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Insect Movement Through Multisensory Landscapes Depends on Cue Integration Across Space, Time, and Changing Internal State

Emma Wilson[1]*, Frederik De Jong[2], Lara Peters[2]

[1]Department of Multisensory Movement and Landscape Navigation, Faculty of Life Sciences, University of Edinburgh, Edinburgh, United Kingdom.
[2]Department of Cue Integration and Internal State, Faculty of Biosciences, Wageningen University, Wageningen, Netherlands.

***E-mail** ✉ emma.wilson@ed.ac.uk

ABSTRACT

Insects rarely encounter ecological information as isolated, continuously reliable signals. Visual structure, odor, airflow, heat, acoustic information and learned spatial cues vary over different distances and timescales, while the usefulness of each signal depends on the current movement task and the animal's physiological condition. Movement models often simplify this complexity by treating cues as independent inputs or by assuming fixed cue weights. Such representations are useful for restricted tasks but become problematic when information is intermittent, modalities alter one another, or an insect switches between search, approach, avoidance and reassessment. This article develops a proposed Dynamic Multisensory Landscape Model in which movement emerges from the interaction among spatial cue availability, temporal reliability, cross-modal transformation and internal-state-dependent valuation. The model separates signal presence from effective information, behavioural synergy from demonstrated neural integration, and laboratory evidence from field-scale inference. The framework predicts that cue weights should change across movement phases, that conflict should trigger context-dependent reweighting or priority switching rather than uniform averaging, and that model validation requires observations spanning controlled sensory manipulations and naturalistic movement. The framework is an organizing synthesis, not an empirically validated universal mechanism.

Keywords: Multisensory integration, Insect navigation, Sensory ecology, Cue reliability, State-dependent behavior, Movement ecology

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Introduction

Insect movement is frequently constructed from several information streams whose ecological value differs across species and tasks. Reviews of insect navigation show that visual, olfactory, mechanosensory and self-motion information may be combined, substituted or used sequentially rather than acting as isolated drivers [1]. Sensory information is also context dependent: a stimulus that is informative for one behavioural state or ecological problem may be weak, irrelevant or misleading in another [2]. This makes cue presence an incomplete description of the information available to a moving insect. The same physical signal can have different behavioural consequences depending on what other signals are present, what the insect has previously learned and what it currently needs.

Navigation studies in ants illustrate this plurality particularly clearly. Path integration can operate alongside learned visual or olfactory information, and familiar cues may correct or redirect movement when accumulated

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positional uncertainty increases [3]. Across insects more broadly, visual navigation itself ranges from local landmark use to orientation over much larger spatial scales, with strategy depending on sensory ecology and task [4]. Visual navigation can therefore coexist with other sensory and self-motion information rather than functioning as a universally dominant channel [1, 4]. Even within a single modality, cue timing can change action. In walking *Drosophila*, odor onset can promote upwind movement whereas odor loss can trigger local search-like responses, demonstrating that transient sensory events can be linked to different motor programs [5]. These findings motivate a framework in which movement is treated as a sequence of information-conditioned states rather than a fixed response to a static sensory scene.

The central problem addressed here is therefore inferential: how should movement ecology represent environments in which sensory information is distributed unevenly across space, changes in reliability through time, interacts across modalities and is revalued as internal state changes? The proposed solution is not a universal algorithm for insect behaviour. Instead, the article develops an explicitly conditional framework that distinguishes four components—spatial opportunity, temporal reliability, cross-modal transformation and internal-state weighting—and asks how their interaction can alter movement decisions. The framework is designed to preserve taxonomic, life-stage and methodological boundaries and to generate testable predictions without equating observed behavioural associations with established neural mechanisms or fitness consequences.

Theoretical methods

This article uses conceptual evidence integration rather than a new empirical dataset. Evidence is organized according to the level at which a source can legitimately support inference: sensory detection, neural processing, behavioural trajectory, movement-state transition or landscape-scale movement. Relationships demonstrated at one level are not automatically transferred to another. This is particularly important for multisensory research because controlled laboratory manipulations can identify cue dependence, yet they cannot by themselves establish how the same relationship functions under natural plume structure, variable wind, heterogeneous vegetation or long-distance displacement.

A second methodological principle is embodiment. Navigation models become more informative when proposed rules are tested within realistic sensorimotor and physical constraints rather than only as abstract decisions. The I2Bot platform demonstrates how multimodal insect-inspired navigation can be evaluated in a closed loop that includes body geometry, sensors, dynamics and environmental structure [6]. Such platforms provide a validation route for theoretical movement architectures, but they do not constitute biological validation of the model proposed here.

A third principle is that movement policy can change with information structure. In male pink bollworm moths, wind-tunnel trajectories and modeling support a shift in exploration–exploitation characteristics with source distance and turbulence [7]. The result is specific to pheromone-guided flight and should not be generalized into a universal insect search rule, but it establishes that movement strategy need not remain constant while the information field changes. Likewise, experiments with *Drosophila* show that bilateral temporal correlations in odor signals can provide directional information distinct from airflow, improving navigation through complex plumes [8]. Thus, the framework treats spatial pattern, temporal pattern and movement state as analytically separable variables whose interaction must be tested rather than assumed.

Spatial distribution of sensory information

A multisensory landscape is not simply a map of stimulus intensity. It is a spatial arrangement of opportunities to obtain information, and different channels can become useful at different distances or positions. Semi-field experiments with *Anopheles gambiae* showed that human scent strongly structured host selection and thermotactic behaviour in a large naturalistic arena, whereas heat without the relevant accompanying host context was comparatively weak [9]. In *Aedes aegypti*, thermal infrared radiation can contribute to host-seeking behaviour when embedded within a broader host-cue context [10]. Together these systems illustrate why a sensory landscape should be described in terms of conditional information fields rather than fixed ranges assigned to individual modalities.

The effective spatial value of one channel may also depend on another. Mosquito spectral preferences can shift when different odors are present, indicating that a visual object is not necessarily assigned a stable behavioural value independently of olfactory context [11]. Conversely, ecological specialization can produce strong task-specific dominance. Oviposition by *Drosophila sechellia* is heavily dependent on olfactory information associated

with its specialized resource, while candidate visual, textural and social alternatives do not account for the tested specialist preference to the same extent [12]. This does not establish a general hierarchy in which olfaction outranks vision; it shows that cue dominance can emerge from the ecology and behavioural task being performed. Spatial information can also be distributed across partly redundant channels. In *Aedes aegypti*, the IR8a pathway contributes to detection of acidic volatiles in human odor, yet disruption of this route does not erase all host-directed attraction because other sensory pathways remain available [13]. A spatial map of "host odor" is therefore biologically incomplete if it is represented as a single scalar field. For the proposed framework, the relevant object is a layered opportunity surface: at a given location, several channels may be detectable, but their behavioural influence depends on sensitivity, task, concurrent signals and the possibility that one channel substitutes incompletely for another.

Temporal reliability

Information changes not only because insects move through space but because signals fluctuate, decay, recur and become outdated. Temporal reliability begins with sensory resolution. In moth olfactory receptor neurons, stimulus duration and offset are encoded early in the olfactory pathway, but discrimination of very brief whiffs becomes less reliable in the tested system [14]. The implication is not that insects share a universal temporal threshold. Rather, any movement model that uses odor intermittency must recognize that environmental fluctuation can exceed the temporal resolution of the sensory machinery measuring it.

Reliability is also history dependent. Experience can retune olfactory processing toward behaviourally relevant odors, altering how later signals are represented [15]. In hymenopteran navigation, learning flights and walks provide a complementary example: bees, wasps and ants perform structured movements during which views are acquired for later orientation [16]. These cases show that movement both consumes information and can actively generate the experience required to interpret future information. Consequently, a cue's reliability cannot always be specified solely from current environmental statistics; it may depend on what the animal has learned and whether the present scene matches that learned context.

Redundancy further complicates temporal interpretation. Knockout of OR39 in *Anopheles coluzzii* removes detection of a particular ligand but does not abolish acquisition of host-seeking behaviour, indicating that a transient or permanent loss of one sensory route need not map directly onto behavioural failure [17]. Temporal robustness may therefore reside in ensembles of channels rather than in persistence of a single signal. Biological time can matter as well. In *Spodoptera littoralis*, female pheromone exposure can synchronize male circadian rhythms and sensory timing [18]. This is a specialized sociosexual system, not a general rule for insect clocks, but it demonstrates that the effective value of a cue can depend on endogenous temporal state in addition to external signal dynamics.

The proposed framework therefore defines temporal reliability as a relation among signal persistence, sensory resolution, recent experience, redundancy and endogenous timing. A cue may remain physically present while becoming behaviourally less useful, or it may be intermittent yet informative because the insect can integrate its temporal structure. This distinction becomes critical once more than one modality is available.

Cross-modal cue integration

Cross-modal integration should not be treated as synonymous with additive summation. In female *Aedes aegypti*, CO_2 exposure alters subsequent visual steering and is associated with modulation of visual processing [19]. Independent 3D flight and genetic experiments further show that CO_2 gates attraction to particular wavelengths and skin-like visual targets [20]. These studies support the species-specific conclusion that olfactory context can alter visual response in *Aedes aegypti* [19, 20], but they do not justify a universal rule that olfaction always gates vision or that all modalities are combined at a common neural stage.

A second integration form is congruence dependence. In male *Bombyx mori* tested in virtual reality, correct relationships among odor, wind and visual information support pheromone-source navigation, whereas selected mismatches degrade performance [21]. Cue conflict therefore may be resolved not by averaging all inputs but by reducing reliance on combinations that are mutually inconsistent. The relative contribution of each modality also need not be equal.

Behavioural synergy represents a third evidential class. In *Stomoxys*, combined visual and olfactory cues can increase attraction relative to isolated components [22]. Because trap response is a whole-animal outcome, however, it does not by itself identify where or how signals are neurally fused. The distinction between

behavioural synergy and demonstrated neural integration is essential for preventing mechanism from being inferred from endpoint behaviour alone.

A fourth form is reciprocal or task-specific cross-modal interaction. During *Anopheles coluzzii* swarming, acoustic information can modify visually guided movement, while visual context also influences responses relevant to conspecific interaction [23]. The result belongs to a social movement context and should not be transferred automatically to host seeking or migration. Collectively, the evidence supports a manuscript-specific classification of cross-modal relationships as conditional gating, congruence-sensitive coordination, behavioural synergy and reciprocal context-specific interaction. These categories describe evidentially different relationships and are not assumed to be exhaustive biological mechanisms.

Because prose alone makes it difficult to preserve the distinction among integration type, evidential level and inference boundary, **Table 1** separates these relationships without converting them into a score.

Table 1. Mechanism–boundary matrix for interpreting cross-modal cue integration in insect movement

Mechanism-localized gating and congruence			
Cross modal comparison dimension	**Conditional sensory gating**	**Congruence-sensitive coordination**	
Movement task	Host-seeking mosquitoes	Pheromone-guided moth navigation	
Empirical signature	One modality changes behavioural or neural response to another	Navigation deteriorates under selected sensory mismatches	
Movement claim	Effective cue value depends on concurrent sensory context	Cross-modal consistency can affect source-directed movement	
Localization boundary	Demonstrated strongly in specific mosquito systems; directionality may be asymmetric	Virtual-reality geometry and species-specific sensory ecology constrain transfer	
Trajectory test and evidence state	Manipulate cue order and presence while measuring trajectory and sensory processing Evidence-supported class	Test conflict under naturalistic plume and wind statistics Evidence-supported class	
Behavior-level synergy, reciprocity, and reliability-conditioned reweighting			
Cross modal comparison dimension	**Behavioural synergy without localized mechanism**	**Reciprocal context-specific interaction**	**Reliability-conditioned reweighting**
Movement task	Biting-fly attraction	Mosquito swarming	Cross-taxon synthesis developed here
Empirical signature	Combined cues produce stronger attraction than isolated cues	Acoustic and visual information alter movement responses in the same social task	Relative informativeness or conflict changes the expected influence of available cues
Movement claim	Multiple modalities jointly affect approach	Relative influence of modalities depends on movement context	Cue influence is proposed to vary with temporal reliability and task
Localization boundary	Endpoint behaviour does not identify neural integration	Social navigation may not transfer to host seeking	Exact weighting rule is not established
Trajectory test and evidence state	Pair free-flight tracking with sensory or neural measurements Evidence-supported behavioural class	Compare identical cue combinations across behavioural states Evidence-supported class	Perturb reliability while holding mean cue intensity constant **Proposed synthesis**

The figure that follows makes explicit a second distinction that is difficult to convey in the matrix: the boundary between what experiments directly measure and what the present article proposes to infer about movement in heterogeneous landscapes.

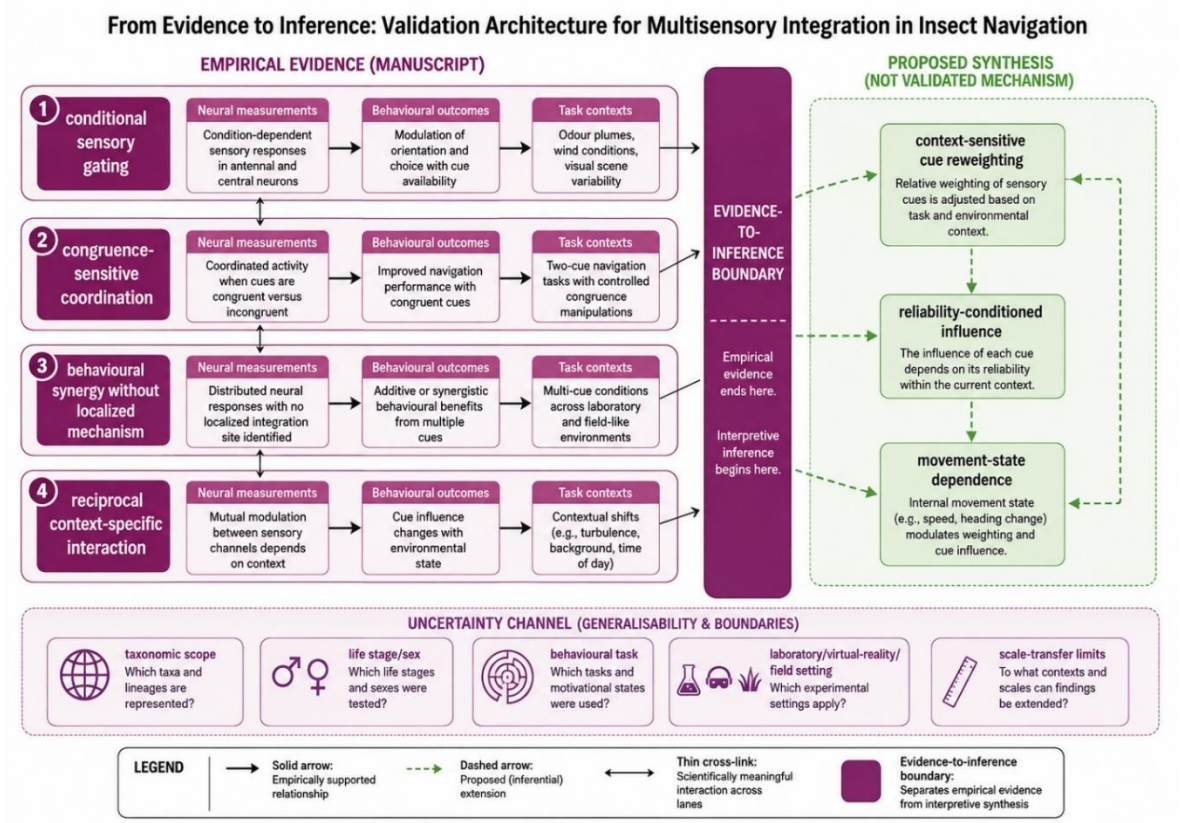


Figure 1. Where cross-modal evidence stops and multisensory movement inference begins

Internal-state weighting

A sensory landscape is not external to the animal because its effective structure changes with physiological state. Reviews of adult *Drosophila* olfaction show that neuromodulatory systems can change odor processing according to internal condition, providing a mechanistic basis for state-dependent sensory valuation [24]. Direct work in *Drosophila* larvae similarly shows that food deprivation alters both search behaviour and function within an early olfactory-processing circuit [25]. Internal state can therefore influence movement before a final choice is expressed; it can modify the sensory representation from which the choice is constructed.

State dependence can begin even earlier in the sensory pathway. In *Bactrocera dorsalis*, starvation alters odorant-receptor regulation through FoxO-associated transcriptional control, and feeding-related reversal indicates that peripheral sensory sensitivity is physiologically plastic [26]. This mechanism is species specific and should not be generalized as a universal controller of insect movement, but it establishes that cue weighting need not arise solely in central integration circuits.

More importantly, state may change cue value rather than merely response magnitude. In *Drosophila* larvae, food deprivation reconfigures early olfactory processing in ways that can alter behavioural valence [27]. A static external map can consequently predict different movements from animals in different states even when the available cues are unchanged. The proposed framework therefore treats internal state as a dynamic modifier of effective information, with at least three conceptually distinct routes: modulation of central sensory processing, altered peripheral sensitivity and state-dependent change in cue valence. These routes remain separate because evidence for one does not establish the others.

This formulation also prevents a common interpretive shortcut. Increased approach under hunger, for example, should not automatically be described as an adaptive strategy or as evidence that a particular molecular pathway optimizes movement. The evidence demonstrates state-dependent changes in sensory processing and behaviour within defined systems. Whether those changes improve fitness, persist across developmental stages or generalize across orders requires separate evidence. In the Dynamic Multisensory Landscape Model developed later, internal state will therefore modify the effective weight and sign of available information, but the exact transformation rule will remain proposed rather than empirically specified.

Movement decisions under cue conflict

Cue conflict does not necessarily imply that an insect averages competing signals. In the *Drosophila* head-direction system, cue influence changes with relative reliability and familiarity, showing that orientation can be reweighted when sources of directional information disagree [28]. This supports a general premise—that cue influence may be relational rather than fixed—but not a claim that insects implement a universal Bayesian rule.

Conflict can also alter behavioural priority. Female *Aedes aegypti* interrupt host-seeking trajectories in response to fast visual threats and can resume host-directed movement after the threat is removed [29]. Looming visual threats likewise reduce blood feeding and evoke escape responses under experimental conditions [30]. Together, these experiments support the restricted conclusion that visual threats can interrupt host-directed behaviour in female *Aedes aegypti* [29, 30]. They do not establish that threat always dominates host cues or that reduced feeding produces a demonstrated fitness cost.

The proposed framework therefore distinguishes reliability reweighting from priority override. Reliability reweighting changes the influence of information while the movement objective remains broadly stable; priority override temporarily changes which objective organizes movement. A third possibility is reassessment, in which conflict weakens commitment without immediately selecting an alternative. These are proposed decision states rather than universally observed insect categories.

Dynamic multisensory landscape model

The proposed Dynamic Multisensory Landscape Model treats the sensory environment as a coupled animal–environment state rather than a fixed external map. At location x and time t, physical signals define opportunities for detection, but effective information depends additionally on sensory resolution, recent experience, cross-modal context and internal state. The framework therefore separates four operations: spatial opportunity determines what can be sampled; temporal reliability determines what remains informative; cross-modal transformation determines how concurrent signals modify one another; and internal-state weighting determines the current behavioural value of that transformed information. No numerical weights or universal transition thresholds are assumed.

The model further allows the integration architecture to change. Genetic disruption of an olfactory pathway in *Aedes aegypti* can increase reliance on heat-related host information, providing a boundary-case demonstration that sensory loss may induce cross-modal compensation [31]. Because this result arises from a perturbed system, it cannot establish that ordinary fluctuations in cue reliability produce the same compensation in wild-type insects. The model therefore treats compensation as a conditional possibility rather than a default rule.

Movement is represented as transitions among proposed functional states: information acquisition, directional commitment, conflict-driven reassessment and renewed search. Evidence from odor-event responses, moth search dynamics, multisensory mismatch, cue reliability and threat interruption supports the separate premises underlying these transitions [5, 7, 21, 28, 29]. Their combination into one state-space architecture is new synthesis. The states are not claimed to be neurally discrete, exhaustive or shared by all insects.

A useful consequence of this formulation is that uncertainty can enter at different points without being collapsed into noise. A signal may be physically absent, present but temporally unresolved, perceptible but cross-modally suppressed, or accurately represented yet assigned little current value. These cases predict different behavioural responses to the same apparent "cue loss." The model therefore treats failure to approach a target as diagnostically ambiguous unless the experiment identifies which informational operation failed. This distinction is especially important when comparisons span species with different receptor complements, life stages with different energetic demands, or behavioural tasks that recruit different sensory systems.

The cross-scale structure of the proposed model is compressed in **Table 2** because its central question is not which cues matter, but where evidence at one level can and cannot justify inference at another.

Table 2. Cross-scale evidence grid for the Dynamic Multisensory Landscape Model

	Information acquisition and commitment	
Multisensory comparison dimension	**Information acquisition**	**Directional commitment**
Immediate information question	Which signals are detectable here and now?	Are available cues mutually informative enough to sustain directed movement?
Evidence level	Receptor, sensory and local behavioural measurements	Trajectory and multisensory behavioural evidence

Movement state represented	Sampling or orientation before commitment	Persistent approach, homing or source-directed motion
Scale boundary	Detection does not establish landscape use	Task-specific trajectories do not establish a universal state
Required test and state	Manipulate spatial availability under naturalistic movement Evidence-supported premise	Compare cue reliability across movement phases **Proposed state built from evidence-supported premises**
Conflict-driven reassessment and renewed search		
Multisensory comparison dimension	**Conflict-driven reassessment**	**Renewed search**
Immediate information question	Do competing cues reduce commitment to the current movement policy?	Has directional information degraded below its current usefulness?
Evidence level	Cue-conflict and orientation experiments	Search-state and odor-loss behaviour
Movement state represented	Reweighting, interruption or temporary loss of commitment	Local search, exploration or reorientation
Scale boundary	Neural weighting and whole-animal priority switching are not equivalent	Search geometry differs among taxa and tasks
Required test and state	Measure competing cues while retaining trajectory history **Proposed synthesis**	Perturb information intermittency rather than mean intensity alone **Proposed synthesis**
Cross-modal compensation and landscape validation		
Multisensory comparison dimension	**Cross-modal compensation**	**Landscape validation**
Immediate information question	Can another channel gain influence after sensory degradation?	Do state-dependent rules survive wind, weather and habitat heterogeneity?
Evidence level	Genetic perturbation plus behaviour	Radar, field and semi-field movement
Movement state represented	Alternative cue dependence	Population-scale directional pattern
Scale boundary	Mutant compensation cannot be assumed in intact animals	Aggregate movement cannot identify sensory mechanism
Required test and state	Test reversible degradation in wild-type insects Evidence-supported boundary case	Link individual cue manipulations to field-scale trajectories Validation requirement

Figure 2 translates these scale boundaries into a state-space architecture in which cue availability, reliability and biological state jointly constrain movement without implying deterministic transitions.

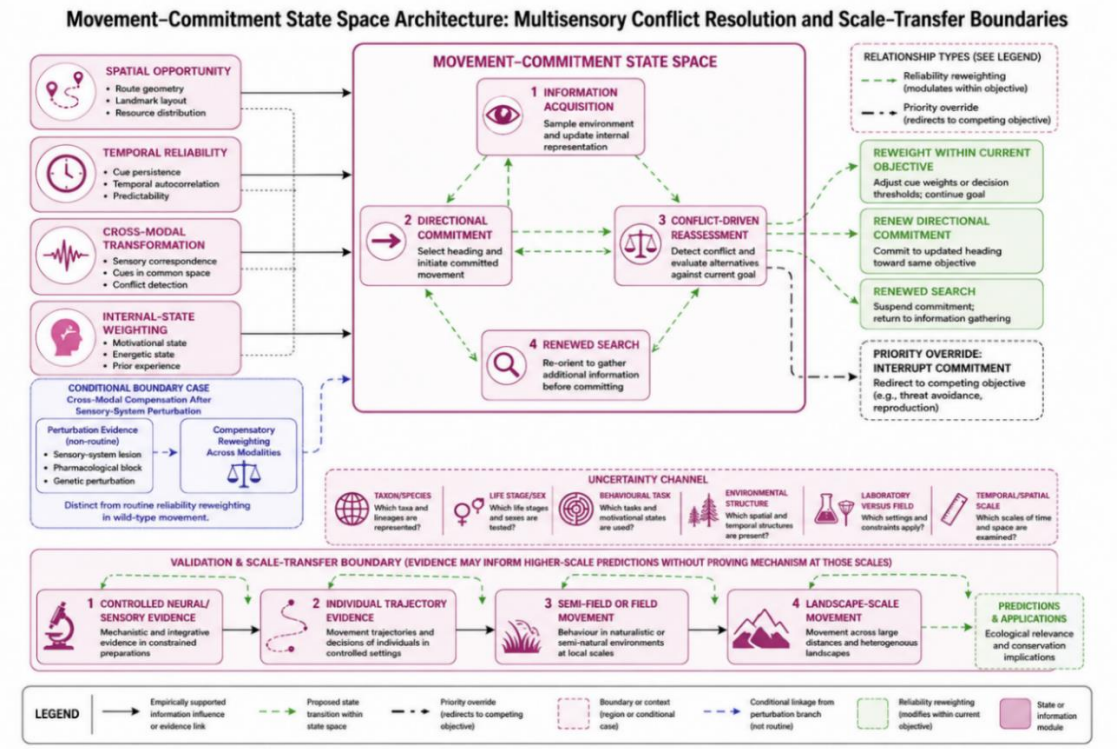


Figure 2. State-dependent movement commitments under changing multisensory information

Predictions across movement phases

The model predicts that cue influence should differ among movement phases. During acquisition, increasing detectability should matter most; during directional commitment, temporal continuity and cross-modal congruence should become more important; during conflict, relative reliability and behavioural priority should govern reweighting or interruption; during renewed search, recent cue loss and memory should shape where information is sampled next. These predictions concern differences among phases, not fixed numerical weights.

The phase predictions should also be asymmetric. A cue that is valuable for initial detection need not retain the same importance during final approach, and information that appears redundant during stable conditions may become decisive after conflict or interruption. Consequently, experiments that measure only terminal choice can miss reweighting that occurred earlier in the trajectory. Continuous movement tracking, coupled where possible to reversible cue manipulations, is better suited to separating acquisition, commitment and reassessment.

A second prediction is that degrading one cue should have the largest behavioural effect when alternative channels are weak, incongruent or unavailable. Redundancy should reduce the effect of isolated cue loss, whereas conflict can make an otherwise detectable cue ineffective. Tests should therefore manipulate reliability independently from mean stimulus intensity and should compare intact animals with temporary, reversible sensory degradation rather than relying only on constitutive mutants.

Cross-scale validation is essential. Radar observations from the Levant show that large-insect migration cannot be reduced to passive transport: movement directions differ systematically from prevailing winds, while migration intensity varies with meteorological conditions [32]. Such observations provide a landscape-scale constraint on movement models, but they do not identify the sensory mechanism generating orientation. A successful framework should therefore predict field movement patterns without treating field correlation as neural validation.

Results and Discussion

The framework changes the unit of explanation from “which cue controls movement?” to “which information is usable for this animal, at this place, at this time, during this movement state?” This shift matters because cross-modal evidence includes gating, congruence dependence, behavioural synergy and reciprocal interaction, which are not mechanistically interchangeable [19]. Likewise, internal state can alter central processing, peripheral sensitivity or cue valence through distinct pathways [24]. Treating all such effects as a single multisensory weight would obscure rather than integrate the evidence.

The main limitation is taxonomic and methodological unevenness. Mosquitoes and *Drosophila* provide unusually strong experimental resolution, whereas other movement systems contribute different forms of evidence. Virtual reality permits controlled conflict, wind tunnels preserve aerodynamic structure better than static arenas, semi-field experiments add naturalistic scale, and radar observes migration but not the sensory computations of individual insects. These approaches are complementary only when their inference boundaries remain explicit.

The proposed model should therefore be evaluated by discriminating tests rather than by asking whether it is broadly plausible. Experiments should alter spatial availability and temporal reliability independently, introduce cross-modal conflict at defined movement phases, manipulate internal state without assuming fitness consequences, and track whether the same individual changes movement policy. Embodied simulations can test whether proposed rules remain physically viable [6], while field validation should determine whether phase-dependent predictions survive atmospheric and habitat variation. Failure under particular taxa or tasks would refine the framework rather than falsify a claim of universality that is not made.

Conclusion

Insect movement through multisensory environments is better represented as dynamic information use than as response to a fixed collection of cues. The proposed framework separates where information is available, how long it remains reliable, how modalities transform one another and how internal state changes effective value. It further distinguishes reliability reweighting, priority override and reassessment as testable movement-level possibilities while preserving boundaries between neural mechanism, behaviour and landscape inference. Its purpose is not to supply a universal sensory algorithm, but to provide a structured basis for experiments that ask when, where and for which insects multisensory information changes movement decisions.

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