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Chemosensory Decisions in Insects Emerge Through Sequential Processing from Receptor Activation to Neural Circuits and Behavioral Action

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ABSTRACT

Chemosensory behavior is often described as though ligand detection is translated directly into attraction, avoidance, feeding, host seeking, or other actions. That shorthand obscures a sequence of biologically distinct transformations. Receptor identity and molecular architecture constrain which chemical signals can enter the nervous system; peripheral sensory neurons regulate sensitivity and can be reshaped by diet or systemic state; first-order circuits preserve some stimulus structure while transforming mixtures and channel combinations; higher-order networks integrate nonchemical cues, internal state, memory, and competing drives; and behavioral output remains subject to sensorimotor feedback. This article develops a proposed neurophysiological framework in which insect chemosensory decisions emerge from sequential but non-isolated processing stages rather than from a single receptor-to-behavior mapping. The framework separates receptor activation, transduction and gain control, primary neural representation, state-dependent integration, decision circuitry, and motor implementation while allowing feedback and cross-level modulation. Evidence from Drosophila, mosquitoes, honeybees, and locusts demonstrates both recurring organizational principles and important departures from canonical models. The framework therefore treats taxon, life stage, sex, stimulus context, and experimental setting as boundary conditions rather than nuisance variation. Its purpose is not to assert a universal insect circuit, but to provide a testable architecture for locating where chemical information is transformed, reweighted, integrated, or lost before action.

Keywords: Insect chemosensation, Olfactory coding, Gustatory circuits, Internal state, Sensorimotor transformation, Decision circuitry

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Introduction

Chemical cues regulate some of the most consequential choices made by insects, including whether to approach food, reject a substrate, orient toward a host, continue ingestion, or prioritize one behavioral program over another. Yet “chemosensory decision” is frequently used as if it described a direct mapping between stimulus detection and action. That compression is biologically misleading. Insect odorant-receptor repertoires differ across lineages and developmental contexts, and their expression and function are themselves products of evolutionary and developmental diversification [1]. Even at the receptor level, odorant receptors and ionotropic receptors differ in

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molecular organization and functional properties, making it inappropriate to treat peripheral chemical detection as one mechanistically uniform input class [2].

The problem becomes sharper when canonical organizational assumptions are transferred between taxa. In *Drosophila*, one-receptor-type-per-neuron logic has often shaped expectations about olfactory coding. In *Aedes aegypti*, however, single-nucleus transcriptomic and physiological evidence shows extensive chemoreceptor co-expression within individual olfactory sensory neurons, creating a broader and less canonical coding arrangement [3]. This is not merely a taxonomic curiosity. It demonstrates that the first stage of a receptor-to-behavior account can vary in how chemical information is partitioned before any central computation occurs.

This article therefore asks a narrower mechanistic question than a general review of insect chemosensation: where, along the path from receptor activation to overt action, is information transformed sufficiently that receptor response can no longer be treated as a proxy for decision? The proposed answer is a sequential circuit-to-behavior architecture with six analytically separable operations: peripheral receptor activation, transduction and gain control, primary neural representation, multisensory and state-dependent integration, decision circuitry, and motor or behavioral implementation. "Sequential" does not mean strictly feed-forward. Later stages can alter earlier ones through systemic or neural feedback, and parallel sensory streams can enter at different points. The framework is therefore a staged inference model, not a universal anatomical chain.

The evidence base is necessarily uneven. Fine-grained circuit causality is dominated by *Drosophila*, whereas mosquitoes provide crucial host-seeking and receptor-organization counterexamples, honeybees provide a distinct olfactory-learning architecture, and locust data help test network principles outside dipterans. Laboratory preparations also vary from purified receptors to free-moving behavior. The central claim is consequently modest: chemosensory action is better interpreted by locating the level at which information is altered than by assuming that peripheral sensitivity, neural representation, behavioral choice, and motor execution are interchangeable readouts.

Peripheral receptor activation

Peripheral receptor activation defines the chemical information that becomes available to the nervous system, but it should not be equated with either valence or behavioral choice. Structural work on the odorant receptor co-receptor Orco showed a tetrameric ion-channel architecture, establishing that receptor activation begins from a molecularly constrained channel system rather than an abstract "odor detector" [4]. Structural analysis of a tuning odorant receptor subsequently identified features underlying ligand recognition and receptor activation, linking odor identity to defined molecular interactions [5]. These studies justify placing receptor architecture at the beginning of the framework, but they do not justify inferring attraction or avoidance from structure alone.

Functional perturbation further shows why receptor necessity must be stated narrowly. CRISPR mutagenesis of *orco* in *Anopheles coluzzii* impaired multiple olfactory functions, confirming the importance of the Orco-dependent pathway for tested odor responses [6]. The result does not imply elimination of all chemosensation, because ionotropic and gustatory pathways remain mechanistically distinct. The correct inference is therefore pathway dependence under specified stimuli, not global sensory deprivation.

Taste provides an even clearer example of why receptor activation and behavioral meaning must be separated. In adult *Drosophila*, OtopLa contributes to attraction toward low concentrations of acid, whereas stronger acidity can still evoke aversion through other channels [7]. Thus, nominally similar chemical stimuli can recruit opposing peripheral pathways depending on concentration and receptor context. Lactic acid provides an additional boundary case: it can recruit sweet-associated gustatory circuitry and promote ingestion rather than simply joining a generic aversive "acid" category [8]. These findings argue against a monotonic receptor-to-valence model.

Within the proposed architecture, receptor activation is therefore best treated as a constrained entry state defined by receptor family, ligand chemistry, receptor combination, sensory organ, and taxon. What enters the nervous system is already structured, but it is not yet a decision. The distinction is particularly important when comparing insects with different receptor-expression rules or when inferring ecological behavior from receptor assays conducted in heterologous systems.

Signal transduction

Once a receptor is activated, the magnitude and persistence of the peripheral neural signal can be modified before central circuits receive it. This second stage matters because a given ligand-receptor interaction need not produce a fixed sensory-neuron output. In *Drosophila* sweet neurons, IR76b can limit sensitivity: reducing its function

increases responsiveness, whereas overexpression lowers sensitivity in the tested context [9]. The finding demonstrates active gain regulation within peripheral sensory neurons and cautions against treating response amplitude as a direct measure of environmental stimulus value.

Peripheral gain is also plastic over longer time scales. Chronic exposure to a high-sugar diet reduces sweet-neuron responsiveness through an O-GlcNAc-transferase-dependent mechanism and is associated with altered feeding behavior [10]. Importantly, this is evidence for diet-induced sensory plasticity, not for adaptive improvement. The laboratory manipulation shows that recent nutritional history can reshape the signal delivered centrally; it does not establish that such remodeling increases fitness or occurs identically across insect taxa.

State-dependent modulation can also arise from signals outside the sensory organ. A gut-to-taste-neuron axis involving Hedgehog signaling links dietary sugar exposure to reduced sweet sensitivity in *Drosophila*, with effects extending to selected olfactory responses [11]. This finding complicates a purely top-down model in which internal state acts only after central sensory representations have formed. Systemic physiological signals can instead alter the effective gain of chemosensory input before information reaches higher-order decision circuitry. The proposed framework therefore separates receptor activation from transduction-level weighting. This separation is mechanistically useful because two insects exposed to the same chemical environment could differ at the peripheral output stage despite similar receptor repertoires. Such differences may reflect acute channel properties, recent diet, endocrine state, developmental history, or other unmeasured conditions. Claims about "increased attraction" cannot therefore be inferred from altered receptor or sensory-neuron responsiveness without demonstrating how later circuit stages interpret that change.

Primary neural representation

Primary neural representation begins when peripheral activity is reorganized into population-level patterns that central circuits can use. In the gustatory system, this transformation can already be combinatorial. Functional dissection of adult *Drosophila* pharyngeal neurons showed that different aversive tastants recruit overlapping but distinct combinations of sensory channels that contribute to feeding avoidance [12]. Thus, even before a putative decision stage, stimulus identity and behavioral relevance may be represented across neuronal combinations rather than by a single labeled line.

Olfactory projection neurons similarly do more than copy receptor-neuron responses. Whole-cell recordings across numerous *Drosophila* glomerular channels found that some aspects of peripheral tuning are preserved while others are transformed in a glomerulus-dependent manner [13]. Local interactions can further alter this representation. For odor mixtures containing components of opposing valence, selective GABAergic inter-glomerular inhibition changes antennal-lobe activity and can bias behavioral responses [14]. These results show that mixture representation is not necessarily a linear sum of receptor inputs.

Higher-order convergence adds another transformation. Mapping of projections from antennal-lobe glomeruli onto lateral-horn neurons revealed structured, non-random combinations of olfactory input [15]. Such organization can constrain which sensory features become jointly available to downstream networks. Connectivity, however, must not be confused with decision causality: anatomical convergence identifies a candidate integration architecture, not the behavioral function of every connection.

Comparative evidence reinforces the need to avoid treating the *Drosophila* sequence as a universal template. Honeybee olfactory coding distributes chemical information across antennal-lobe and mushroom-body processing in ways shaped by learning and task context [16]. In female *Aedes aegypti*, human and nonhuman host odors evoke distinguishable glomerular combinations, including channels particularly responsive to chemical features enriched in human odor [17]. At a more abstract network level, work comparing *Drosophila* and *Schistocerca americana* shows that convergence and nonlinear network properties can generate stereotyped downstream responses despite variable connectivity, although the effect depends on sparsity and other network parameters [18].

Primary neural representation should therefore be understood as a family of transformations rather than a single coding stage. Peripheral information may be preserved, suppressed, combined, decorrelated, or selectively converged. The analytical question is not whether an odor or tastant "has a representation," but which stimulus dimensions survive the first central transformations and which new combinations are constructed before state and choice mechanisms act on them.

Multisensory and state-dependent integration

Chemical information rarely arrives in isolation. Host-seeking female *Aedes aegypti* integrate olfactory and visual cues, and the influence of one modality on behavior depends on the presence and timing of the other rather than following a fixed additive rule [19]. This establishes an important boundary for chemosensory inference: even a well-characterized odor representation may change behavioral relevance when a nonchemical cue alters search, orientation, or approach.

Internal state introduces another form of conditional weighting. In *Drosophila*, hunger and thirst do not merely raise a generic motivational gain. Leucokinin-dependent modulation helps determine whether sugar-associated or water-associated memories are expressed, with different dopaminergic circuits recruited according to deprivation state [20]. A separate circuit links internal glucose sensing to fructose-responsive neurons through tachykinin signaling, making fructose drive contingent on satiety [21]. These mechanisms support a model in which state selects or suppresses particular sensory-action mappings rather than uniformly amplifying all chemosensory signals.

Brain-wide imaging further shows that different internal states can operate at different spatial scales. Metabolic and reproductive state alter food choice through partly distinct neural distributions, with some effects broadly distributed and others more localized within the sensorimotor pathway [22]. “Internal state” should therefore not be represented as a single scalar input. It is better treated as a set of physiologically specific modulators that can enter the chemosensory sequence at different levels.

For the present framework, multisensory and state-dependent integration is the first point at which chemical evidence is explicitly reweighted against information that may have different origins, time courses, and biological meanings. The same odor or tastant can consequently support different actions without any change in the external stimulus itself. That variation need not imply noise; it may reflect a shift in which information is permitted to dominate the next stage of processing. At the same time, evidence from mosquitoes and flies should not be fused into one anatomical mechanism. The transferable principle is conditional reweighting, whereas the neurons and circuit loci implementing it remain species-, sex-, task-, and state-dependent.

The distinction is easier to recover when evidence is organized by the kind of reweighting being performed rather than by sensory modality alone. **Table 1** therefore separates major integration states according to what changes, what remains observable, and which inference becomes unsafe.

Table 1. When chemical evidence changes meaning: integration states that separate sensory availability from behavioral relevance

Where weighting occurs			Behavioral consequence	How the interpretation is tested		
Integration gate	**Detected evidence**	**Organismal setting**	**Change in behavioral meaning**	**Perturbation or comparison**	**Transfer boundary**	**Evidential standing**
Cross-modal weighting						
Cross-modal gating of chemical relevance	Behavior or neural responses differ between odor-only and odor-plus-visual conditions	Host-seeking adult female mosquitoes	Chemical information can gain or lose behavioral influence depending on concurrent nonchemical cues	Manipulate cue order, timing, and reliability rather than testing odor in isolation	Laboratory cue timing, stimulus geometry, and sex-specific host-seeking state constrain transfer	Evidence-supported principle
Internal-state access						
Deprivation-specific memory access	Different deprivation states recruit distinct modulatory pathways and change which learned resource cue is expressed	Adult Drosophila under hunger or thirst	Internal state can select among stored chemosensory associations instead of scaling all of them equally	Compare the same learned cue across matched deprivation states and circuit perturbations	Learned-memory paradigm; state effects need not generalize to innate responses	Evidence-supported principle
Satiety-dependent nutrient drive	Internal glucose-sensitive circuitry alters fructose-responsive sensory drive	Adult Drosophila evaluating fructose	Metabolic state can gate a nutrient-specific chemosensory pathway before action selection	Test whether analogous state gates exist for other nutrients without assuming shared circuitry	Nutrient specificity and laboratory feeding context limit generalization	Evidence-supported principle

Distributed state modulation	Brain-wide activity changes occur at different anatomical scales for different states	Adult Drosophila food choice under metabolic and reproductive conditions	"State" should be decomposed into physiologically distinct modulators acting at different processing levels	Map where each state enters the sensorimotor sequence rather than assigning one central state node	Functional imaging defines correlated and perturbable loci but not a universal insect state architecture	Evidence-supported principle
Proposed reweighting layer						
Proposed conditional-reweighting layer	Same external chemical can produce different downstream relevance when modality, state, memory, or physiological condition differs	Cross-taxon synthesis derived from the preceding evidence	Receptor activation should be separated from the later weighting that determines whether a signal influences choice	Test identical chemical inputs while varying one contextual dimension at a time and measuring both neural and behavioral outputs	Exact neural implementation is expected to vary across species, sex, life stage, and task	Proposed synthesis

Decision circuits

A chemosensory decision becomes analytically distinct from sensory representation when neural activity reflects selection among incompatible actions rather than merely stimulus identity. In adult *Drosophila* confronted with appetitive and aversive food information, a fan-shaped-body neuronal ensemble changes activity with hunger, prior experience, and the option ultimately rejected, supporting a role for higher-order circuitry in context-dependent choice [23]. The finding does not establish a universal decision center. It instead demonstrates that a circuit can represent the relative behavioral relevance of competing sensory evidence after earlier transformations have occurred.

Anatomical connectivity can narrow candidate mechanisms but cannot substitute for this functional criterion. The synaptic-resolution adult *Drosophila* brain volume provides a powerful substrate for tracing possible information routes [24]. A synaptic connection, however, does not by itself establish sign, necessity, sufficiency, state dependence, or behavioral consequence. Decision-circuit claims therefore require stronger evidence than anatomical adjacency alone.

Competition can also occur between whole behavioral programs. In male *Drosophila*, feeding and courtship are oppositely reweighted by starvation, food quality, sexual state, and tyraminergic modulation [25]. This illustrates a decision architecture in which chemosensory evidence is evaluated in relation to competing drives rather than converted independently into separate motor commands. Its sex and assay specificity are important: the result supports a mechanism of action prioritization in the tested male system, not a universal insect rule.

The proposed framework consequently defines a decision circuit operationally as a neural configuration in which alternative action tendencies become conditionally prioritized after sensory evidence has already been represented and contextualized. This definition deliberately excludes receptor responses, anatomical convergence, and motor activity when those measurements alone cannot distinguish selection from transmission. The framework also allows discordance: strong peripheral or central sensory evidence may coexist with weak choice because internal state favors another action, competing programs suppress execution, or the relevant circuit has not been functionally engaged.

These discordances are scientifically useful rather than inconvenient. They identify where an apparently simple receptor-to-behavior explanation fails and where additional levels must be tested. **Figure 1** therefore organizes decision evidence around concordant and discordant states while keeping anatomy, state-dependent weighting, competing programs, and behavioral commitment analytically separate.

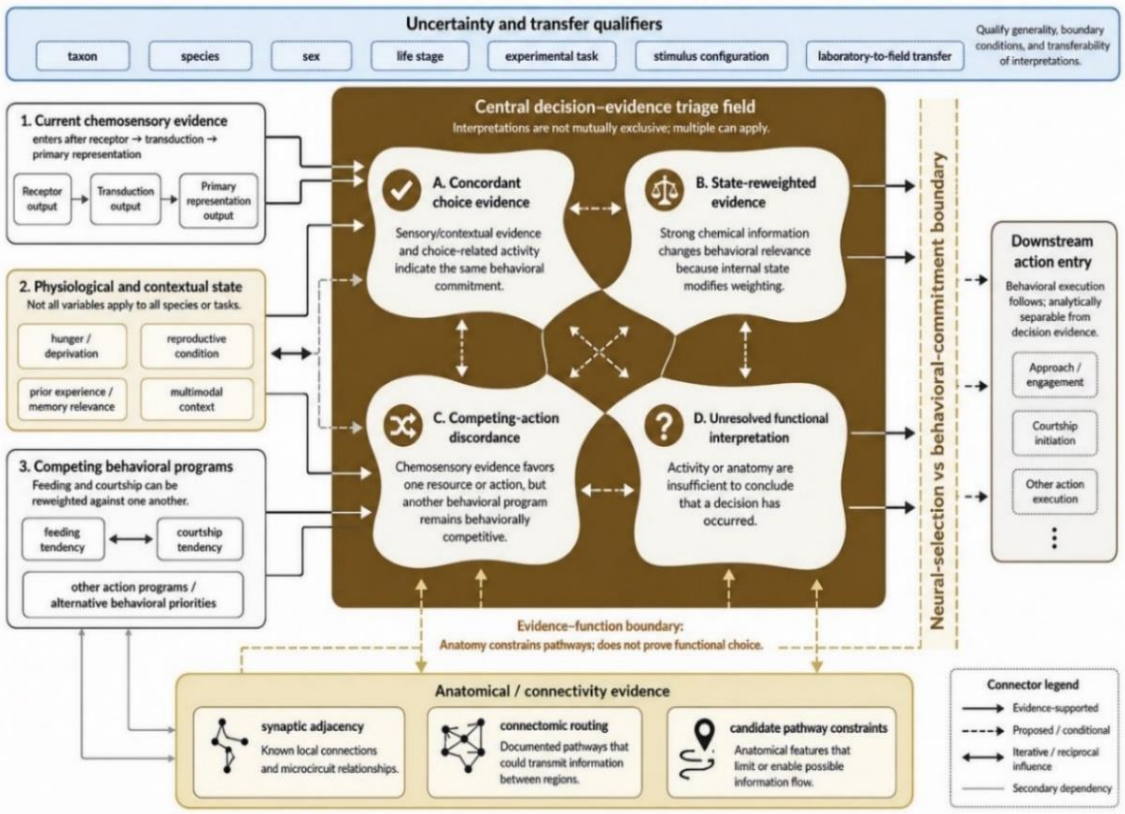


Figure 1. Decision-evidence discordance identifies where chemosensory information ceases to predict action directly

Motor and behavioral output

Choice is not the final transformation. Once an action begins, sensory and motor systems continue to interact. Larval *Drosophila* feeding circuitry contains parallel mono- and polysynaptic routes from sensory inputs toward motor output, indicating that execution need not depend on one serial path [26]. Because these data are developmentally specific, they support the existence of parallel sensorimotor architectures without establishing that adult insects use the same wiring.

Ongoing ingestion can itself generate new sensory information. In adult *Drosophila*, pharyngeal mechanosensory and gustatory signals converge on circuitry that regulates feeding, and properties such as food viscosity alter the sensory conditions encountered during a meal [27]. Motor output is therefore not merely an endpoint. It changes the animal–stimulus interaction and can feed back into continuing acceptance, rejection, or meal termination.

Navigation makes this recursive structure especially clear. Odor and wind information converge within circuitry involved in oriented movement, providing a mechanism by which chemical detection becomes directionally organized behavior [28]. The broad multimodal conclusion is useful, although later qualification of exact cellular identity makes overly precise assignment inappropriate. In a complementary paradigm, bilateral temporal correlations in odor arrival provide motion information that improves navigation of complex plumes beyond what airflow alone supplies [29]. Such effects are demonstrated under controlled or virtualized conditions and should not be equated automatically with cue weighting in every natural plume.

These cases produce several apparently conflicting observations—strong sensory activity without action, action altered by feedback after initiation, or similar chemical input producing different trajectories. **Table 2** reconciles those patterns by locating the level at which receptor-to-action correspondence breaks down.

Table 2. Reconciling mismatches between chemosensory evidence and observed motor action

Parallel routing			
Parallel sensory-to-motor routing			
Route topology	Drosophila larval feeding	**Observed basis**	Multiple pathways of different synaptic depth connect sensory input with feeding output

Why action and sensory evidence diverge	Similar actions need not imply one serial decision route			
Constraint	Larval wiring cannot be assumed for adults	**Intervention**	Compare latency and perturbation sensitivity across candidate parallel routes	*Evidence-supported*
Action-generated feedback				
Action-generated sensory feedback				
Route topology	Adult Drosophila ingestion	**Observed basis**	Pharyngeal mechanical and taste signals vary during ongoing feeding	
Why action and sensory evidence diverge	Behavioral output can modify the evidence used to continue or stop the same action			
Constraint	Food mechanics and laboratory feeding context constrain transfer	**Intervention**	Measure neural state before and during execution rather than only before movement	*Evidence-supported*
Spatial implementation				
Multimodal spatial implementation				
Route topology	Adult Drosophila odor-guided navigation	**Observed basis**	Odor-related and wind-direction information jointly influence orientation	
Why action and sensory evidence diverge	Chemical evidence acquires motor meaning through spatial-context signals			
Constraint	Exact cellular assignment and laboratory wind conditions require caution	**Intervention**	Perturb odor and directional streams separately and jointly	*Evidence-supported*
Plume-motion guidance				
Route topology	Walking adult Drosophila	**Observed basis**	Bilateral temporal odor correlations improve navigation in complex-plume paradigms	
Why action and sensory evidence diverge	Temporal structure of chemical encounters can guide successive motor corrections			
Constraint	Virtual or controlled plume statistics may differ from natural environments	**Intervention**	Test whether the same temporal cue remains informative under field-realistic turbulence	*Evidence-supported*
Output-discordance rule				
Proposed output-discordance rule				
Route topology	Cross-level synthesis	**Observed basis**	Sensory strength, choice state, and executed action need not covary	
Why action and sensory evidence diverge	A mismatch should trigger localization of the transformation rather than be labeled sensory noise			
Constraint	Requires measurements spanning at least two processing levels	**Intervention**	Pair behavioral readouts with upstream neural measurements and ongoing feedback	*Proposed synthesis*

Sequential circuit-to-behavior architecture

The evidence supports a sequence of transformations, but not one invariant anatomical pathway. Receptor organization can differ even among dipterans [3], and the first central relay can selectively reformat peripheral activity rather than simply transmit it [13]. The proposed architecture therefore treats each stage as an inference boundary: evidence obtained at one level licenses conclusions about that level, but behavioral meaning must be demonstrated rather than propagated automatically downstream.

Internal state further prevents a purely feed-forward interpretation. Different physiological states can influence different portions of the sensorimotor system [22]. Choice-related circuitry can then represent context-dependent alternatives after that weighting has occurred [23]. The architecture is therefore sequential in analytical order while remaining recurrent in biological operation.

Three rules follow. First, preserve level identity: receptor activation, sensory-neuron gain, population representation, contextual weighting, choice, and execution are not interchangeable measurements. Second, localize discordance: when neural and behavioral readouts disagree, test intervening transformations before invoking noise. Third, preserve evidence class. Multisensory behavior demonstrates conditional interaction [19], whereas connectomic anatomy identifies candidate routes [24]; neither should be made to carry the other's inferential burden. Navigation evidence similarly supports odor–direction integration [28], but not universal field transfer.

This localization strategy also clarifies what constitutes meaningful disagreement among experiments. A receptor manipulation that changes neural sensitivity but leaves behavior intact may indicate redundancy, downstream compensation, or a context in which that channel is not behaviorally limiting. Conversely, behavioral switching without a detectable peripheral change directs attention toward central integration, competing drives, or execution. The framework does not prescribe which explanation is correct; it identifies the next level at which competing explanations should be discriminated. This makes discordance a diagnostic feature of experimental design rather than evidence that one measurement must be wrong.

Experimental predictions

The framework generates testable predictions rather than validated performance claims. First, reducing an early sensory signal should not always produce a proportional behavioral change when parallel receptor systems or state-dependent modulation remain available. Orco disruption provides a tractable early-stage perturbation [6], whereas peripheral Hedgehog signaling shows that physiological context can independently alter sensory gain [11]. Brain-wide state effects predict additional downstream compensation or reweighting [22].

Second, holding the chemical stimulus constant while changing context should change action probability when integration or competition occurs after receptor activation. Visual context alters odor-guided mosquito behavior [19]. Choice under sensory conflict varies with internal conditions [23], and competing feeding and courtship programs are reweighted by physiological state [25]. Experiments that factorially vary stimulus, state, and alternative action opportunity should therefore distinguish receptor failure from decision-level reassignment.

A third prediction concerns temporal order. If decision formation and action remain coupled through feedback, then neural signals measured before movement should differ in explanatory value from signals measured after contact, ingestion, or plume interception. Feeding feedback provides a concrete precedent for such updating [27]. Navigation likewise shows that successive odor encounters can supply information unavailable from a single instantaneous concentration measurement [29]. Time-resolved experiments should therefore distinguish pre-action evidence accumulation, commitment-related activity, and feedback generated by the action itself.

Finally, stronger validation should connect anatomy, physiology, perturbation, and behavior without assuming equivalence among them. Connectomic routes can define candidates [24]; functional navigation experiments can test how directional information enters those routes [28]; and plume-motion paradigms can test whether temporal odor structure changes action [29]. Comparative validation should also ask whether homologous-looking stages perform the same computational role. Similar behavioral outputs across species may arise from different receptor organizations or circuit implementations. Generalization should therefore be demonstrated at the level of transformation and function, not inferred from superficial anatomical or behavioral resemblance.

Conclusion

Chemosensory decisions in insects are best understood as emergent outcomes of successive, interacting transformations rather than direct consequences of receptor activation. Molecular receptor properties determine what can be detected, peripheral physiology regulates effective gain, early central circuits restructure sensory patterns, multisensory and internal-state information alters relevance, decision circuits prioritize alternatives, and motor output creates further sensory consequences.

The proposed sequential architecture is therefore an inferential discipline as much as a circuit model. It specifies where evidence should stop: receptor activity is not automatically valence, neural representation is not automatically choice, connectivity is not automatically function, and choice-related activity is not automatically executed behavior. Its strongest current mechanistic support comes from a limited set of experimentally accessible insects, especially *Drosophila*, with mosquitoes, honeybees, and locusts providing essential comparative boundaries. Progress will depend on experiments that measure more than one processing level in the same animal,

manipulate state and competing actions explicitly, and test whether laboratory-defined transformations remain predictive under natural sensory complexity.

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