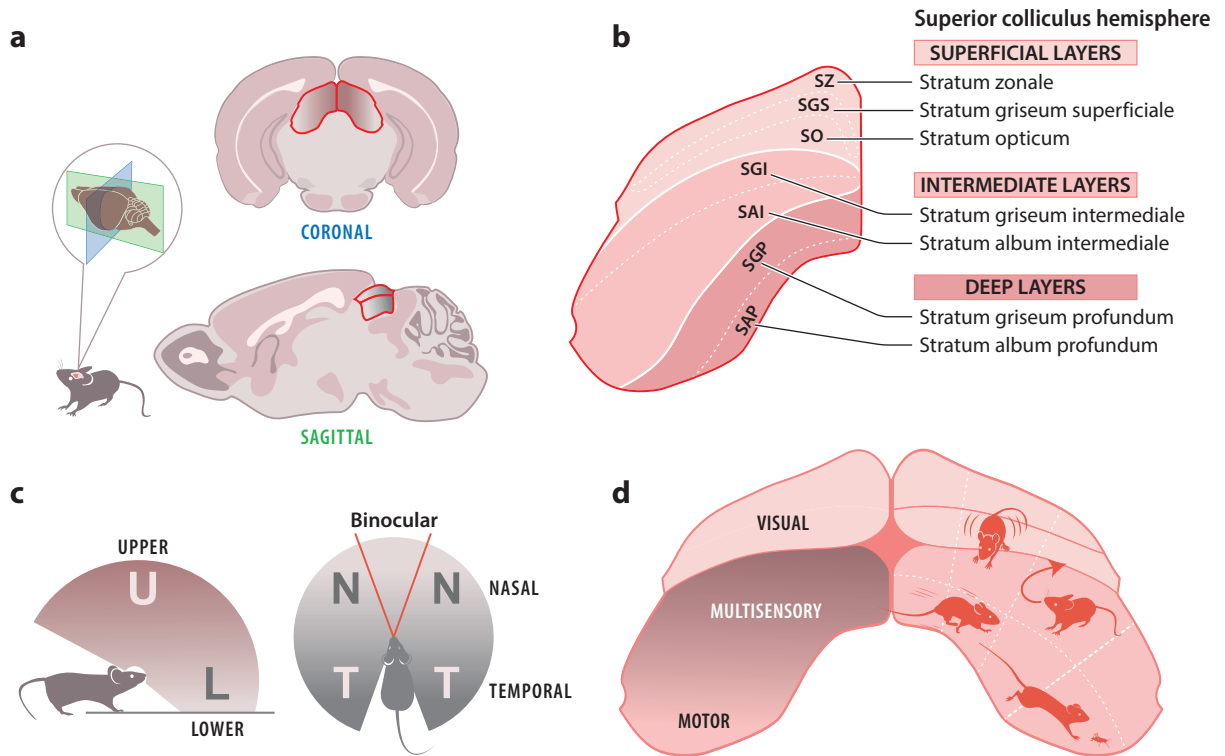


Figure 1

Blueprint of the superior colliculus. (a) Location of the superior colliculus in the mouse brain, including a coronal and sagittal view. (b) The seven layers of the mouse superior colliculus (coronal view). (c) The extent of the visual field of the mouse, including the upper (U) to lower (L) extent (left), as well as the nasal (N) to temporal (T) extent (right). (d) The function (left) and behaviors (right) associated with different regions of the superior colliculus. Panels a and c adapted from Hoy & Farrow (2025).

Gharaei et al. 2018; Ito et al. 2021; Knudsen 1982; Meredith & Stein 1986). Work in owls and ferrets demonstrates that the alignment between different collicular maps relies on visual experience, where shifting of visual input using a prism drives a corresponding shift in auditory and motor maps, illustrating an activity-dependent mechanism that aligns the collicular maps (Brainard & Knudsen 1998; King et al. 1988, 1998; Knudsen & Brainard 1991). In addition, the congruence between sensory and motor maps is a defining property of the colliculus. Pharmacological and electrical stimulation experiments demonstrated that local activation of the collicular surface evokes movements directed toward the corresponding region of visual space (Apter 1946, Sparks 1986). This spatial coupling between input and output maps is conserved across vertebrate species.

The topographic organization across the collicular surface is accompanied by regional specialization aligned with ecological and behavioral demands. In rodents, the medial colliculus, representing the upper visual field, is preferentially engaged in defensive behaviors such as freezing and escape, whereas the lateral colliculus, representing the lower field, supports approach behaviors including exploration and prey capture (Dean et al. 1989, Evans et al. 2018, Hoy et al. 2016, Sahibzada et al. 1986, Shang et al. 2018). This regional specialization reflects the statistical structure of natural scenes and experience, where upper-field stimuli often signal aerial threats and lower-field stimuli correspond to ground-level features or conspecifics. Similar biases are

observed in primates, where neurons representing the upper visual field exhibit smaller and denser receptive fields (Hafed & Chen 2016, Hafed et al. 2023).

Within the superficial layers, neurons cluster into modules that share orientation or motion preference, forming patch-like columns roughly 100–200 μm in diameter (Ahmadlou & Heimel 2015; de Malmazet et al. 2018, 2024; Feinberg & Meister 2015; Li et al. 2020). Orientation-selective neurons are arranged in radial patterns centered on the point of fixation, whereas direction-selective neurons exhibit a global organization aligned with optic flow during forward locomotion and a net bias for upward-nasal motion in the upper visual field (Ahmadlou & Heimel 2015, de Malmazet et al. 2018, Li et al. 2020). Comparable modularity is found in the deeper layers, where *Pitx2*-expressing neurons form a tiled array associated with spatially targeted head movements (Masullo et al. 2019).

These structural regularities indicate that the collicular map is not a uniform representation of space but one weighted toward behaviorally salient regions. Local tuning and connectivity preferences are biased to link ecologically relevant stimuli to appropriate motor outputs, ensuring that the same spatial coordinates guide both sensory selection and motor execution.

3. CELL TYPES OF THE SUPERIOR COLLICULUS

3.1. Morphological and Genetic Framework

Identifying the neuronal components of a brain region has often provided a foundation for understanding its circuit logic and function (Sanes & Masland 2015, Xu et al. 2020, Zeng & Sanes 2017). This is proving to be the case for the colliculus. Classical anatomy distinguished a recurring set of morphological cell types. This included narrow-field, wide-field, horizontal, stellate, piriform, and marginal cells in the superficial layers, as well as multipolar or pyramidal neurons in the deeper layers (May 2006). Like in the retina and other brain regions, morphology was a good predictor of both projection target and response properties. For example, in mice, Gale & Murphy (2014, 2018) established a systematic link between genetic, anatomical, and functional classification of collicular neurons (**Figure 2**). Using Cre-driver lines combined with quantitative morphology and electrophysiology, they identified four principal classes in the retinorecipient layers: wide-field neurons (Ntsr1-GN209-Cre) reside in the optic fiber layer and project to the lateral posterior thalamus; stellate neurons (Rorb-Cre) project to the dorsal and ventral geniculate and the parabigeminal nucleus (PBG); horizontal neurons are GABAergic (Gad2-Cre) and project locally or to the visual thalamus and the PBG; and narrow-field neurons (Grp-KH288-Cre) project to the deeper layers and the PBG. Identification of mouse lines labeling these and other specific cell types in the colliculus enabled a series of specific studies to understand the role each cell type plays in mediating approach and avoidance behaviors (Hoy et al. 2019; Li et al. 2023; Sans-Dublanc et al. 2021; Shang et al. 2015, 2018; Wu et al. 2022).

3.2. Molecular Diversity

The use of single-cell and single-nucleus transcriptomics has revealed the expression profiles of thousands of genes in individual cells that allow for the clustering of cells into subtypes based on their distinct transcriptomes (Byun et al. 2016, Cheung et al. 2024, Liu et al. 2023, Zeng & Sanes 2017). One key advantage of this approach is the identification of specific marker genes that enable the selective targeting and manipulation of select populations.

In the superficial layers of the colliculus, transcriptomic studies have uncovered extensive cellular heterogeneity, identifying 28–30 distinct populations including 23 inhibitory and 7 excitatory subtypes (Liu et al. 2023). Transcriptomic classification reliably links molecular types to traditional anatomical and functional roles (Chen et al. 2025, Liu et al. 2023). For example, in mice, excitatory

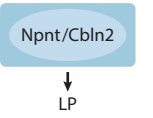
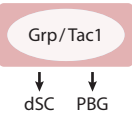
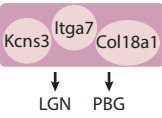
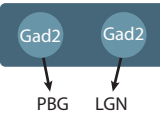
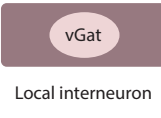
	WIDE-FIELD	NARROW-FIELD	STELLATE	HORIZONTAL PROJECTION	INTERNEURON
Strata zonale griseum superficiale opticum					
Excitatory or inhibitory	Excitatory	Excitatory	Excitatory	Inhibitory	Inhibitory
Visual encoding	Looming Small moving Object motion	Looming Small stationary Direction selective	Small slowly moving	Looming Large moving Large stationary	Looming Large moving Large stationary
Transgenic lines	Ntsr1-GN209-Cre Cbln2-IRES-Cre	Grp-KH288-Cre	Rorb-Cre	Gad2-Cre	Gad2-Cre, Rorb-Cre, and vGat-Cre
Subpopulations	 LP	 dSC PBG	 LGN PBG	 PBG LGN	 Local interneuron
Behaviors	Arrest Freezing Hunting	Escape Orienting Pursuit	Not applicable	Orienting Modulate freezing and escape	Not applicable
Retinal inputs	ON and OFF alpha Small field transient	Direction selective	Not applicable	ON and OFF alpha Direction selective Small field transient	Not applicable

Figure 2

Cell type composition of the superficial superior colliculus. Major anatomically, genetically, and functionally characterized cell classes of the superficial superior colliculus are wide-field (WF), narrow-field (NF), stellate, and horizontal cells (inhibitory projection neurons) as well as *Gad2*⁺ and *Rorb*⁺ interneurons. The main visual response properties and transgenic lines are reported, together with known genetically specific or projection-specific subpopulations. Where known, mediated behaviors and major retinal inputs are listed. Abbreviations: dSC, deep superior colliculus; LGN, lateral geniculate nucleus; LP, lateral posterior nucleus of the thalamus; PBG, parabigeminal nucleus.

wide-field cells, which project to the pulvinar, are marked by the expression of *Cbln2* (cerebellin 2) and *Npnt* (nephronectin) (Chen et al. 2025, Liu et al. 2023, Tsai et al. 2022), and *Cbln2* is a conserved marker for wide-field neurons across different species, including tree shrews and humans (Chen et al. 2025, Kipcak & Erisir 2026). Further, systematic comparison between transcriptomic results and in vivo imaging has successfully matched molecular profiles to functional response types, identifying the inhibitory subtype defined by the molecular marker *Cbln4* (cerebellin 4) as critically involved in direction selectivity and accounting for ~40–50% of direction-selective cells in the superficial layers of the colliculus (Liu et al. 2023). While direction-selective cells have been associated with various morphological types, including narrow-field neurons, the identification of *Cbln4*⁺ neurons provides a clear genetic determinant for a major functional population.

In a separate study, viral tracing was combined with RNA sequencing across the depth of the colliculus and identified 25 excitatory subtypes. This approach revealed two subtypes in the deeper layers that stand out with their specific projection targets: *Pitx2*⁺ neurons send axons to the paramedian pontine reticular formation, while *Rxfp2*⁺ neurons target the mediorostral part of the lateral pulvinar (Cheung et al. 2021). Transcriptomic analyses have further enabled the selective identification and investigation of the *Pitx2*⁺ glutamatergic neuron subclass (Masullo et al. 2019). These *Pitx2*⁺ neurons are concentrated in the intermediate layer (stratum griseum intermediale), accounting for ~23% of stratum griseum intermediale neurons. Anatomically, they are clustered into arrays that tile the intermediate layer, providing a modularly organized spatial-motor register

for movement vectors. Functionally, *Pitx2*⁺ neurons mediate spatially tuned head movements and encode prey-specific tactile cues (Masullo et al. 2019, Xie et al. 2021).

3.3. Functional Properties

The first single-cell recordings of visual responses in the mammalian colliculus were performed in the 1960s and 1970s, mostly in cats, primates, and rabbits (Humphrey 1968, Jassik-Gerschenfeld & Ascher 1963, Masland et al. 1971, McIlwain 1975, Schiller & Koerner 1971, Spear et al. 1972). Together with lesion studies, these experiments proposed the function of the colliculus in visual attention (Sprague & Meikle 1965), expanding on its already established role in head and eye movements. In mice, recent functional classification using high-throughput physiological recordings during visual stimulation has revealed ~24 functional subtypes of visual neurons in the superficial layers of the colliculus (De Franceschi & Solomon 2018, Gale & Murphy 2014, Liu et al. 2023, Wang et al. 2010). Like in the retina, collicular neurons differ in their ON-OFF polarity, contrast preference, motion tuning, direction- and orientation-selectivity, size preferences, and so forth. The similarity of collicular response types and the representation of visual information in the retina decreases with increasing depth within the colliculus, consistent with associated progression of signal processing and sensory integration (Lee et al. 2020, Li & Meister 2023, Si et al. 2025). In particular, the deeper layers show increased feature selectivity and spatial invariance and are more likely to respond to auditory stimuli, consistent with computations that trigger looming-evoked escape and orienting behaviors.

Critically, not only are the numbers of functionally (~24) and genetically (~30) identified types in the superficial layers similar, but different classes of functional cell types also map well onto the genetic cell types identified by Cre lines and using single-nucleus RNA sequencing (Chen et al. 2025; Gale & Murphy 2014, 2018; Liu et al. 2023). For example, wide-field neurons labeled in *Ntsr1*-Cre mouse lines preferentially transmit information about the low-speed motion of small objects across a large visual field to the pulvinar, while *Grp*⁺ narrow-field neurons send information about looming objects as well as the direction of movement of small objects to the PBG and the deeper layers of the colliculus. Local excitation is provided by *Rorb*⁺ stellate cells, which preferentially respond to small and stationary visual stimuli and also send axons to the lateral geniculate nucleus (LGN) and the PBG. GABAergic *Gad2*⁺ horizontal cells respond to large stationary stimuli as well as looming stimuli and can be separated into two subtypes: (a) a type of projection neuron targeting the LGN and the PBG and (b) *Rorb*⁺ or *Gad2*⁺ interneurons (Figure 2). In the deeper layers, *Pitx2*⁺ neurons are the main genetically identified type that has been functionally characterized, revealing its responses to tactile rather than visual stimuli (Xie et al. 2021).

While the complete repertoire of visual response types likely exceeds those identified with standard stimuli, the convergence of molecular, anatomical, and physiological datasets supports a model where the colliculus condenses high-dimensional retinal information into a compact set of motor-relevant features. These include direction, motion onset, and spatial expansion, which are routed down defined projection channels.

3.4. Projection-Specific Functional Modules

The sparse and selective projections of the neurons of the colliculus give rise to a projection-specific organization of its circuits, where distinct populations of neurons, often defined genetically, are dedicated to processing specific sensory features and projecting to discrete downstream targets to mediate particular behaviors. Evidence for this modularity came from studies in rodents, revealing a regional specialization corresponding to distinct behavioral pathways: The

lateral colliculus, representing the lower visual field, mediates orienting and approach behaviors, while the medial colliculus, representing the upper visual field, mediates avoidance and defensive behaviors. This organizational principle links visual field representation to ethological necessity (e.g., approaching ground food versus escaping aerial predators).

Within the superficial layers, several distinct cell types form projection-specific modules, which route visual information to specific downstream targets that mediate different behaviors. Wide-field neurons, for instance, almost exclusively project to the pulvinar and are the (almost) sole input from the colliculus to the pulvinar, placing them in a unique position to convey information about predator- and prey-like stimuli to higher cortical areas (Beltramo & Scanziani 2019, Bennett et al. 2019, Gale & Murphy 2014). In accordance with their visual response properties, these neurons sample from a small and specific subset of retinal ganglion cells that encode both small and slowly moving objects as well as looming stimuli (Kühn et al. 2025, Reinhard et al. 2019). In addition, wide-field neurons sample different types of visual inputs along different sections of their massive dendritic trees, a subcellular organization that allows for de novo computation of motion features (Kühn et al. 2025). Similarly, collicular neurons that project to the PBG have been found to sample from a partially distinct but overlapping set of retinal inputs, which, in contrast to the wide-field inputs, includes direction-selective retinal ganglion cells (Krizan et al. 2024, Reinhard et al. 2019). This corresponds with direction-selective responses found in the PBG itself as well as in the different PBG-projecting neurons, such as narrow-field cells (Krizan et al. 2024, Reinhard et al. 2019). In fact, narrow-field neurons have been shown to inherit their selectivity for movement direction directly from ON-OFF direction-selective retinal ganglion cells (Krizan et al. 2024).

Projection-specific modules arise not only from specific connections between retinal inputs and collicular targets but also in the connectivity of nonretinal inputs to different subpopulations of collicular neurons. For instance, GABAergic *Gad2*⁺ horizontal cells that project to the LGN or the PBG both sample from similar retinal inputs and encode comparable visual features (Gale & Murphy 2014, Li et al. 2023, Whyland et al. 2020). However, their brain-wide inputs significantly differ where, for instance, tactile- and motor-related brain areas preferentially target PBG-projecting *Gad2*⁺ neurons (Li et al. 2023). This architecture sets out a projection-specific logic that rapidly converts visual input into action while still permitting flexibility by allowing internal state and context to selectively modulate activity within each pathway (**Figure 3**). This circuit structure suggests that the different output pathways embody a projection-specific logic for routing visual features (detection and pursuit) for robust, innate behaviors while providing the key circuit infrastructure for flexibility, enabling the selective modulation of feedforward visual threat signals based on the animal's internal state or context.

4. CIRCUITS UNDERLYING DISTINCT BEHAVIORS

The projection-specific modules of the colliculus support a set of innate behaviors that allow animals to respond rapidly and appropriately to ethologically salient sensory stimuli. Here we discuss how the circuits of the colliculus support classical orienting movements of the eye, head, and body before illustrating how these principles generalize to support innate avoidance and approach behaviors, including freezing, escape, and prey capture. Lastly, we illustrate how recent studies show that these hardwired, conserved circuits can be modulated by different brain regions to match the current brain state and context an animal finds itself in.

4.1. Orienting Movements of the Eye, Head, and Body

To interact effectively with their surroundings, animals orient toward salient stimuli. The colliculus has long been recognized as central to this function. As early as in the nineteenth century,

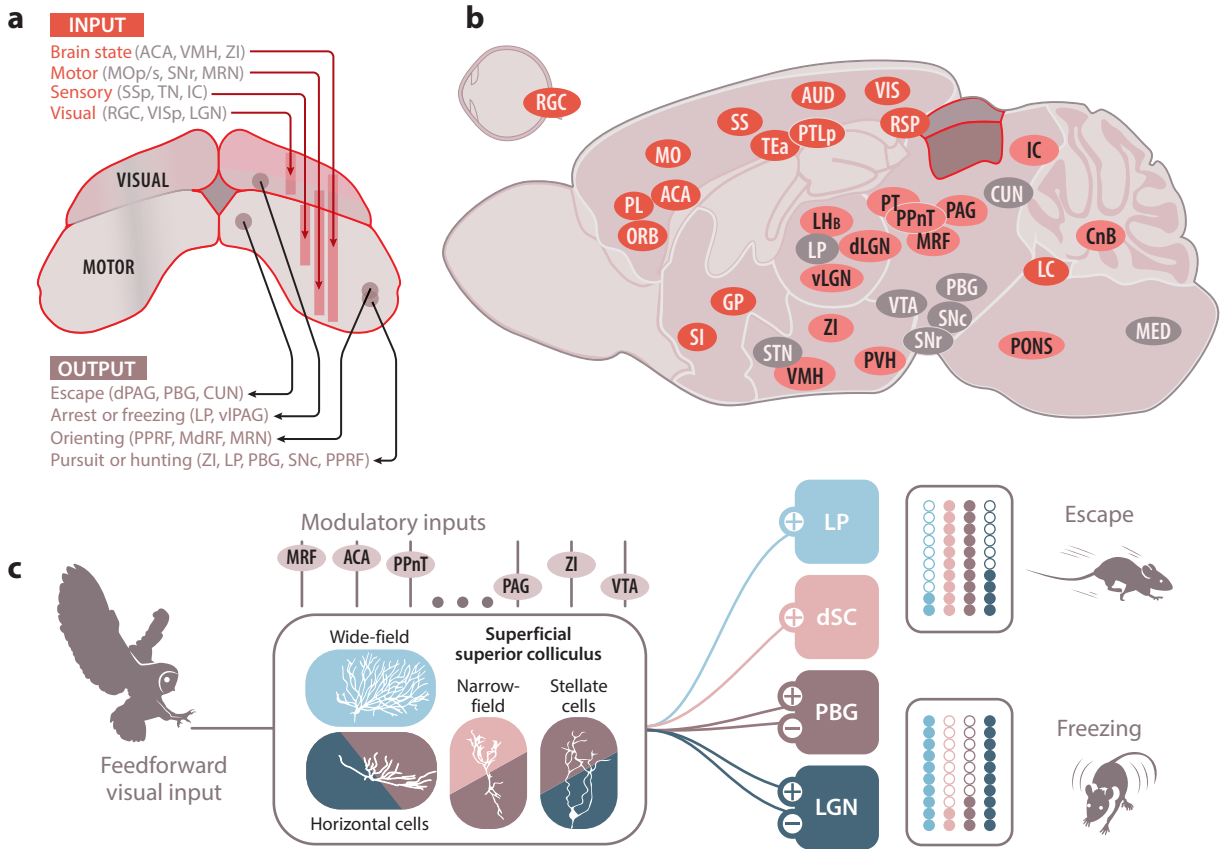


Figure 3

Organization of inputs and outputs of the superior colliculus and capacity for adaptive behaviors. (a) Laminar organization of input and output pathways of the superior colliculus. (b) The major nuclei that provide inputs and/or receive outputs from the mouse superior colliculus (sagittal view). (c) A proposal of how feedforward sensory and modulatory brain-wide inputs may interact to modify the activity in different output pathways of the superior colliculus to influence which behavior is triggered by the same visual stimulus. Abbreviations: ACA, anterior cingulate area; AUD, auditory cortex; CnB, cerebellar nuclei; CUN, cuneiform nucleus; dLGN, dorsal lateral geniculate nucleus; dPAG, dorsal periaqueductal gray; dSC, deep superior colliculus; IC, inferior colliculus; GP, globus pallidus; LC, locus coeruleus; LGN, lateral geniculate nucleus; LHb, lateral habenula; LP, lateral posterior nucleus of the thalamus; MED, medulla; MdRF, medullary reticular formation; MO, motor cortex; MRF, midbrain reticular formation; MRN, midbrain reticular nucleus; MOp/s, primary/secondary motor cortex; ORB, orbital area; PAG, periaqueductal gray; PBG, parabrachial nucleus; PL, prefrontal area; PONS, pons; PPnT, posterior paralaminae nuclei of the thalamus; PPRF, paramedian pontine reticular formation; PT, pretectal area; PTLp, posterior parietal association areas; PVH, paraventricular nucleus; RGC, retinal ganglion cell; RSP, retrosplenial cortex; SI, substantia innominata; SNc, substantia nigra pars compacta; SNr, substantia nigra pars reticulata; SS, somatosensory cortex; SSp, primary somatosensory area; STN, subthalamic nucleus; TEa, temporal association areas; TN, tegmental nucleus; VIS, visual cortex; VISp, primary visual cortex; vLGN, ventral lateral geniculate nucleus; vIPAG, ventral lateral periaqueductal gray; VMH, ventral medial hypothalamus; VTA, ventral tegmental area; ZI, zona incerta. Panels a and b adapted from Hoy & Farrow (2025).

Adamük (1870) observed that electrical stimulation of the colliculus in cats produced movements of the eyes, which were later demonstrated by Apter (1946) to correspond to the visual location of the site of stimulation. These observations laid the foundation for the concept of a sensory-motor spatial map within the colliculus. In primates, Goldberg and Wurtz later showed that neurons in the superficial, visual layers possess receptive fields corresponding to restricted regions of the visual field, while neurons in the deeper, motor-related layers discharged just before saccadic eye

movements (Cavanaugh & Wurtz 2004; Goldberg & Wurtz 1972a,b; Wurtz & Goldberg 1972). Together, these findings established the colliculus as a structure that transforms spatially organized sensory inputs into coordinated motor outputs.

When animals are allowed to freely move their heads, activity in the colliculus reflects the coordinated control of eye and head movements, where the relative contribution of eye and head motion varies systematically with species and body size (Freedman et al. 1996; Guillaume & Pélisson 2001, 2006). In mice, the cell types mediating these movements have been identified. They are *Pitx2*-expressing glutamatergic neurons, which form clustered premotor modules in the intermediate layers and generate 3D, saccade-like head movements (Masullo et al. 2019). Their firing precedes natural movements, and their axons descend through the predorsal bundle to the paramedian pontine reticular formation and medullary motor nuclei that jointly determine gaze endpoints (Cheung et al. 2021). In addition, these *Pitx2*⁺ modules receive convergent input from superficial visual neurons and from deep-layer multisensory and cortical sources, providing a selective locus where spatially coherent signals are transformed into motor vectors (González-Rueda et al. 2024). Complementary optogenetic stimulation of individual modules in freely moving mice evokes stereotyped combinations of head and eye motion that terminate at consistent endpoints, highlighting the modular and topographic organization of premotor circuits in the deep colliculus (Zahler et al. 2023).

4.2. Avoidance and Defensive Behaviors

Instinctive avoidance and defensive behaviors (De Franceschi et al. 2016, Yilmaz & Meister 2013) depend on sensorimotor transformations mediated by the colliculus. These transformations rely on its superficial layers, where visual inputs mimicking overhead threats reliably trigger escape or freezing. Starting in the superficial layers of the colliculus, neuronal activity diverges into anatomically and molecularly distinct output pathways, each associated with a specific behavioral response.

Visually evoked arrest and freezing behaviors are associated with the set of excitatory neurons projecting to the lateral posterior thalamus (pulvinar), identified in a series of activation and inhibition experiments on different sets of neurons (Sans-Dublanc et al. 2021, Shang et al. 2018, Wei et al. 2015, Xie et al. 2021). Activation of CaMKII- or parvalbumin-positive neurons projecting to the lateral posterior thalamus reliably triggers long freezing responses (Sans-Dublanc et al. 2021, Shang et al. 2018, Wei et al. 2015). As parvalbumin and CaMKII are not specific markers of individual cell types in the colliculus, it is likely that they include the wide-field neurons labeled in *Ntsr1*-GN209-Cre and *Cbln2*-IRES-Cre mice (Gale & Murphy 2014, Gerfen et al. 2013, Liu et al. 2023, Sans-Dublanc et al. 2021, Xie et al. 2021). More specific manipulation of wide-field neurons labeled in those Cre lines illustrates their importance in mediating both arrest and freezing behaviors (Sans-Dublanc et al. 2021, Xie et al. 2021). Note that freezing behaviors are more likely to be mediated by the medial colliculus, which samples the upper visual field (Sans-Dublanc et al. 2021, Wei et al. 2015). Evaluation of commonly used transgenic mouse lines showed that little *Ntsr1* is expressed in the wide-field neurons; hence, Cre expression in *Ntsr1*-GN209-Cre mice is not driven by endogenous *Ntsr1* expression (Chen et al. 2025). Instead, nephronectin (in mice) and cerebellin 2 (across species) have been identified as reliable markers of wide-field neurons (Chen et al. 2025, Cheung et al. 2021, Liu et al. 2023, Tsai et al. 2022, Xie et al. 2021), providing a tool for future dissection of the wide-field neuron pathway across species (Kipcak & Erisir 2026).

The pathways associated with escape appear more diverse than those mediating arrest and freezing behaviors. They include two pathways originating with narrow-field neurons in the superficial layers of the colliculus and two output pathways from the deeper layers of the colliculus.

In the superficial layers, excitatory projections to the PBG and deep layers of the colliculus have been demonstrated to drive escape behaviors (Krizan et al. 2024; Shang et al. 2015, 2018; Wu et al. 2022). *Grp*⁺ narrow-field neurons project from the superficial layers of the colliculus to each of these targets and are reliably labeled in Grp-KH288-Cre mice (Gale & Murphy 2014). These neurons respond well to looming stimuli and are direction-selective, and optogenetic activation commonly triggers escape behaviors (Gale & Murphy 2014, Krizan et al. 2024, Wu et al. 2022). Similar to activating *Grp*⁺ neurons, general activation of excitatory neurons projecting to the PBG triggers escape behaviors (Deichler et al. 2020; Shang et al. 2015, 2018). Consistent with these results, inhibition of PBG-projecting *Gad2*⁺ neurons leads to increased likelihood and vigor of visually evoked escape behaviors (Li et al. 2023). However, specific activation of neurons projecting to the deeper layers of the colliculus has not yet been possible, and the roles of each projection remain intertwined.

From the deep layers of the colliculus, outputs to the cuneiform and dorsal periaqueductal gray (dPAG) have been shown to drive escape behaviors (Bandler & Depaulis 1991, Dean et al. 1989, Mitchell et al. 1988, Sahibzada et al. 1986, Zhang et al. 1990). In mice, the output to the dPAG is best understood. Using a complementary set of activation, inhibition, and calcium recordings experiments, it has been demonstrated that the glutamatergic projections from the deeper layers of the medial colliculus to the dPAG encode threat intensity and the probability of escape, while excitatory neurons in the dPAG are active at the initiation of escape (Evans et al. 2018). In vitro patch-clamp and optogenetic experiments demonstrated that neurons in the deep medial colliculus form weak monosynaptic connections with the dPAG. Together with recurrent excitatory connections within the colliculus, this circuit acts to accumulate evidence about threat levels, and only after reaching a threshold will glutamatergic neurons in the dPAG fire and initiate escape (Evans et al. 2018). In both mice and rats, a direct projection from the colliculus to the cuneiform nucleus has been found, bypassing the PAG (Benavidez et al. 2021, Caggiano et al. 2018, Mitchell et al. 1988, Redgrave et al. 1988). Activation of this projection from the deep layers of the colliculus, including the surrounding midbrain reticular formation, also reliably triggers defensive behaviors, including escapes, but which behavior is elicited varies depending on the environment (Isa et al. 2020). Finally, the intermediate and deep layers of the colliculus contain glutamatergic projections to the ventral tegmental area, which is known for its role in learned appetitive and aversive behaviors (Huang et al. 2021, Zhou et al. 2019). There, amygdala-projecting GABAergic neurons, involved in both conditioned and innate fear behavior, receive direct excitatory inputs from the colliculus and respond to looming stimuli. Inhibition and activation of these neurons modulate escape to a nest (Zhou et al. 2019).

4.3. Hunting and Approach Behaviors

Hunting is another type of instinctive behavior that uses rapid sensorimotor transformations. It is a complex process that we can subdivide into different phases: detection of the prey, subsequent shifting of an animal's body and attention toward the target, initiation of pursuit, and capture of the prey.

Hunting is an evolutionarily conserved behavior, and the involvement of the colliculus/optic tectum has been found in multiple species. Ethological studies in toads provided some of the first evidence of the involvement in the detection of different visual stimuli by the colliculus/optic tectum and how the features of these stimuli can lead to hunting versus avoidance (Beck & Ewert 1979, Ewert 1969). In larval zebrafish, the size of a moving visual stimulus leads to initiation of different behaviors: While a small moving object leads to hunting, a large moving object leads to escape behaviors (Barker & Baier 2015, Yin et al. 2019). In addition, multiple rodent species are

reported to use vision to guide hunting behaviors (Dean & Redgrave 1984, Langley 1989, Polsky 1978). More recently, laboratory mice have been shown to hunt cockroaches (Shang et al. 2019, Zhao et al. 2019) and crickets (Hoy et al. 2016, 2019).

On a circuit level, wide- and narrow-field neurons are not only involved in avoidance behaviors but also play distinct roles in predatory hunting behaviors. While wide-field neurons are responsible for rapid prey detection and the initiation of an approach, narrow-field neurons are essential for continuous approach and for the accurate orienting movements during pursuit (Hoy et al. 2019, Krizan et al. 2024). The downstream pathways through which the different steps of hunting are mediated are less well known. Shang et al. (2019) used an activity-dependent genetic labeling approach to identify pathways from the intermediate and deeper layers of the colliculus that are activated during hunting behavior, which included projections to the zona incerta (ZI) and the substantia nigra pars compacta (SNc). Activation of projections from the colliculus onto GABAergic ZI neurons drives hunting behaviors (Shang et al. 2019, Zhao et al. 2019). These ZI-projecting neurons encode prey-related sensory cues, which in the ZI are translated into motivational cues for predatory attack (Shang et al. 2019, Zhao et al. 2019). The colliculus–ZI pathway may specifically participate in predatory hunting since activation of this pathway did not induce food intake, social aggression, or exploration, and inhibition did not affect visually triggered escape (Shang et al. 2019). In addition, this pathway appears to simultaneously initiate hunting and inhibit aversive behavior, both through projections to the ventrolateral and lateral PAG (Chou et al. 2018, Zhao et al. 2019).

Pitx2⁺ neurons, earlier discussed for their role in head movements, also project to the ZI. Consistent with the findings on the colliculus–ZI pathway, inactivation of *Pitx2*⁺ collicular neurons impaired prey capture, without affecting looming-evoked defensive responses (Xie et al. 2021). Interestingly, in this study, the *Pitx2*⁺ neurons responded strongly to contralateral whisker stimulation but not to the small moving black circle, suggesting a role of this circuit in the tactile rather than visual aspects of prey capture (Xie et al. 2021).

The second main collicular target that is activated during hunting behavior is the SNc, which is involved in appetitive locomotion (Huang et al. 2021, Shang et al. 2019). Glutamatergic colliculus neurons innervate dopaminergic neurons in the SNc and modulate dopamine release in the striatum. These SNc-projecting colliculus neurons encode locomotion speed and are recruited during appetitive but not during defensive locomotion (Huang et al. 2021). However, the question remains on how locomotion information is transmitted to the colliculus. The authors hypothesize a possible role for the strongly motor-related substantia nigra pars reticulata since it has GABAergic projections to the lateral part of the deep layers of the colliculus (Kaneda et al. 2008) where the SNc-projecting neurons are located. Furthermore, it has been shown that the inhibition and excitation of the substantia nigra pars reticulata predict the initiation and suppression of locomotion, respectively (Freeze et al. 2013). This is in line with another study that showed that activating the substantia nigra pars reticulata–colliculus projection reduced active avoidance behavior and increased approach to a robo-beetle (Almada et al. 2018).

4.4. Context Matters: Modulatory Inputs Influencing Behavior

Behaviors mediated by the colliculus may appear stereotyped, almost reflex-like. However, to ensure survival, even very fast and essential behaviors need to be adapted to the current situation under which they are elicited. Contextual changes may even lead to completely different strategies, as has been shown, for example, for the presence or absence of a shelter that triggers mice to switch between escape and freezing behaviors in response to the very same stimulus (Vale et al. 2017). Dissection of the anatomical organization of nonretinal inputs to the different output

pathways of the colliculus provides an important step in understanding how contextual information about the internal state or about the surroundings can be integrated to flexibly modulate behavior (**Figure 3**). Li et al. (2023) traced the brain-wide inputs that innervate the *Gad2*⁺ inhibitory neurons of the superficial layers. These experiments revealed two separate populations of *Gad2*⁺ neurons: one projecting to the PBG (Gad2-PBG) and one projecting to the LGN (Gad2-LGN). While both populations receive information from similar retinal ganglion cells and encode comparable visual features, they diverge in their nonretinal inputs. Of the 69 labeled input areas of *Gad2*⁺ neurons, 51 had a significant bias toward one of the populations. For instance, cognition-related and visual areas had a bias toward the Gad2-LGN circuit, while motor-related and somatosensory areas preferred the PBG-projecting *Gad2*⁺ neurons. Both pathways influence innate defensive behaviors in distinct ways, with circuit-specific modulation by nonretinal inputs allowing threat responses to be flexibly adjusted according to the animal's activity, internal state, and surroundings. While inhibition of Gad2-PBG resulted in increased escape responses, inhibition of Gad2-LGN led to increased and prolonged freezing responses. The balance between these two behaviors could hence be shifted by activation of circuit-specific inputs, for example, from the ZI and the anterior cingulate areas. Furthermore, Gad2-PBG neurons are strongly modulated by locomotion, which is in line with a bias for motor-related input areas to this circuit. Similarly, selective modulation of looming responses by locomotion was found for *Ntsr*⁺ neurons (Relota et al. 2025). This suggests that self-motion may impact escape reactions and is a further indication of contextual modulation of different output circuits of the colliculus.

A special focus of other studies has been on the modulation of colliculus-mediated visual behaviors by the ventral lateral geniculate nucleus (vLGN). Inhibition of GABAergic neurons in the vLGN led to increased escape to shelter (Fratzl et al. 2021) or increased and prolonged freezing (Salay & Huberman 2021). On the other hand, activation of these neurons increased exploration of the environment (Fratzl et al. 2021, Salay & Huberman 2021). Activity of the vLGN axons in the medial colliculus was low right before escapes and higher in nonescape trials, indicating an important role for the vLGN in perceiving the level of threat and habituation (Fratzl et al. 2021). Most vLGN recipient neurons are located in the optic layer of the colliculus and immediately below. vLGN inputs tune the preference of these colliculus neurons toward smaller stimuli through broad surround suppression, which facilitates approach toward small moving dots in the lower visual field (Li et al. 2023). In addition, glutamatergic neurons in the vLGN project to the colliculus and have an opposing effect to the GABAergic projections: While inhibition of glutamatergic vLGN neurons leads to a decrease in defensive behaviors, activation leads to an increase (Salay & Huberman 2021).

Another example of modulatory input is the locus coeruleus (LC). Stressed mice show accelerated defensive responses to looming, which are mediated by a TH⁺ LC–colliculus projection (Li et al. 2018). The TH⁺ neurons in the LC are activated by repeated stress, and chemogenetic inhibition of these neurons or blocking of adrenergic receptors in the colliculus abolishes the enhanced defensive behaviors. This suggests a strong role for the LC–noradrenergic pathways to link contextual information on stress and anxiety with innate defensive behaviors.

A useful organizing analogy is to view the colliculus as a control center coordinating rapid, spatially organized actions. Inputs from the cortex, thalamus, and midbrain converge on collicular circuits to bias the selection and vigor of visually evoked behaviors according to the animal's current circumstances.

5. COMPARATIVE AND EVOLUTIONARY PERSPECTIVES

The coarse anatomy of the colliculus and optic tectum is based on a layered and retinotopic organization and is conserved across species. The separation into superficial, intermediate, and deep

layers found in mice is a general blueprint of the mammalian colliculus. A similar organization can also be found in zebrafish, where the optic tectum is split into a superficial retino-recipient zone and a central and periventricular zone involved in various motor outputs, with further subdivision into a total of six layers (Baier & Scott 2024). In birds such as chickens and pigeons, the optic tectum has 15 distinguishable layers (Ramón y Cajal 1909), and similar to other species, retinal inputs enter into the superficial layers (Angaut & Repérant 1976). In addition to this dorsoventral layering, the colliculus and optic tectum also have a conserved retinotopic organization along their anteroposterior and mediolateral axes in rodents (Molotkov et al. 2023), fish (Stuermer 1988), birds (McGill et al. 1966), and primates (Dilbeck et al. 2022).

Furthermore, similar cell types can be identified across species. On a molecular level, conserved neuronal composition of the colliculus across mice, tree shrews, and humans has been found, and transcriptomic analysis shows a high correspondence across species as well (Kipcak & Erisir 2026, Liu et al. 2025). For instance, *Cbln2* labels a subset of pulvinar-projecting wide-field neurons of the superficial layers in both tree shrews and mice. Anatomically, such wide-field neurons whose dendritic arbors span dozens of degrees of visual angle have also been described in rats, voles, hamsters, lizards, chickens, and squirrels (Hilbig et al. 1999, Luksch et al. 1998, Major et al. 2000, May 2006, Mooney et al. 1985, Ramón y Cajal et al. 1995, Valverde 1973). Some other subtypes of collicular neurons are species specific, and various genes are differently enriched in different species, most notably genes related to the primary cilium (Liu et al. 2025). In contrast to the cortex, synapse-related genes associated with neurotransmitter receptors, cell adhesion, and the extracellular matrix are found to be highly conserved across mammalian species, including mice, tree shrews, and humans (Liu et al. 2025). This conservation, which spans species separated by more than 96 million years of evolution, includes functional categories such as post-synaptic organization, synapse assembly, vesicle organization, vesicle-mediated synaptic transport, and neurotransmitter regulation.

The common anatomical organization is a substrate for conserved functional properties: Preferences for ethologically relevant stimuli that signify danger or food or have social relevance have been found in the retino-recipient neurons of any investigated species (Georgy et al. 2016, Hoy et al. 2019, Lee et al. 2020, Temizer et al. 2015, Wu et al. 2005). In particular, collision-sensitive neurons, important for detecting approaching danger, have been described in mice (Gale & Murphy 2016), pigeons (Wu et al. 2005), frogs (Nakagawa & Hongjian 2010), zebrafish (Temizer et al. 2015), and cats (Liu et al. 2011) as well as in the optic lobe of crabs (Oliva et al. 2007) and flies (de Vries & Clandinin 2012) (**Figure 4**). Accordingly, the colliculus and optic tectum are involved in mediating aversive, appetitive, and social behaviors, including escape and freezing (De Franceschi et al. 2016, de Vries & Clandinin 2012, Dunn et al. 2016, Yilmaz & Meister 2013), gaze and head movements (Guitton et al. 1980; Kardamakis et al. 2015, 2016; Kurtz & Butter 1980; Wilson et al. 2018), and approach and capture of prey (Ewert 1969, Filosa et al. 2016, Hoy et al. 2019), across a wide variety of animals.

Despite these similarities in overall architecture and function, the colliculus and its homologues exhibit convergent specializations that reflect ecological demands (Basso et al. 2021, Isa et al. 2020, Wylie et al. 2009). For instance, in zebrafish, rabbits, mice, and pigeons, >80% of all retinal output neurons project to the colliculus, but in primates it is only ~10% (Ellis et al. 2016, Perry & Cowey 1984). It remains unclear whether this means that fewer information channels, that is, retinal ganglion cell types, are routed to the primate colliculus. Alternatively, visual tasks involving the colliculus might require a specific spatial resolution, independently of the species, rather than scale with each species' maximal visual accuracy. Indeed, considering that a mouse retina contains ~50,000 retinal ganglion cells (RGCs) distributed over ~14 mm² (Claes & Moons 2022, Jeon et al. 1998, Remtulla & Hallett 1985) and a 1° visual angle covers 33 μm on the retina

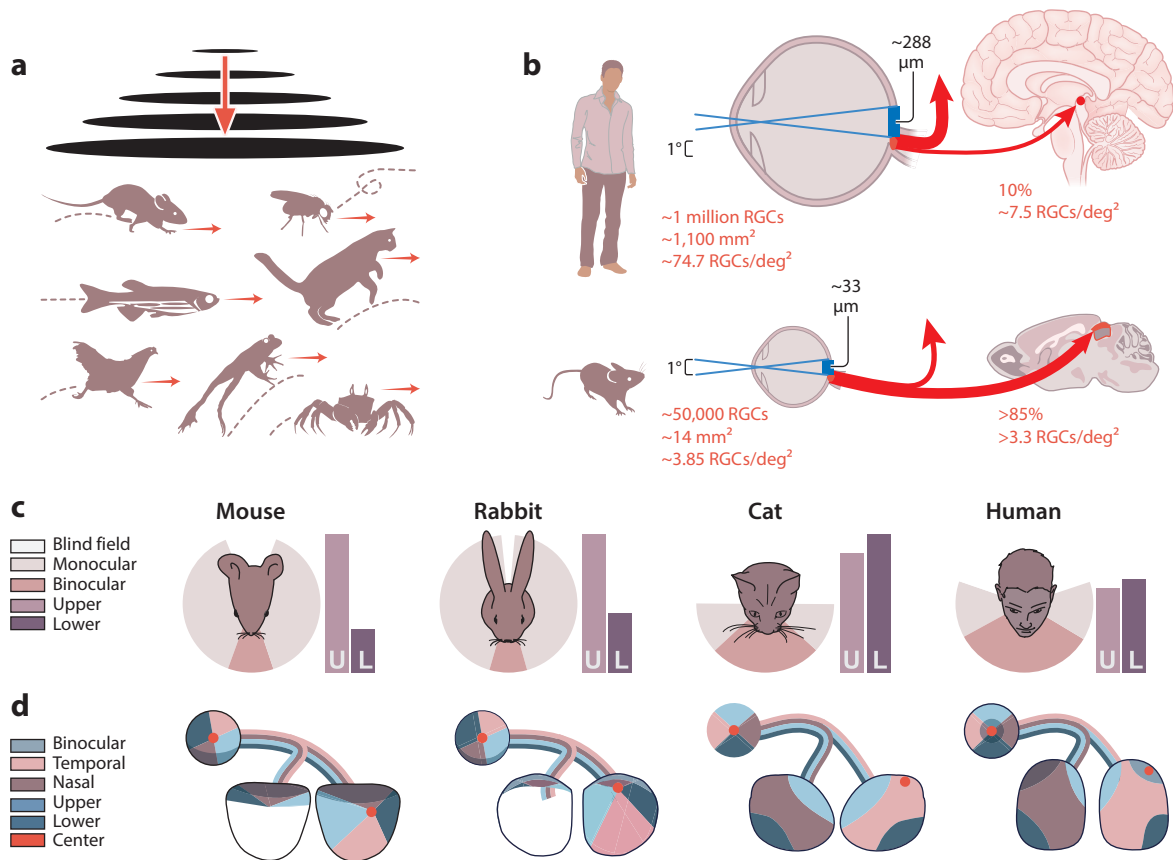


Figure 4 Comparative behavioral roles and visual field representations in the superior colliculus of different species. (a) Looming-evoked avoidance behaviors are conserved across species. (b) While the relative amount of visual information being sent to the superior colliculus in mice is much higher than in primates, the relative resolution (ganglion cells per degree of visual space) is comparable. (c) The extent of the visual field in mice, rabbits, cats, and humans. (d) Representation of the visual field within the superior colliculus of mice, rabbits, cats, and primates. Abbreviations: L, lower; RGC, retinal ganglion cell; U, upper.

(Schmucker & Schaeffel 2004), there are ~ 3.85 RGCs/deg². In humans, the retina measures $\sim 1,100$ mm² and contains ~ 1 million RGCs, and 1° covers 288 μ m (Kolb 1995; Sjöstrand et al. 1999), resulting in ~ 74.7 RGCs/deg². Hence, if evenly sampled across the retina, the resolution of the retinal information sent to the colliculus is comparable in both species (> 3.3 RGCs/deg² versus ~ 7.5 RGCs/deg²) (Figure 4).

Beyond innervation density differences, the primate colliculus has been implicated in cognitive functions such as gestalt and face recognition (Georgy et al. 2016, Nakano et al. 2013), aspects that have not been attributed to the colliculus in other species, granted they probably have not been tested in other animals. Work in primates further supports the view that the colliculus participates not only in orienting movements but also in target selection and visual attention (Anderson & Rees 2011, Katyal et al. 2010, Krauzlis et al. 2013, Lovejoy & Krauzlis 2010, Nummela & Krauzlis 2010, Robinson & Kertzman 1995, Schneider & Kastner 2009, White et al. 2017). In birds, work on the owl optic tectum and associated isthmus circuitry further shows that target selection depends on competitive circuits in the optic tectum that enhance behaviorally and ethologically relevant

stimuli and suppress distractors (Allen et al. 2021; Knudsen 2018; Mysore et al. 2010, 2011; Wylie et al. 2009; Zhang & Mysore 2025). Together, these studies indicate that in birds and primates the colliculus contributes to target selection by biasing competitive visuomotor representations, extending its role beyond motor execution. It remains to be investigated whether similar circuit mechanisms are in place in other species, such as rodents.

The largest variation among species will likely be found in nonretinal inputs to the colliculus and in its precise innervation of downstream targets. In mice, the colliculus receives cell type-specific and circuit-specific inputs from dozens of other brain areas, which allows for modulation of sensory inputs and/or motor output (Benavidez et al. 2021, Li et al. 2023). It is conceivable that depending on a species' habitat, sensory exposure, and social interactions, these inputs may vary in type and strength to flexibly adapt innate behaviors to context. Further species-specific adaptation may arise from the wiring of the output pathways of the colliculus. In *Mus*, the main targets of the superficial and deeper layers of the colliculus and their function are rather well described, and they are thought to be conserved across species. For instance, the colliculus–pulvinar axis has been confirmed in humans (Kragel et al. 2021), and work in *Octodon degus* further supports the possible role of the colliculus–PBG circuit in escape behavior (Deichler et al. 2020), while the role of the dorsomedial periaqueductal gray (dmPAG) circuit as the main escape initiator has also been shown in rats (Deng et al. 2016) and cats (Bandler & Depaulis 1991, Zhang et al. 1990). However, while this dmPAG function is also conserved in the deer mouse *Peromyscus maniculatus*, in its very closely related sister species, *Peromyscus polionotus*, the dmPAG does not mediate escape (Baier et al. 2025). This suggests not only rewiring or repurposing of the colliculus–dmPAG circuit in an evolutionarily speaking short time span but also the evolution of an alternative principal escape pathway. We hence argue that while model organisms remain critical for detailed circuit dissection, it is important to perform comparative research to gain a deeper understanding of which elements are conserved and which are adaptive.

6. DISCUSSION

The colliculus brings together a rich set of circuit motifs that transform visual input into behavior. Across species, this structure preserves a shared blueprint that includes a set of layered topographic maps, as well as tight alignment between sensory representations and motor commands. Yet the growing catalog of collicular cell types shows that this conserved blueprint contains fine-grained specializations that shape how each species deploys vision for its ecological needs. Recent work in mice, tree shrews, primates, and other vertebrates now provides the resolution needed to link molecular identity, circuit position, and behavior.

New molecular and physiological datasets show that the colliculus contains a far richer diversity of neuronal subtypes than previously recognized. Transcriptomic profiling identifies numerous excitatory and inhibitory populations, many with characteristic laminar positions, visual response properties, and projection targets. These cell types form modular circuits that transform visual signals into behavior via distinct pathways. In particular, wide- and narrow-field, stellate, and multiple inhibitory cell types each make specific contributions to visuomotor transformations. Their selective engagement in looming detection, prey capture, spatial localization, and head-orienting movements supports the view that the colliculus is not a single integrative hub but rather a set of interlinked channels, each tuned for a particular behavioral function.

This modular structure clarifies long-standing observations about the coexistence of feature-detecting and event-detecting responses within the same anatomical layers. It also explains how the colliculus can simultaneously support rapid yet flexible innate responses to salient stimuli and influence higher-order perceptual judgments. Recent work in mice extends this view by showing

that colliculus circuits contribute to visual selection and perceptual decision-making behaviors, not just the execution of orienting or defensive responses (Cone et al. 2024; Cover et al. 2026; Hu & Dan 2022; Wang et al. 2020, 2022, 2026). As molecular tools uncover more precise correspondences between transcriptomic classes and projection-defined circuits, the colliculus is becoming a model for understanding how neuronal diversity enables dedicated behavioral algorithms within a shared anatomical structure.

Despite this diversity, the broad architectural plan of the colliculus is remarkably conserved across species. Common organizational motifs are shared by fish, birds, rodents, and primates: layered maps of visual space, alignment between sensory input and motor output, and a division between superficial sensory layers and deeper premotor zones. Yet comparative studies also show systematic differences across species. Primates emphasize event detecting in the superficial layers that support rapid saccades and visual attention. Rodents express feature-detecting modules tuned for looming threats and small moving prey. Tree shrews combine primate-like visual specialization with rodent-like inhibitory enrichment. These differences reflect ecological priorities rather than departures from a common plan.

An emerging principle is that evolution modifies the colliculus through differential deployment of a conserved set of cell types. Some projection-defined modules, such as the *Cbln2*-expressing circuit targeting the pulvinar, appear deeply conserved. Others, especially inhibitory subclasses, show some divergence across mammals. This pattern suggests that adaptive changes in behavior arise less from new circuit motifs and more from adjusting the balance, connectivity, and recruitment of shared neural components. Comparative analyses position the colliculus as a powerful system for studying how evolution shapes sensorimotor circuits while preserving a core circuit architecture.

A growing set of work across different species suggests that differences are primarily due to adjustments of a conserved circuit architecture rather than the creation of new circuits. Synaptic genes and core cell types are strongly preserved across mammals, with differences occurring in specialized cellular domains such as cilia-related transcripts and a limited set of inhibitory cell types. These molecular differences parallel ecological specializations: primates emphasize event detection, while rodents rely on feature selectivity to drive innate behaviors.

Emerging tools now allow collicular circuits to be probed across different species. Spatial transcriptomics, projection-specific viral strategies, and deep-brain imaging can be deployed in mice, tree shrews, and primates, enabling cell types and pathways to be identified using shared molecular criteria. Combined with high-density recording and behavioral assays in freely moving animals, these methods make it possible to link homologous cell types to conserved or divergent computations. As these approaches expand across model systems, they provide a common framework for comparing how evolution tunes a shared collicular blueprint for different ecological demands.

SUMMARY POINTS

1. The superior colliculus preserves a conserved architectural blueprint across species, with layered maps that align sensory inputs with motor outputs.
2. Within this structure, a diverse set of excitatory and inhibitory cell types create modular channels that support behaviors such as looming detection, prey capture, and orienting.
3. Molecular identity often predicts projection targets and functional roles, revealing a close link between cell type, visual function, and behavior.

4. Collicular processing is dynamically shaped by behavioral state, including neuromodulatory influences, motor context, and top-down signals from cortical and subcortical areas.
5. Understanding collicular computation requires studying neural activity during naturalistic behaviors and considering how species-specific ecology and evolutionary history shape circuit organization and function.

FUTURE ISSUES

1. How do collicular circuits combine multisensory input, internal state, and motor context during natural, freely moving behavior, and how can these computations be measured in such conditions?
2. How do neuromodulatory signals shape collicular activity in real time and adjust sensorimotor transformations to current behavioral demands?
3. How do different collicular cell types interact within and across layers to support flexible, context-dependent behaviors?
4. How do developmental programs establish laminar, topographic, and regional specializations in the superior colliculus, and which aspects of this organization remain plastic in response to experience?
5. How do the parallel output pathways of the superior colliculus interact in downstream circuits of the thalamus, midbrain, and brainstem to generate appropriate behaviors across contexts and species?

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.

AUTHOR CONTRIBUTIONS

The authors contributed equally to all aspects of this work and share authorship.

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