Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2024, Volume 4, Issue 1, Page No: 76-85
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Available online at: www.esvpub.com/

Sensory Competition, Internal State, Learning, and Action Selection Together Shape the Architecture of Attention in Insects

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ABSTRACT

Insects routinely encounter more sensory information than can be translated into simultaneous action. Yet studies of selective behavior are often partitioned into separate literatures on multisensory integration, stimulus salience, physiological state, learning, neuromodulation, and motor control. This fragmentation makes “attention” difficult to define mechanistically and encourages either overly narrow circuit interpretations or broad cognitive labels that exceed the evidence. This article develops a proposed behavioral-neuroscience architecture in which attention is treated as dynamic allocation of processing priority rather than as a single conserved center or unitary faculty. The framework distinguishes competition among external cues from modulation by physiological state and experience, separates sensory filtering from learned valuation, and places action selection within the architecture rather than treating movement as a passive endpoint. Evidence from mosquitoes, flies, honey bees, and bumblebees shows that cue reliability, hunger, reproductive state, threat, sleep, associative history, memory comparison, and neuromodulatory signals can each alter which information influences behavior. These effects occur at different neural and behavioral levels and cannot be collapsed into one mechanism. The proposed architecture therefore emphasizes conditional weighting, recurrent sensorimotor feedback, and explicit taxonomic and methodological boundaries. It generates testable predictions for experiments that manipulate cue reliability, internal state, experience, and action opportunity factorially while measuring both sensory processing and behavior.

Keywords: Sexual satisfaction, Pregnant mothers, Healthy mothers, Candidate vaginitis

Received: 08 May 2024
Revised: 11 June 2024
Accepted: 13 June 2024

How to Cite This Article: Ramirez C, Torres E, Ortega P, Mendes S. Sensory Competition, Internal State, Learning, and Action Selection Together Shape the Architecture of Attention in Insects. Entomol Appl Sci Lett. 2024;4(1):76-85.
https://doi.org/10.51847/Qq5uCr0wMc

Introduction

An insect moving through a natural environment rarely receives a single, isolated cue. Odor plumes fluctuate, visual objects compete for retinal representation, mechanosensory events can signal immediate danger, and learned or physiological priorities can change within minutes or across a reproductive cycle. Mosquito neurobiology illustrates this problem particularly clearly because host seeking depends on combinations of olfactory, visual, thermal, and state-dependent information rather than on one invariant stimulus–response channel [1]. Bumblebee foraging likewise shows that floral recognition can recruit several modalities and that learned cross-modal relations can affect recognition and choice [2]. These examples make an operational definition of

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attention necessary: here, attention refers to the selective allocation of processing priority that changes which available information most strongly influences current behavior. This definition does not require consciousness, a mammalian-style executive controller, or a single anatomical locus.

A second difficulty is architectural. Insect studies often identify selective processes at different levels and then describe them with the same vocabulary. The central complex provides one important example because it lies between sensory representations, navigation variables, and premotor control in several insects [3]. In Drosophila, a dense connectome of the central complex reveals recurrent, convergent, and context-sensitive network motifs that are structurally compatible with flexible action selection, although connectivity alone does not establish the function of every motif [4]. Thus, the problem is not simply to locate "attention" in one brain region. It is to determine how sensory competition, state-dependent valuation, experience, neuromodulatory gating, and action requirements are coordinated across levels.

This article proposes that insect attention is best treated as a distributed allocation architecture. The proposal does not assert that all insects share homologous circuitry or that every form of sensory filtering is attentional. Instead, it organizes established findings into a sequence of questions: which inputs compete, what makes one input effectively salient, how physiological state changes that weighting, how experience modifies or interferes with it, how modulatory systems gate candidate responses, and how selected information is converted into action. The framework is therefore intended to separate evidence-supported mechanisms from a higher-order synthesis that remains to be validated across taxa, life stages, ecological contexts, and experimental paradigms.

Competing sensory inputs

Competition begins before a discrete behavioral choice is visible. Multiple cues may be redundant, complementary, noisy, or mutually misleading, and their joint effect depends on the reliability of the individual components. In bumblebees trained with degraded cues, multimodal combinations improved response accuracy when component information was noisy, showing that integration can compensate for uncertain evidence rather than simply add more signal [5]. Honey bees provide a related boundary condition: multimodal gain followed the principle of inverse effectiveness, with larger benefits when the unimodal components were relatively weak [6]. Multimodal processing should therefore not be represented as a fixed enhancement term. Its contribution varies with signal quality and with the baseline effectiveness of the channels being combined.

Cross-modal interaction can also occur before overt selection. In female Aedes aegypti, exposure to carbon dioxide changed visual responsiveness and steering toward visual features during host-seeking behavior, demonstrating that an olfactory/contextual cue can alter the behavioral influence of a visual channel [7]. This result is stronger than a claim that mosquitoes merely "use smell and vision together," but narrower than evidence for a general attentional mechanism: it is a host-seeking-specific interaction observed under controlled conditions.

Competition also depends on how complex inputs are represented. Human and nonhuman host odors produce distinguishable combinations of activity in the Aedes antennal lobe, and human-associated odor features can be compressed into selective neural representations that contribute to host discrimination [8]. At the same time, antennal-lobe recordings show combinatorial population coding across odor identity and concentration rather than a simple one-odor/one-neuron scheme [9]. These findings imply that competition among biologically relevant inputs is already constrained by distributed sensory coding. They do not, however, show that every distributed code is an attentional representation. The proposed architecture therefore treats early sensory coding as the substrate over which later weighting operates, not as synonymous with attention itself.

Salience and stimulus selection

Salience is often treated as if it were an intrinsic physical property of a stimulus, but insect behavior shows that effective salience can be altered by learning and task context. In bumblebees, reward history changed the distribution of visual inspection time during search, providing a behavioral proxy for learned reallocation of attention toward previously valuable floral regions [10]. Because reward quality and visual properties cannot be completely separated in every condition, the result supports experience-dependent search allocation rather than a claim that a single neural salience variable has been identified.

At the neural level, selective processing can be associated with distinct temporal and pathway-specific signatures. In Drosophila, central-brain oscillatory activity became phase locked to attended visual features during competing visual tasks, linking selected features with measurable population dynamics [11]. This relationship is a neural correlate, not proof that the oscillation itself is a universal cause of selection. Complementary evidence comes

from the visual system: T3 columnar neurons contribute specifically to saccadic bar tracking while other visuomotor functions can remain comparatively spared, indicating that feature processing can be routed toward action-specific outputs rather than through one undifferentiated visual-selection channel [12].

Selection also changes with the statistics and temporal history of stimulation. Early visual neurons can alter temporal filtering as stimulus conditions and behavioral state change, showing that sensory transformations themselves are flexible [13]. Olfactory habituation likewise recruits temporally distinct circuit mechanisms as repeated stimulation proceeds [14]. Habituation reduces responsiveness to repeated input, but it should not be equated with attention: repeated-stimulus adaptation can occur without competition among alternatives. Together, these studies support a more precise distinction. Physical intensity, learned value, sensory adaptation, and pathway relevance can all influence whether a stimulus dominates behavior, but they do so through partially separable processes.

Within the proposed architecture, effective salience is therefore not a single stimulus attribute. It is the current consequence of stimulus evidence interacting with the state of the sensory pathway and the animal's task history. This formulation is proposed rather than empirically established as a unified mechanism, and it predicts that the same nominal stimulus can change behavioral priority without changing its physical properties.

Internal physiological state

Internal state can alter behavioral priority at several biological levels. In Aedes aegypti, neuropeptide F and RYamide vary across the gonotrophic cycle and exert reciprocal effects on host attraction, linking feeding and reproductive physiology to the probability that host cues will control behavior [15]. A related study showed that NPY-like receptor signaling contributes to the post-blood-meal suppression of host seeking and that pharmacological receptor agonism can reduce host-directed behavior [16]. These findings demonstrate state-dependent gating of a major behavioral goal, but they do not establish a universal insect "attention hormone," and pharmacological suppression should not be treated as identical to the natural endogenous sequence.

State can also alter the meaning of a cue rather than simply its gain. In Drosophila, a transient threat state produced by mechanical disturbance caused an otherwise neutral visual object to become aversive through tachykinergic neural activity [17]. In larvae, food deprivation can reconfigure early olfactory processing so that the behavioral response to particular odors reverses between fed and hungry states [18]. The life-stage distinction is important: larval sensory circuits and adult behavioral demands differ substantially, so the larval mechanism should not be generalized to adult insects. What these studies jointly show is that state-dependent weighting can be implemented at different processing stages.

Dopaminergic population activity provides another level of conditionality. Mushroom-body dopaminergic neurons encode combinations of valence and current physiological or behavioral state rather than a single invariant value signal [19]. Yet state effects are not interchangeable. Sleep deprivation increases visual distractibility in Drosophila, whereas several other tested stress manipulations did not reproduce the same selective-attention phenotype [20]. This negative comparison is important because it argues against treating "internal state" as a generic arousal variable. The proposed architecture therefore requires state identity to be specified: hunger, reproductive state, threat, sleep pressure, and locomotor state may alter selection through different pathways and at different timescales.

Learning and prior experience

Experience changes selection not only by strengthening remembered value but also by altering how memories are compared and retrieved. In Drosophila, the specificity of learned odor memory depends on which alternatives are available at test, showing that a stored association can be expressed differently when the comparison set changes [21]. This supports a distinction between memory content and memory-guided selection: behavioral expression at retrieval is conditional on the options currently competing for control.

Learning can also assign new value to sensory inputs. Closed-loop optogenetic experiments show that taste responses can acquire appetitive or aversive value through defined reinforcement pathways [22]. Higher-order conditioning further demonstrates that interactions among dopaminergic circuits can allow previously learned predictors to support new associations [23]. These results establish that experience can reorganize future valuation, but they should not be generalized to natural learning without qualification because the conditioning paradigms deliberately isolate selected reinforcement pathways.

Prior experience can also impair subsequent performance. Genetic dissection of consecutive learning tasks in Drosophila separates proactive from retroactive interference, demonstrating that an earlier or later memory can reduce expression of another under particular timing and task conditions [24]. Bumblebees reveal a different limitation: after learning reward relations in separate contexts, they can rely on ordinal ranking when making novel comparisons, implying that relative memory structure may guide choice even when absolute reward information is not available or is not retrieved in the same form [25]. Learning therefore cannot be represented in the framework as a monotonic increase in attentional efficiency.

A further interaction between internal context and learned search is suggested by bumblebees exposed to caffeine paired with a floral odor. This treatment biased initial choices toward the learned target odor, but the effect was transient and was measured in an artificial foraging environment [26]. The appropriate interpretation is that biochemical and reward context can modulate the later priority of learned cues, not that caffeine universally improves attention or pollination performance.

These findings create several distinct experience-dependent states that prose alone can easily conflate. **Table 1** separates how comparison-dependent retrieval, acquired valence, higher-order association, interference, relative memory, and transient priming alter what can legitimately be inferred about stimulus priority.

Table 1. Experience-dependent routes by which prior learning changes the behavioral priority of competing cues

Evidential standing	Biological setting · Evidence	Consequence for stimulus selection	Limits and uncertainty · Research or test
	Comparison-dependent retrieval		
Evidence-supported	Adult Drosophila memory-guided choice The same learned cue is expressed differently when the available alternatives change	Current competitors help determine which remembered value controls choice	Retrieval context may alter expression without rewriting stored memory Manipulate the comparison set while holding training constant
	Acquired sensory valence		
Evidence-supported	Adult Drosophila associative learning Reinforcement assigns appetitive or aversive value to a sensory input	Previously neutral input can gain or lose behavioral priority after learning	Laboratory reinforcement isolates selected pathways Compare learned valuation with naturalistic reinforcement
	Hierarchical learned significance		
Evidence-supported	Adult Drosophila higher-order conditioning A learned predictor becomes capable of supporting a subsequent association	Priority can depend on relations among memories, not only direct reinforcement	Demonstrated within a specific conditioning architecture Test whether higher-order weighting generalizes across modalities and taxa
	Consecutive-memory interference		
Evidence-supported	Adult Drosophila sequential learning Earlier and later tasks impair one another under defined conditions	Prior experience can reduce, rather than increase, access to task-relevant information	Direction and magnitude depend on timing and task structure Include interference controls in repeated attention training
	Relative-value memory		
Evidence-supported	Bumblebee foraging choice Novel decisions follow previously learned ordinal relations	Choice can be guided by relative ranking rather than recovered absolute value	Does not show that absolute information was never encoded Separate encoding, retention, and retrieval in comparative-choice tests
	Transient biochemical priming		
Evidence-supported	Bumblebee odor-guided search Reward chemistry paired with target odor biases early search	Internal/reward context can temporarily raise learned cue priority	Effect is short-lived and laboratory-specific Measure persistence and ecological transfer before claiming durable benefit
	History-sensitive priority updating		
Proposed synthesis	Cross-domain synthesis Combined pattern across comparison, reinforcement, interference, and priming	Prior experience is treated as a conditional weight on current competition rather than a simple memory-strength term	No single circuit or parameter has been validated across insects Factorially manipulate learning history and current competitors

Neuromodulatory gating

Neuromodulation is one mechanism by which sensory and learned values can be translated into changes in behavioral priority, but the evidence argues against a unitary "attention transmitter." In Drosophila, Dop1R1 signaling in different central-complex populations has opposing effects on the temporal organization of locomotion and turning, showing that dopamine can bias candidate action patterns in a cell-type-dependent manner [27]. This is best interpreted as modulation of action architecture rather than as direct measurement of an abstract attentional resource.

Learned value can also be routed into specific motor strategies through identifiable downstream circuits. In Drosophila, mushroom-body output pathways conveying learned olfactory valence converge on neurons that promote wind-oriented movement, providing a circuit-level example of how memory can be transformed into an action appropriate to odor-guided navigation [28]. The result supports a bridge between valuation and action selection, but it remains specific to the tested olfactory and navigational context.

Gating is not exclusively chemical. Visual processing in flying Drosophila is selectively suppressed during course-changing turns but is not equivalently suppressed during course-stabilizing optomotor turns [29]. Thus, the current action can feed back onto sensory gain in an action-specific manner. This distinction is central to the proposed architecture: neuromodulatory signals, endocrine state, and motor-related feedback may all alter which information controls behavior, but they should remain analytically separate because they operate through different mechanisms and timescales. The next step is therefore not to search for a single gating center, but to determine how these distinct gating processes are coordinated when several sensory cues and several possible actions are simultaneously available.

Action selection

Attention becomes behaviorally consequential only when selected information changes what the insect does. Action selection therefore cannot be treated as a terminal readout of an already completed attentional process. In flying Drosophila, distinct visual features converge through LPLC2 and descending pathways to support rapid evasive turning [30]. This circuit provides a task-specific example in which several sensory features acquire significance because they map onto an immediately available action. It does not establish a general decision circuit, but it shows that selection can be organized around behavioral consequences rather than around stimulus representation alone.

The same principle applies in social contexts. Quantitative analysis of Drosophila courtship shows that the probability of particular actions depends on structured features of the partner and on recent interaction history [31]. Current sensory evidence is therefore interpreted against a temporally evolving behavioral context. Collision avoidance offers a complementary mechanistic example: LPLC1 combines object and motion information with spatially structured inhibition so that particular geometries preferentially promote slowing [32]. Neither system should be relabeled as "attention" in isolation. Together, they show that selection can arise through feature conjunctions whose relevance is defined by the candidate action.

Action selection also changes subsequent sampling. Odor-guided walking in Drosophila is expressed through graded changes in locomotor state rather than a single reflexive command [33]. During flight, head and body movements temporally organize when stable visual information is acquired, producing punctuated patterns of visual sampling [34]. Combined with the action-specific visual suppression described above, these findings make a one-way sensory-to-motor pipeline inadequate. The proposed architecture therefore places action inside a recurrent loop: current sensory competition influences action, while the selected action changes sensory gain, position, timing, and the evidence available for the next selection.

This recursive logic is compressed in **Figure 1**. The figure deliberately keeps established task-specific mechanisms separate from the article's proposed cross-domain architecture so that evidence from host seeking, learned navigation, visual escape, courtship, and active sensing is not mistaken for a single conserved circuit.

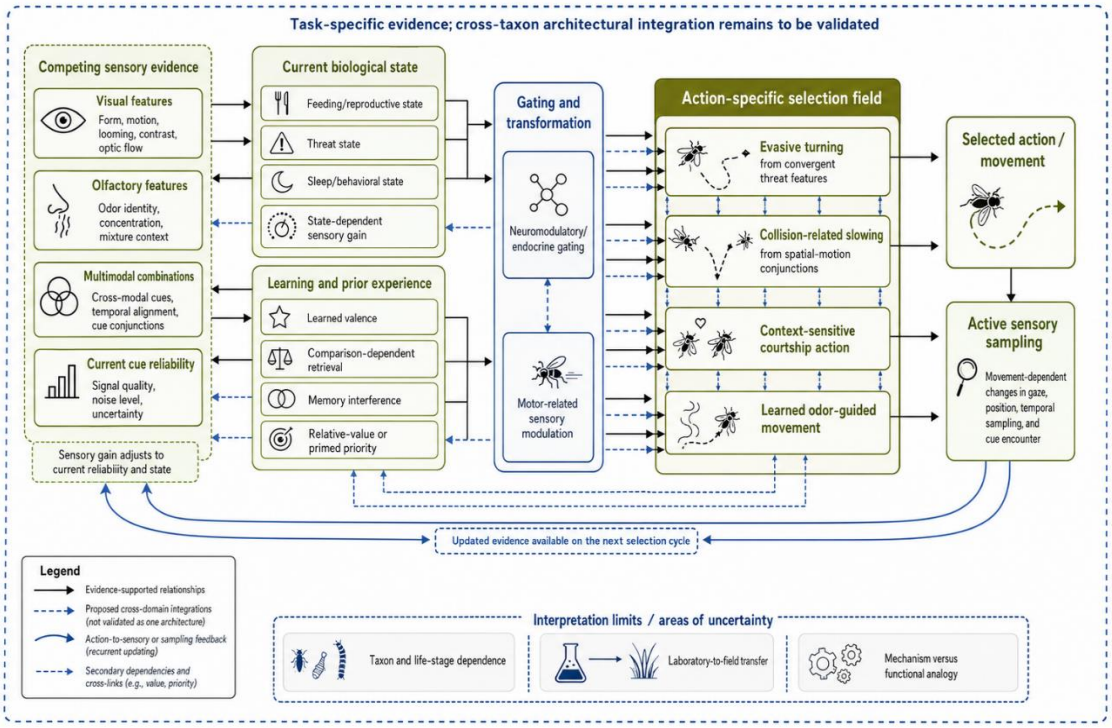


Figure 1. Action-dependent resolution of sensory priority across state, memory, and motor feedback

Attention as dynamic resource allocation

The evidence reviewed above supports a distributed interpretation but not a literal, measurable pool of "attention." Here, dynamic resource allocation is therefore a proposed functional description: processing priority is repeatedly redistributed among available signals and actions as cue reliability, physiological state, remembered value, and current movement change. No single weighting term is assumed to reside in one neuron class. The value of the formulation is analytical: it specifies which variables must be dissociated experimentally before selective behavior is attributed to a unitary attentional mechanism.

Three properties follow. First, allocation is conditional. Multimodal benefit can increase when individual cues are weak [5], whereas learned search can redirect inspection toward previously rewarding targets [10]. Second, allocation is state dependent: hunger can change early sensory output [18], so a shift in behavior need not originate at a late decision stage. Third, allocation is recursive. Learned value can be transformed into directed movement [28], while ongoing movement can suppress or restructure subsequent visual processing [29]. Thus, input priority and action opportunity are mutually constraining on behaviorally relevant timescales.

Cross-taxon generalization requires particular caution. Related Drosophila species differ in object-tracking strategies in association with visual ecology [35]. Such variation is compatible with context-dependent allocation, but the comparative association does not demonstrate that ecological differences adaptively produced each neural or behavioral strategy. The proposed architecture therefore treats species, life stage, and environment as potential parameters of allocation rather than as nuisance variables.

Table 2 is needed because the framework contains different evidential statuses: some allocation operations have direct neural or behavioral support, some are supported only within particular tasks, and the cross-domain links are proposed. Mapping those distinctions exposes where experimental coverage is strong and where apparent architectural continuity still depends on inference.

Table 2. Where dynamic allocation is evidenced, bounded, or untested across insect selective behavior

Allocation operation	Discriminating test	Evidence	Interpretation within this article · Principal boundary or gap	Biological context represented · Evidential standing
Reliability-dependent cue weighting	Manipulate modality reliability independently while	Performance changes as component cues become weak or noisy	Relative cue reliability can alter processing priority	Bee multimodal foraging Evidence-supported

	recording behavior and neural responses		Mostly controlled associative tasks	
State-conditioned sensory weighting	Hold stimulus constant while changing defined physiological state	Same cue class gains or loses behavioral control with physiological state	Internal state can alter priority before or during selection Mechanisms differ across taxa and life stages	Mosquito host seeking; fly feeding and threat states Evidence-supported
History-conditioned priority	Cross learning history with a novel competitor set	Retrieval, ranking, interference, and priming change later choice	Prior experience modifies current competition rather than simply strengthening memory Different learning paradigms measure different processes	Fly and bumblebee learning Evidence-supported
Action-specific convergence	Present identical features while altering available actions	Distinct feature combinations predict or cause task-specific actions	Selection is partly defined by the action that sensory evidence can support Strongly Drosophila-weighted	Fly escape, collision avoidance, courtship, and odor navigation Evidence-supported
Action-to-sensory return	Record sensory activity before, during, and after alternative actions	Movement changes neural gain or timing of sensory acquisition	Allocation can be recurrent rather than purely feed-forward Limited modalities and laboratory behaviors	Fly turning and active visual sampling Evidence-supported
Cross-domain allocation architecture	Factorial multimodal, state, learning, and action manipulation across taxa	Convergence of separately established patterns	Attention is treated as repeated conditional reweighting across levels No insect-wide validation or common parameterization	Proposed across sensory, state, memory, and action domains Proposed synthesis

Experimental predictions across insect taxa

The framework makes predictions about interactions rather than fixed effect sizes. If dynamic allocation is useful, manipulating cue reliability should change which modality controls behavior most strongly, and that shift should itself depend on current state or learned value. A factorial design is more informative than separate "attention," hunger, or learning experiments because an architecture of conditional weighting predicts interactions among these variables rather than only independent main effects.

A second prediction concerns locus. The same physical stimulus should be capable of supporting different actions under different internal or learned conditions without requiring a change at the receptor. Existing state-dependent and memory-to-action mechanisms make this plausible, but the framework does not predict that modulation must occur centrally. Peripheral sensitivity, early sensory circuits, valuation circuits, and premotor pathways are competing explanations that should be measured rather than assumed.

A further prediction concerns temporal scale. A cue that dominates at initial encounter should not necessarily retain priority after habituation, reinforcement, satiety, or movement changes the available evidence. Repeated measures should therefore estimate transitions in selection rather than summarize an entire trial with one endpoint. The framework predicts that apparent inconsistency across experiments may sometimes reflect observations made at different points in the same changing allocation process.

Variation should also be retained rather than averaged away. Individual honeybees differ in their use of social information during learning [36], while comparative Drosophila work shows species-level differences in visual tracking strategy. The proposed framework predicts that some between-individual and between-taxon heterogeneity will appear as systematic differences in cue weighting, state sensitivity, or action coupling. Demonstrating that interpretation will require repeatability, common-task comparisons, and, for evolutionary claims, designs able to separate ecology from phylogenetic history.

Research priorities

The first priority is measurement across levels. Behavioral proxies such as inspection time are valuable but cannot identify where selection occurs. Experiments should combine competing stimuli with neural measurements and

explicit action readouts whenever technically feasible, while preserving the distinction between correlation, necessity, and sufficiency. State variables should be defined biologically rather than collapsed into "arousal," because sleep, hunger, reproductive physiology, threat, and locomotor state need not influence the same pathways. Methodologically, the decisive tests are those that pit the framework against simpler alternatives. For example, a state-dependent behavioral switch should be accompanied by measurements capable of distinguishing altered peripheral sensitivity from central valuation or premotor gating. Likewise, apparent learning-dependent "attention" should be tested against memory retrieval and motor persistence, and action-related sensory suppression should be separated from global movement artifacts. Negative results are informative: failure of one component to modulate selection can define where conditional allocation does not apply.

The second priority is ecological transfer. Laboratory isolation is indispensable for circuit analysis, but natural signal statistics may change the competition being studied. Multimodal noise, intermittent odor plumes, moving backgrounds, changing floral displays, and unrestricted movement can alter which cue is useful. Validation should therefore test whether mechanisms identified in constrained preparations continue to organize selection when animals can actively sample their environment.

The third priority is taxonomic and developmental breadth. Much of the circuit-resolution evidence comes from adult Drosophila, whereas mosquito studies are concentrated on female host seeking and bee studies commonly use adult foragers. Larval state-dependent sensory recoding shows why life stage cannot be assumed irrelevant [18]. Comparative tests should preserve species, sex, developmental stage, and individual identity as explanatory variables. The objective is not to prove that every insect implements the same architecture, but to determine which allocation principles recur, which mechanisms are lineage- or task-specific, and which apparent similarities dissolve under matched experiments.

Finally, comparative work requires shared operational definitions. "Attention" should not be inferred from different proxies in bees, mosquitoes, and flies and then treated as directly equivalent. Matched manipulations of distractor strength, cue reliability, internal state, and action opportunity would permit stronger cross-taxon comparisons even when neural methods differ. Such designs could reveal conserved computational principles without presuming conserved anatomy.

Conclusion

Insect attention is most usefully approached as a problem of selective control under simultaneous sensory, physiological, mnemonic, and motor demands. Existing evidence establishes multiple mechanisms that can alter cue influence, sensory gain, learned value, and action probability, but it does not establish one conserved attention center or one universal mechanism. The contribution developed here is therefore explicitly architectural: attention is proposed as repeated, conditional allocation of processing priority across sensory competition, internal state, experience, gating, and action. This formulation preserves the mechanistic diversity of insects while making stronger experiments possible. Its value will depend on whether factorial, multilevel, and cross-taxon tests can distinguish genuine recurrent allocation from simpler explanations such as sensory adaptation, motivation, memory retrieval, or task-specific sensorimotor control.

Acknowledgments: None

Conflict of Interest: None

Financial Support: None

Ethics Statement: None

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