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Review

The Sensory Basis of Planarian Behavior

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Over the past few decades, planarians have emerged as a powerful model for regeneration research. Planarians can repair and regenerate their entire nervous system—including their brain and nerve cords—a rare ability among common model organisms. The planarian nervous system supports several sensory modalities, including vision, extraocular photosensation, chemosensation, thermosensation, mechanosensation, and nociception. This diverse array of sensory modalities gives rise to a wide range of behaviors and makes planarian worms a remarkable model for the study of sensory neuroscience. Furthermore, studying the processes that mediate the efficient repair and reorganization of their complex nervous system upon injury may yield new insight into the maintenance and regeneration of sensory systems in other organisms, including humans. In this review, we discuss the existing literature on the molecular drivers of planarian sensation, as well as the behaviors resulting from their sensory systems and multisensory integration.

Key words: **ethogram; invertebrate sensory biology; neuroethology; neuro-regeneration; planarian behavior; sensory regeneration**

Introduction

Planarians are free-living flatworms from the phylum Platyhelminthes, which they share with other flatworms, such as flukes and tapeworms (Hyman, 1951). While some planarians live in marine or terrestrial environments, the most commonly studied species live in freshwater streams, where they hunt for small live prey or bottom-feed (Vila-Farré and Rink, 2018). Planarians are a widely used model system for the study of regeneration, as they can regenerate a complete body from any fragment of tissue that contains stem cells, called neoblasts (Morgan, 1898; Stevens, 1907; Pedersen, 1959; Agnes and Brøndsted, 1961). They retain this ability indefinitely, making them "immortal under the edge of a knife", which means amputations or cuts do not kill them (Dalyell, 1814). Moreover, individual animals can constantly replace damaged cells and tissues, and they age in an atypical fashion, where regeneration may trigger "global rejuvenation" of their tissues (Dai et al., 2025). As such, they may live for millions of years—although whether they can truly be considered to remain the same animal over such long timespans is a philosophical question (see Ship of Theseus; Blackburn, 2016). Importantly, however, they can regenerate their entire nervous system (Child, 1911; Brøndsted, 1955).

The planarian nervous system is complex and centralized. The central nervous system is organized into two anterior cephalic ganglia (a "brain"), two ventral nerve cords projecting ventroposteriorly from the brain, and two eyespots which sit atop the brain and form ipsi- and contralateral projections on the brain to relay light information (Fig. 1*a*; Best, 1967; Okamoto et al., 2005). There are transverse neurons that project across the ventral nerve cords, as well as peripheral sensory neurons throughout the head, body, and pharynx, which is the sensorimotor apparatus used for both feeding and excretion (Hyman, 1956; Baguñà and Ballester, 1978). The planarian nervous system does not have a fixed size or number of neurons; instead, it flexibly scales according to the size of an individual worm (Oviedo et al., 2003).

The planarian centralized nervous system supports a complex set of sensory modalities such as vision, chemosensation, and thermosensation (Hyman, 1951). However, they also exhibit some less common sensory abilities, such as extraocular photosensation (Shettigar et al., 2017). Several sensory modalities integrate to drive typical invertebrate behaviors. For example, planarians typically avoid light in favor of darkness, but this tendency is overcome in the presence of an appetitive stimulus such as liver in a light-exposed area (Inoue et al., 2015).

In the early years of planarian neuroscience, several research articles on planarian behavior stirred up controversy, especially a series of articles positing that memory transfer could occur from trained planaria (which had "learned" to avoid a stimulus) to untrained (control) planaria through cannibalization of the trained planaria (McConnell, 1966). Several papers exploring planarian memory, learning, and behavior were found to have poor controls and some unreproducible results; this came to be known as the "planarian controversy" (Deochand, et al., 2018). However, recent advances in understanding of planarian biology, as well as in behavioral studies, have encouraged researchers to return to studying planarian neuroethology. To set the scene for these studies, we compiled existing data on the behaviors and sensory systems of planaria. For each sensory modality, we will first describe the ecology and relevant behavioral repertoire, followed by the molecular and cellular drivers of planarian behavior.

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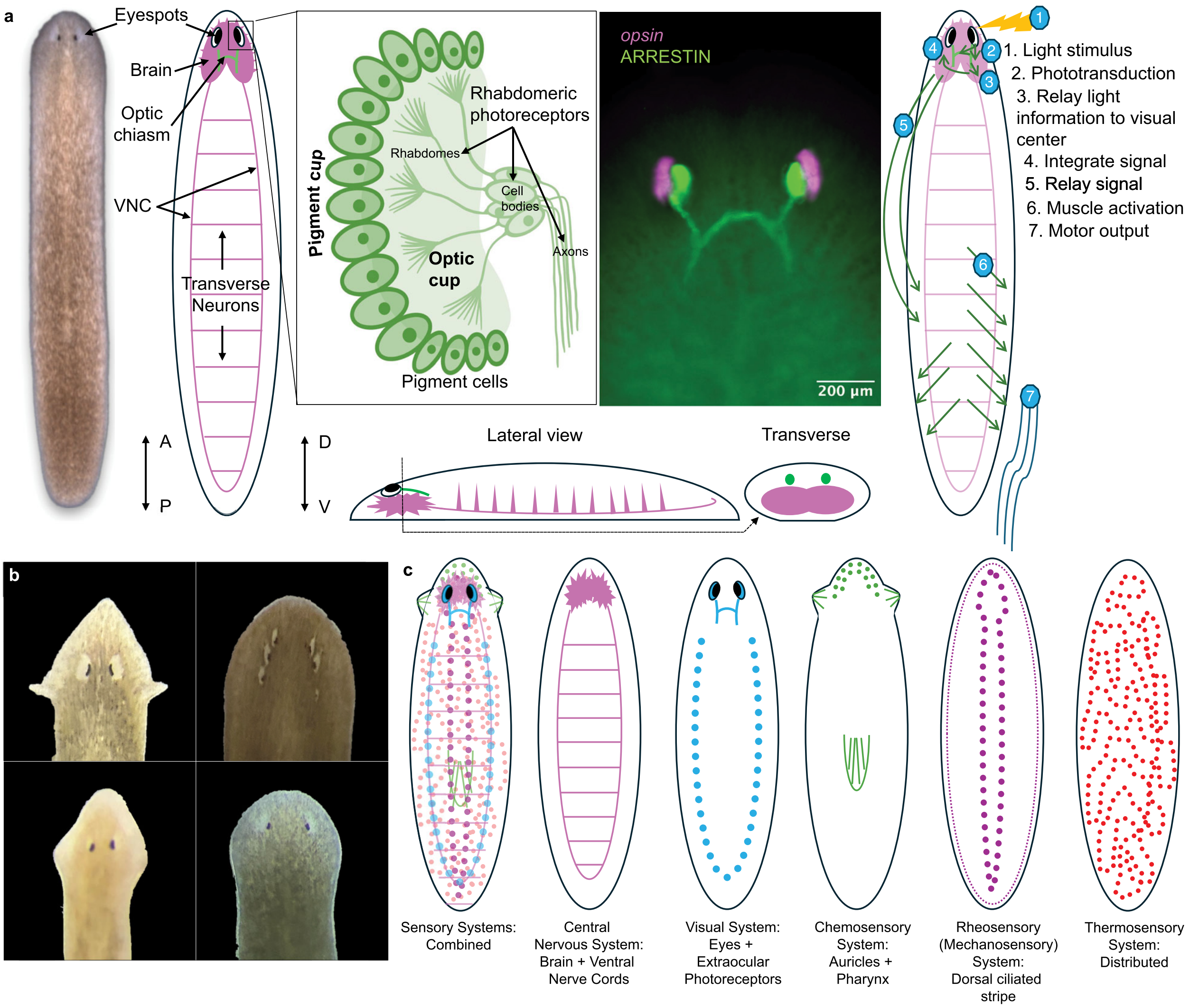


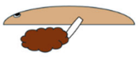
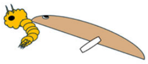
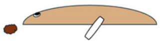
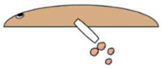
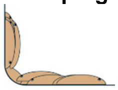
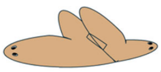
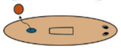
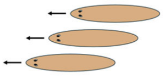
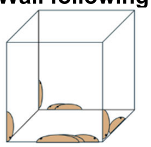
Figure 1. Major sensory systems in freshwater planarians. ***a***, The planarian nervous system in the dorsal, lateral, and transverse view. A schematic displays the structure the visual system, consisting of photoreceptor cells and pigment cup cells, which form an optic chiasm, as shown using an opsin FISH and ARRESTIN antibody stain. The final panel (right) highlights the steps of visual information relay in the planarian. ***b***, Four different planarian species (clockwise from top left) *D. dorotocephala*, *S. polychroa*, *S. mediterranea*, and *D. japonica*, highlighting their different eyespot and auricle structures. ***c***, Simplified areas of concentrated sensory organs or cells, divided by major sensory modality: visual, chemosensory, rheosensory (mechanosensory), and thermosensory.

Photosensation

Light provides important cues for shelter, foraging, and predator avoidance, with several combined evolutionary pressures leading to many aquatic animals adopting nocturnal or light-avoidant behaviors (Gaston, 2019). Planaria are typically light averse (Parker and Burnett, 1900; Lemke, 1935; Marriott, 1958; Stasko and Sullivan, 1971). Negative phototaxis—movement away from light—is consistent across planarian species (Table 1; Hyman, 1951). The reaction time between light stimulus presentation and movement away from light varies across different studies and different species, especially with different intensities of light but is usually within the range of seconds to 1 or 2 min (Fig. 1*a*; Akiyama et al., 2018). Of the wavelengths on the visible spectrum, planarians seem to be most behaviorally sensitive to shorter wavelengths (blue-greens) and least sensitive to longer wavelengths (red; Paskin et al., 2014). Typical behavioral assays for vision are based on either ON–OFF areas of light (Fig. 2*a*) or a gradient of light (as in Inoue et al., 2004; Atabay et al., 2018, Fig. 2*a*). While both assays achieve similar results, they are different in ecological relevance, as planaria typically live under rocks in shallow streams and lakes (Mirolli, 1961; Vila-Farré and Rink, 2018), likely with little exposure to drawn-out light gradients as one might encounter in deep seawater, but with more exposure to light off/on transitions (i.e., under rock/not under rock).

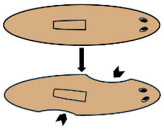
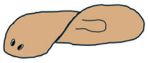
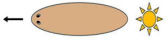
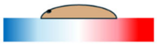
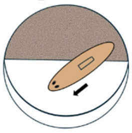
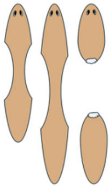
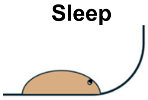
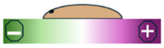
The majority of photosensitive behaviors is driven by the visual system. The planarian visual system consists of two eyespots that each contain two cell types: pigment cells and rhabdomeric photoreceptor neurons (Fig. 1*a*; Carpenter et al., 1974). The pigment cells form a pigment cup in and around which the rhabdomeric photoreceptor neurons' rhabdomes receive light signals (Fig. 1*a*; MacRae, 1964). Photoreceptor neurons form the optic cup; these neurons relay light information through axons that project ipsi- and contralaterally to the brain, forming a bridge-like structure called the optic chiasm (Fig. 1*a*; Okamoto et al., 2005). The presence of an optic chiasm suggests that planarian worms have binocular vision, with two slightly overlapping receptive fields of vision (Akiyama, et al., 2018). Current research

Table 1. Planarian ethogram

	Behavior	Description	Stimulus	Sensory Modality	Source
Eating Behavior	**Eating** 	Sensing appetitive chemical cue, pharynx protrusion, food intake	Chemo-attractant	Chemosensation, possibly vision	Sheiman et al., 2002
	Predation 	In response to prey such as mosquito larvae	Chemo-attractant, or visual stimulus	Chemosensation and/or vision	Lombardo et al., 2011; Tranchida et al., 2009
	Cannibalism 	Eating members of the same species; can occur under predation or stress context	Starvation	Chemosensation, vision	Hull, 1947
	Foraging 	Searching, pharynx protrusion, may involve head-swinging	Chemo-attractant	Chemosensation, mechanosensation, possibly vision	Sheiman et al., 2002
	Floating 	After eating, some worms may “float” without swimming or adhering to any surfaces	Eating sufficiently or overeating; higher oxygen demand during digestion	Chemosensation, rheosensation	Hyman, 1951
	Defecating (Excretion) 	After eating and digesting, worms excrete food waste products through the pharynx (pictured)	Undigested food; stress can also trigger premature excretion	--	--
Prosocial Behavior	**Clumping** 	Congregating in corners/edges over each other	Stress	Chemosensation, vision	Allee & Wilder, 1939
	Mating 	“Tail sandwich” conformation, followed by lining up gonopore openings and exchanging sperm	Reproductive; seasonal	Chemosensation, mechanosensation, possibly vision	Anthes, 2010
	Capsule-laying 	Releasing a capsule from gonopore	Reproductive; stress; periodical	--	Guo et al., 2016
Loco-motive Behavior	**Gliding** 	Locomotive gait - steady-state swimming motion	Several	Chemosensation, vision, rheosensation	Sabry et al., 2019
	Wall following 	Exhibited “wall preference” likely due to chance encounter with wall and lack of other stimuli to avoid wall.	Visual-mechanical	Thigmotaxis, mechanosensation, vision	Akiyama et al., 2015

(*Table continues.*)

Table 1. Continued

	Scrunching 	Body/muscle contraction upon noxious stimulus; may also serve as a "startle" or "escape" response	Can be mechanical, visual, chemical, heat, or noxious stimuli	Vision, mechanosensation, chemosensation, nociception	Sabry et al., 2019
	Peristalsis 	Locomotive gait similar to scrunching, like inching	Ciliary disruption	Nociception	Sabry et al., 2019; Reho et al., 2022; Rompolas et al., 2013
	Righting Reaction 	Correcting by flipping or twisting to be dorsal-side up after agitation or movement that causes their ventral side to be exposed	Distinct dorsal-ventral chemical and mechanical stimuli	Rheosensation, chemosensation	Reddien, 2022; Hyman, 1951; Pearl, 1903
Survival Behavior	**Negative phototaxis** 	Movement away from light	Light (visible and UV)	Vision, nociception	Inoue et al., 2004
	Thermotaxis 	Movement toward ideal temperature ranges (10-30°C)	Extreme temperatures (outside of planarian range)	Thermosensation	Inoue et al., 2014
	Thigmotaxis 	Movement toward smooth textures to swim on, and away from rough textures	Tactile	Rheosensation, mechanosensation	Inoue et al., 2015
	Fissioning 	Asexual reproduction	Stress; may also be a seasonal trigger depending on whether the strain is flexibly sexual-to-asexual	Chemosensation, mechanosensation, nociception	Hammoudi et al., 2018; Herath & Lobo, 2020; Malinowski et al., 2017; Sheiman et al., 2003
	Sleep 	Still, unmoving, attached to surface	Circadian triggers, likely light	Vision, mechanosensation	Omond & Lesku, 2023
	Cathodic electrotaxis 	Movement toward cathode in an electric field	Electric stimuli	Electrosensation	Sabry et al., 2022
	Gammataxis 	Movement away from gamma radiation	Radiation, extent of behavior dependent on season	--	Brown & Park, 1964

suggests that planarians can sense light intensity and direction and may not perceive images, given the lack of a lens and other structures necessary for image formation (Mannini et al., 2004; Land, 2005; Land and Nilsson, 2012). As they do have binocular vision, there are interesting opportunities to develop novel behavioral paradigms and use them to explore whether they might possess depth perception similar to humans, motion parallax similar to fruit flies, or other complex visual abilities.

In many animals, vision is mediated by dedicated photoreceptor neurons, which in invertebrates are typically rhabdomeric and in vertebrates are typically ciliary. These neurons express specific GPCRs known as opsins, that associate with a light-sensitive chromophore (Asano et al., 1998; Palczewski et al., 2000; Shettigar et al., 2017; Supplementary Table 1). The planarian worm is thought to encode 5 opsins: rhabdomeric opsin, peropsin, xenopsin, and two noncanonical rhabdomeric opsins

(Shettigar et al., 2021). Only some of these opsins are found in photoreceptor neurons in the planarian eyespots (Shettigar et al., 2021). In some organisms, two opsins can be coexpressed, such as in the photoreceptor cells of a larval mollusk, which coexpresses xenopsin and r-opsin (Arendt, 2017; Vöcking et al., 2017). Interestingly, planarian eyes express essential components of both rhabdomeric and ciliary photoreceptor signaling cascades (Lapan and Reddien, 2012); whether these cascades can both function, or even have distinct functions, in planarian photoreceptors remains to be determined.

Gene expression analysis in the planarian visual system suggests that it involves conserved neuronal proteins and receptors, such as the scaffolding protein β-arrestin and the ion channel TRPC-1, making the planarian eye a relevant system for studying photoreceptor evolution and regeneration (Lapan and Reddien, 2011, 2012). Further immunocytochemical analysis suggests that planarian photoreceptors have concentrated histamine expression, supporting the hypothesis that they use histamine for neurotransmission (Panula et al., 1995). However, electrophysiology would be required to validate whether planarian photoreceptor neurons indeed release histamine, as do many invertebrates such as *Drosophila melanogaster* and other arthropods, or another neurotransmitter such as glutamate, which is the more common excitatory neurotransmitter in vertebrates but is also the main neurotransmitter in cephalopod photoreceptors (Panula et al., 1995; Pungor and Niell, 2023). Dissection and activity analysis (through calcium imaging, for instance) of the visual center may allow for further understanding of synaptic receptors and postsynaptic excitation and inhibition. Already, negative phototaxis behavior is consistent with the electrophysiological response at the eye as measured by the ocellar potential, which is maximally sensitive at 508 nm (green light; Brown et al., 1968). Tracing the relay of visual information, starting from the photoreceptor's ocellar potential–through the visual center, down to bodily movements away from light–especially throughout the regenerative process, may help uncover the mechanisms of negative phototaxis in planaria and how it can be restored after injury.

The planarian visual system regenerates fully after head amputation, in roughly 5–7 d, with some differentiated eye cells appearing as early as 2 d after amputation (Inoue et al., 2004). Several genes drive the re-establishment of the planarian visual system; two that have been well described are *ovo* and *six1/2*, both transcription factors required for the differentiation of eye cells (Lapan and Reddien, 2012). Eye loss or injury triggers differentiation of eye progenitor cells which exist in the pre-pharyngeal region of the worm (Atabay et al., 2018). These cells subsequently migrate to an anatomical target zone for repatterning and formation of the eye (Atabay et al., 2018). After injury, eye loss, or eye transplantation, specific muscle cells function as guideposts to help axon guidance for proper repatterning of the optic chiasm (Scimone et al., 2020). Behavioral recovery, however, seems to precede full morphological recovery, such that worms exhibit negative phototaxis even before the visual system is fully reformed (Inoue et al., 2004).

Planarians also possess some form of extraocular photosensation. Extraocular cells expressing noncanonical rhabdomeric opsins drive UV-light sensitivity, including after head amputation (Shettigar et al., 2021). Headless worms "scrunch" in response to UV light and often move away from it, despite not having eyes (Shettigar et al., 2021). Scrunching, the planarian escape response, is a characteristic and well-described planarian behavior that recruits muscle for full-body contraction (Cochet-Escartin et al., 2015; Reho et al., 2024). The ion channel TRPA1 was also reported to mediate planarian extraocular photophobic behavior in response to near-UV light (Birkholz and Beane, 2017). Extraocular photosensation puts planarians in the company of brittle stars, sea urchins, and fly larvae, which also possess some form of extraocular photosensation, whether to UV or visible light (Xiang et al., 2010; Sumner-Rooney et al., 2020). It is currently unknown whether dispersed photoreceptors throughout the body use the same mechanism of transmission as the centralized visual system in the eyespots. Further, it will be interesting to find whether and how signals from the eyes and the dispersed photoreceptors are integrated to possibly modulate circadian rhythms or other nonvisual light-dependent functions and behaviors. These topics form promising areas for further investigation and may even further our understanding of other systems with some extraocular photosensation, including humans.

Chemosensation

The ability to sense chemical triggers is essential to locate food, avoid toxic compounds and possibly to drive social behaviors and avoidance of predators. Indeed, chemosensation is another sensory modality that produces robust behavioral outputs in planarians: in spite of planarian aversion to light and extreme temperatures, they will venture out into these conditions, or forage, in the presence of an appetitive food stimulus, exhibiting positive chemotaxis (Inoue et al., 2015; Table 1). Planarians also exhibit negative chemotaxis to several compounds, including frog extract (Cho et al., 2019). There are currently several different assays for chemosensory behavior. Many paradigms involve placing liver paste as an attractant on one end of a dish or in the center and placing planarians on the other end and observing the time-to-reach-stimulus (Inoue et al., 2015; Miyamoto et al., 2020; Fig. 2*b*). However, some chemosensory assays have not controlled for light (i.e., the possibility that planaria may use vision in addition to chemosensation to find food). Conducting chemosensory assays in the dark or in red light can resolve this issue. A maze assay can also control for this possibility and does not hinder chemotactic ability (Roberts-Galbraith et al., 2016). One common hurdle in these assays has been the use of biological materials that are poorly controlled and difficult to reproduce as chemosensory stimuli. These paradigms invite exploration of standardized foods (e.g., commercial fish food) or diluted chemical stimuli (e.g., defined salts) to increase the reproducibility of chemosensory assays. There is also an opportunity to explore the planarian chemosensory behavior repertoire using techniques like electrophysiology to identify individual responding neurons and the stimuli to which they respond.

Besides foraging behavior for immobile food stimuli, planarians also exhibit predatory behavior, with some documented instances of planarians preying on mosquito larvae and other small freshwater organisms such as frog embryos and ribbon worms (Pearl, 1903; Melo and Andrade, 2001; Segev et al., 2015). Planarians also cannibalize each other, in particular when they have been starved (Hay and Ball, 1979). In addition, planaria do seem to exhibit some predator-avoidance behavior in a chemosensory context, as represented by their avoidance of frog extract (Cho et al., 2019). All these aforementioned behaviors entail chemosensory ability for feeding and/or survival.

The planarian chemosensory system is primarily located in the auricles, which are two peripheral structures at either side of the head, and in the pharynx, a feeding and excretion apparatus (Hyman et al., 1924; MacRae, 1967; Agata et al., 1998). The morphology of the auricles varies across species: triangle-headed

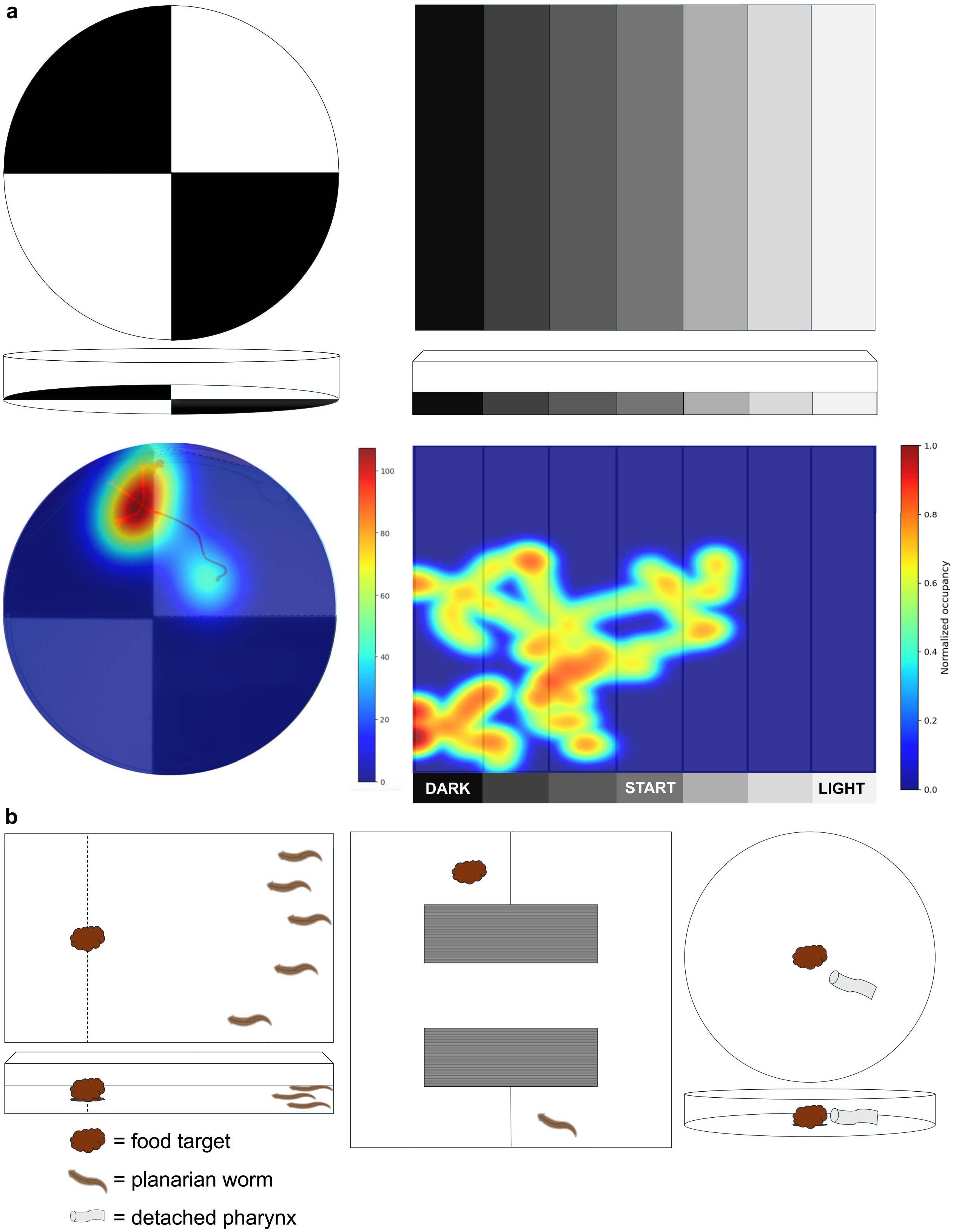


Figure 2. Common behavioral assays in freshwater planarians. ***a***, Several setups for testing vision in planaria, with corresponding sample heatmap traces of where planaria may migrate in each assay. The left panel shows a light ON/OFF binary model, with a corresponding heatmap below showing the trajectory over the course of 2 min of a single worm placed in the light ON (top right) quadrant. The right panel demonstrates a gradient light assay, wherein the corresponding heatmap below is the aggregate heatmap for 10 worms individually allowed to explore the assay for 1 min. The worms start at the center of the assay, taking several seconds to flip and discern the direction of light while in the center, and then typically migrate toward the darker side of the gradient. Heatmaps and traces generated using ezTrack (Pennington et al., 2021). ***b***, Three different setups for testing chemosensation in planaria, including chemoattractant gradient assay (left; Inoue et al., 2015), a maze-like assay (middle; Roberts-Galbraith et al., 2016), and isolated pharynx assay (right; Miyamoto et al., 2020).

species such as *Dugesia dorotocephala* have very clear protruding auricle structures, whereas in more round-headed species such as *Schmidtea mediterranea* the chemosensory neurons are embedded in similar lateral positions at the head rim (Fig. 1*b*; Okamoto et al., 2005). The auricles are rich in chemosensory neurons, and their removal abolishes food-seeking behavior (Almazan et al., 2021). The auricles are quick to regenerate after removal: 2 d after auricle removal, food-seeking behavior is re-established (Almazan et al., 2021). Based on data from *Girardia dorotocephala*, auricles express several common neuronal receptors associated with chemosensation such as dopamine, glutamate, and acetylcholine receptors, as well as ENaC-like receptors (data from Almazan et al.) There are also chemosensory neurons throughout the body of the worm, although higher concentrations are found in and around the brain, with *cintillo*$^+$ putative chemosensory neurons marking the very edges of the head (like a *cintillo*, Spanish for "headband"; Oviedo, et al., 2003).

Chemoreceptors, which are proteins involved in chemical signal transduction, have been extensively studied in fruit flies, nematodes, zebrafish, and mice, among others. Such receptors are typically identified by functional screens, including electrophysiological and behavioral assays, as well as genomic and structural analyses (Benton and Himmel, 2023). Chemosensory neurons in planaria express homologs of genes that encode chemoreceptors in other species, such as the *CNG-1* gene, which encodes a cyclic-nucleotide gated receptor in several species; in planarians, *CNG-1* may underlie chemosensory behavior based on its expression in brain branches, which are also implicated in chemosensation (Roberts-Galbraith et al., 2016; Fig. 1*c*). *Polycystic kidney disease-like (pkdl)* genes, also expressed in the brain branches and implicated in diverse cellular functions spanning cilia and ER, are also required for chemosensory behavior in planarians (Ross et al., 2024). *S. mediterranea* also expresses genes that are homologous to well-characterized *D. melanogaster* chemosensory receptors, such as the ionotropic receptor *Ir31a*, which is sensitive to 2-oxopentanoic acid in flies (Silbering et al., 2011). *Caenorhabditis elegans*, a nematode that can live in both terrestrial and aquatic environments, has distinct odor and gustatory receptors that are responsive to specific chemical compounds (Bargmann, 2006). Chemosensory behavior experiments in combination with receptor knockdowns may also be useful in identifying compounds that planarians detect in addition to the molecular mechanisms and logic of chemosensation.

One of the unanswered questions in planarian and other aquatic animal chemosensation is how olfactory and taste stimuli may be distinguished in an underwater environment; for example, how is the source of diffuse long-range stimuli determined? Do planarians compare stimulus intensity across auricles to determine the direction of a stimulus, similar to how blind moles use two nostrils to determine the source of a smell or how humans use two ears to determine the source of a sound (Alain et al., 2001; Catania, 2013; Wu et al., 2020)? Do planarians encounter and interact with chemical stimuli that require close contact or tactile interaction, similar to how octopodes use tentacles to search for prey (Sepela et al., 2025)? Do planarians have discrete chemosensory systems that distinguish taste and smell, as there are in some fish species (Valentinčič, 2004) or are they integrated into one broader chemosensory system?

The planarian pharynx is both a chemosensory and mechanosensory organ, responsible for both feeding and excretion (Miyamoto et al., 2020). The pharynx can be isolated from the planarian body and, remarkably, can execute the majority of the feeding behaviors by itself; an amputated pharynx can move toward food stimuli and away from aversive stimuli, indicating that it has both the sensory and motor components required for carrying out its feeding functions independently of the brain (Miyamoto et al., 2020). An interesting problem for the future is whether and how chemosensory information from the head region is integrated with that from the pharynx, and how these cues drive planarian feeding behavior.

Thermosensation

Planarians have a quite narrow temperature range in which they can live, and thermotactic behavior therefore is probably important for planarian survival. Planarians tend to tolerate temperatures in the range of 10–30°C, with very little mobility at temperatures below 10°C and death after a few days living in temperatures above 30°C (Hammoudi, et al., 2018). Planarians exhibit scrunching in response to sudden high temperatures and are lethargic and die at extremely high temperatures (>30°C); at very low temperatures, planarian behavior is typically dampened, and their locomotive ability seems hindered (Inoue et al., 2014). Behavioral assays for thermosensation often involve gradients of temperature established with heatblocks underneath water containers, where the planarians are given a few seconds or minutes to exhibit thermotactic behavior (Mast, 1903; Inoue et al., 2014).

Based on studies in *D. melanogaster* and *C. elegans*, thermosensation is typically mediated by transient receptor potential (TRP) channels (Tobin and Bargmann, 2004; Himmel et al., 2017). *TRPM*, a planarian homolog of the Transient Receptor Potential Melastatin family, is expressed in thermosensory neurons, which are located throughout the planarian body (Inoue et al., 2014). Thermosensation relies not only on thermosensory neurons but also requires brain signal integration, such that in the absence of proper brain regeneration after RNAi, planarians lose thermosensory ability (Inoue et al., 2014). *TRPA1*, another Transient Receptor Potential family member, modulates noxious heat sensation; this is further described in the section on nociception (Arenas et al., 2017).

Mechanosensation

Mechanosensation provides planarians with the ability to sense mechanical or tactile stimuli, such as touch and pressure. One of the most important mechanical stimuli for planarians is water flow, which may be variable in their native freshwater streams (Pearl, 1903; Allen, 1915; Ratner and van Deventer, 1965). Rheosensation is a type of mechanosensation that refers specifically to this ability to sense changes in water flow (Ross et al., 2018). Rheosensory behavior involves bodily contraction; when water is squirted over the surface of the animal, it contracts (Allen, 1915; Hyman, 1951; Ratner and van Deventer, 1965; Ross et al., 2018). Evidence also suggests that planarians exhibit positive rheotaxis to weak water currents (Pearl, 1903).

Rheosensation is typically mediated by ciliated cells. Cilia are present all over the ventral and dorsal epidermis of planarians, as well as in dedicated cells of their secretion system (protonephridia; Rink et al., 2011). A particularly densely ciliated stripe (Fig. 1*c*), located on the dorsal midline of the worm and enriched in the anterior region, is rich in sensory neurons thought to be responsible for planarian rheosensation (Stringer, 1917; Ross et al., 2018). The transcription factor *SoxB1-2* marks progenitor cells that give rise to neural and epidermal cells, including those in the dorsal ciliated stripe (Ross et al., 2018, 2024). The *SoxB1* gene plays a critical role in regulating gene expression required for the differentiation and normal function of sensory neurons (Ross et al., 2018, 2024). Behavioral assays show that RNAi knockdown of genes downstream of *SoxB1-2*, which includes *pkdl* family genes, leads to defects in rheosensation and vibration sensation (Ross et al., 2018, 2024). *SoxB1-2* knockdown however also results in decreased density of cilia in the dorsal ciliated stripe, in the auricles, and in the dorsal and ventral surfaces, as detected by staining of *acetylated tubulin*; this finding revealed that *SoxB1-2* broadly regulates cilia across planarian structures, rather than driving a neuron-specific effect (Ross et al., 2018).

Other mechanical stimuli that planaria are sensitive to include vibrations. A mechanical tapping assay where an automated lever taps the planarian dish to create vibration showed that planarians contract in response to these water vibration stimuli (Ross et al., 2018, 2024). PIEZO receptors, which are mechanically-gated ion channels, are known for driving mechanosensation in humans and many vertebrates, as well as many invertebrates including hydra and spiders (Coste et al., 2010; Johnson et al., 2021; Alzugaray et al., 2025). While the genetic drivers of other kinds of mechanosensation are still relatively unknown, planarians do possess PIEZO homologs, indicating these receptors might be relevant in driving reactions to mechanical stimuli. Finally, planarians can also recognize different surface textures and have at least some memory of such environmental parameters (Shomrat and Levin, 2013). However, the sensory basis for this remains unclear.

Nociception

Survival is contingent on the ability to recognize harmful stimuli. Nociception is defined as the detection and encoding of noxious —i.e., harmful—stimuli (Kavaliers, 1988). In planarians, we interpret some forms of locomotion as an expression of the perception of noxious stimuli (Cochet-Escartin et al., 2015). Nociceptive behavior in planaria typically involves movement away from noxious stimuli, as well as scrunching (McConnell, 1966; Cochet-Escartin et al., 2015). For instance, in response to UV and near-UV light, low pH, high temperature, and cuts, planarians scrunch (Cochet-Escartin et al., 2015; Reho et al., 2024). This results in a shortening of the animal along the anterior-posterior axis (see Fig. 1*a* for axis reference). For some planarian species, scrunch is a faster gait than typical gliding, whereas the reverse is true for others (Cochet-Escartin et al., 2015). Increased mucus secretion accompanies scrunching and may serve as an additional defense mechanism against predators, as it may have an unpleasant taste (Cochet-Escartin et al., 2015). Other nociceptive behaviors include twisting, seizure-like activity, and hyperkinesia (Reho et al., 2024).

Some nociceptive sensory systems consist of many free nerve endings specialized to detect noxious stimuli. In vertebrates, these nociceptive neurons are classified by the characteristics of their axons, either myelinated or unmyelinated; however, this level of complexity is typically not present in invertebrate models (Smith and Lewin, 2009). Still, across classes of invertebrate animals, nociceptive neurons contain various conserved ion channels such as transient receptor potential (TRP) ion channels specialized in detecting noxious stimuli, among others (Tracey et al., 2003). Invertebrate TRP channels are not uniquely associated with nociception; they are also implicated in many other kinds of signaling, including vision and thermosensation (Montell, 2003). The main families of TRP receptors involved in nociception are TRPA, TRPV, and TRPM, which are expressed throughout the planarian head and mesenchyme (Inoue et al., 2014; Arenas et al., 2017). Expression of TRPA and TRPM is more dense in the head, while TRPV is more evenly distributed throughout mesenchymal cells (Inoue et al., 2014). The scrunching reactions of planarians to TRP agonists confirmed the function of these channels in nociceptive behavior and response to noxious stimuli (Sabry et al., 2019). Further experiments demonstrated the loss of heat avoidance upon treatment with RNAi against TRPA1, which is a *S. mediterranea* homolog of the aforementioned *D. japonica* TRPA, suggesting that TRPA1 functions in the detection of excessive heat (Arenas et al., 2017; Reho et al., 2024).

Other Sensory Systems

Planarians may have the ability to detect several other environmental signals. There is indication that planarians possess some form of electrosensation (Pearl, 1903; Sabry et al., 2022). *D. melanogaster* larvae also exhibit electrosensation, navigating toward the cathode (negative pole) in an electric field, which is mediated by two *Gr66a+* sensory neurons at the lateral periphery of the head (Tadres et al., 2025). Weakly electric fish similarly can sense electric fields, although these are often self-generated and aid with navigation and prey localization (Nelson, 2011). Additionally, amphid sensory neurons mediate *C. elegans* crawling toward cathodes in an electric field (Gabel et al., 2007). While the literature on planarian electrosensation is extremely limited, there is evidence that planaria exhibit cathodic electrotaxis—that is, movement toward the cathode end of a static electric field (Sabry et al., 2022). Planarians also seem to be responsive to voltage, not current. Interestingly, this response was found to be more robust in larger animals. This phenomenon is thought to be due to interfering signals from the head, likely the brain, that override bodily response to the electric signals; in larger worms the body size is disproportionally larger compared with the head, so the larger worms would be more likely to exhibit cathodic electrotaxis (Sabry et al., 2022). Finally, there are other documented behaviors, such as negative gammataxis—movement away from gamma radiation—that have received little study but may also be relevant to planarian sensory physiology and ecology (Brown and Park, 1964). Very few studies focus on behavioral avoidance of gamma radiation; however, in birds, spatial avoidance of radiation has been documented (Zach and Mayoh, 1985). Additionally, micro- and hypergravity conditions, created respectively by a random position machine and a large centrifuge, can also impact planarian regeneration to a limited extent, suggesting that the worms may also be sensitive to or sense gravitational fields (Adell et al., 2014). A slight impact on planarian mobility has been demonstrated with high-gradient magnetic fields, and planarian fissioning was found to be higher in the presence of weak magnetic fields (Novikov et al., 2008; Lu et al., 2018; Cao et al., 2020). To the best of our knowledge, there is no research on planarian audition, although sounds causing large vibrational changes may activate rheosensory functions.

Multisensory Integration

Multisensory integration refers to the process of obtaining several sensory inputs (e.g., light, chemical stimuli) and forming a coherent perception of these in the brain (Stein and Stanford, 2008). In planarians, several behaviors arise from what may be multisensory integration (Inoue et al., 2015), possibly including social behaviors. Planarians exhibit at least some social and group behaviors. Some of the most common social behaviors in planaria are those involved in reproduction. Planarians employ two modes of reproduction: sexual and asexual. Some planarian strains or species do not have reproductive organs and thus can only reproduce asexually through a behavior known as fissioning

(Table 1; Grasso and Benazzi, 1973; Stocchino and Manconi, 2013; Nodono and Matsumoto, 2022). Other species of planarians are obligatorily sexual or can alternate between reproducing asexually or sexually, partly based on seasonal reproductive cycles (Nodono and Matsumoto, 2022). Planarian mating is naturally limited to the sexual strains and species of planarians, which are typically cross-fertilizing hermaphrodites, possessing both male and female gonads that develop postembryonically (Chong et al., 2011).

Mating may involve several sensory modalities, such as chemosensation and mechanosensation. The process begins with the screening of mate candidates, likely through a combination of chemosensory, mechanosensory, and visual cues (Anthes, 2010). It is unclear if planarians secrete any pheromones for mating, but observations of planaria in culture suggest they secrete more mucus either to induce or respond to group aggregation (Reynierse, et al., 1969); whether this mucus secretion actually contains pheromones or contributes meaningfully to group or social behaviors is unclear. Mate selection seems to occur through a sort of encounter-based screen; size-dependent mate choice is likely to occur in some planarian species (Anthes, 2010). Upon positive mate selection, one planarian may "sandwich"—or line up—against the other (Anthes, 2010). This sandwiching then leads to an aligning of the gonopores (the reproductive organ), which allows for mutual penis insertion for the transfer of sperm from one planarian to the other (Anthes, 2010).

Certain marine flatworms engage in an intriguing behavior known as penis fencing in which they try to pierce each other's skin to inject their sperm—although this has not yet been reported in freshwater planaria (Michiels and Newman, 1998). To the best of our knowledge, there are no specific behavioral assays for scoring mating rituals or later capsule-laying behaviors in planarians; this is fertile ground for scientific exploration.

Asexual worms reproduce through a process called fissioning (Curtis, 1902; Child, 1906). In this process, the planarian adheres to a surface and then mechanically stretches its body from both the anterior and posterior poles using muscular contraction, until it rips into two halves (Best et al., 1969). Many factors may impact fissioning. As it is an irregular occurrence, long-term (i.e., months long) recordings of planarians in an open space may be required to record sufficient fissioning events in order to draw conclusions about inducers or inhibitors of fissioning behavior (Malinowski et al., 2017). Some cues that seem to induce higher rates of planarian fissioning include low population density, high temperature, and low light intensity (Best et al., 1969; Sheĭman et al., 2003; Malinowski et al., 2017; Hammoudi et al., 2018; Herath and Lobo, 2020). It is possible that changes in food availability or starvation state may also play a role in planarian fissioning frequency (Nentwig and Schauble, 1974). Broadly, it appears that environmental cues, particularly stressors, may drive this behavior. However, it is unclear whether, for instance, low population density drives fissioning because of an evolutionary need for species survival or if high population density halts fissioning because of increased competition, social behavior, or other pressures to stay intact.

In addition to reproduction-related behaviors, planaria exhibit social protective behaviors upon stress or exposure to aversive stimuli such as UV radiation; in these cases, they cluster together such that many worms become protected from damage (Deochand et al., 2018). They also exhibit these behaviors in laboratory settings under homeostasis; they may cluster together at the walls or corners of their containers, known as a thigmotactic behavior (Reynierse and Scavio, 1968). Several studies suggest that planarians aggregate at homeostasis (Reynierse, 1967; Reynierse and Scavio, 1968; Reynierse and Gleason, 1975), but more recent assays for shoaling—a group clustering behavior in aquatic animals—are limited and do not support the hypothesis that planarians may be attracted to the visual or chemosensory cues of other planarians at homeostasis (i.e., without reproductive, chemical, or other stressors; Martinez et al., 2021). These social behaviors may therefore be driven by combinations of several sensory modalities, depending on the triggering stimulus or stressor.

Another kind of multisensory integration is through pairing of different sensory stimuli for learning. Early studies of memory concluded that, through classical or operant conditioning, planarians could learn to discriminate between directions in a maze assay, or when an unconditioned stimulus (shock) was paired with a conditioned stimulus (light) to establish learned behaviors (scrunching; Best and Rubenstein, 1962a,b; Griffard and Peirce, 1964; Block and McConnell, 1967; McConnell, 1967; Deochand et al., 2018), as well as demonstrating spatial localization (Qian et al., 2023). Recent studies of learning and memory have supported the hypothesis that worms can be conditioned to choose one direction, texture, or stimulus in a maze or Petri dish (Abbott and Wong, 2008; Shomrat and Levin, 2013). Whether these memories are maintained long-term is still unclear; however, one recent study claimed that memory was retained after head amputation and regeneration, suggesting memories may be stored in some form outside of the brain (Shomrat and Levin, 2013).

Conclusions and Future Directions

Regeneration in planarians is a complex and effective process, wherein even the fragments of amputated planarians can exhibit behavioral outputs similar to intact worms (Le et al., 2022; Tellakula et al., 2025). This makes the planarian worm a remarkable model for interrogating sensory neuroscience and physiology, as well as how sensory systems respond to injury and regenerate. Additionally, they can be an intriguing model to investigate how memories are retained throughout replacement of cells and neuronal structures. There are many unanswered questions about planarian neuroscience and regeneration that invite exploration. The planarian scales allometrically, meaning that the number of cells in a tissue type increases as the worm increases in size, but interestingly, the scaling is not proportional; for example, as a worm gets larger, it has a higher proportion of intestinal cells, but as it gets smaller, it has a higher proportion of neuronal cells (Oviedo et al., 2003; Emili et al., 2025). How does the nervous system flexibly scale during starvation or regeneration to achieve similar sensations and behaviors, using fewer neurons (Le et al., 2022)? How do injured and regenerating neurons find their appropriate targets, even after several consecutive rounds of injury, wound-healing responses, and regeneration? Further, understanding the complex sensory world of invertebrates is a compelling challenge that the planarian model may help solve. What are the evolutionary pressures for these animals to have developed brains or binocular vision? How do differing chemical cues (long-range and close-contact) interact with different sensory organs, like the auricles and pharynx? How do these multiple sensory systems interact to modulate behavior in the wild?

The planarian's sensory systems may provide new insight into these questions, as well as perhaps having translational implications for human diseases and disorders of the nervous system.

There are a multitude of human diseases and disorders that implicate the loss or injury of neurons and sensory abilities, including neuropathies, ataxias, and others. Lessons from planarian sensory regeneration may then be particularly helpful to inspire novel strategies for application in instances of human nervous system lesions (e.g., spinal cord injury) or degeneration (e.g., age-related visual or olfactory neuron death). Ultimately, the planarian sensory nervous system, and its accompanying behavioral repertoire, is a unique model for its complexity and extensive regenerative abilities and may prove to be a true treasure trove for uncovering the principles of functional sensory nervous system regeneration.

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