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Insect Navigation Under Imperfect Information Depends on Sensory Integration Across Spatial and Temporal Scales

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ABSTRACT

Insects rarely navigate with a single perfectly informative signal. Self-motion, terrestrial structure, celestial information, wind, airflow, optic flow and other cues differ in availability, persistence and usefulness across habitats and tasks. The central theoretical problem is therefore not simply how insects detect cues, but how navigational systems preserve useful behavior when information is incomplete, conflicting or valid only over limited spatial and temporal ranges. This behavioral framework synthesizes evidence from ants, bees, dung beetles, moths, butterflies and *Drosophila* while separating behavioral demonstrations, computational sufficiency, neuroanatomical capacity and neural mechanism. It distinguishes four properties that are often conflated: information availability, sensory detectability, behavioral influence and navigational validity. The framework argues that cross-modal integration should be treated as a set of conditional transformations rather than as obligatory cue averaging. Information can be weighted, switched, converted between reference frames, retained in memory or ignored according to task state and environmental conditions. Navigation failure can therefore emerge from discordant cues, inappropriate strategy selection, outdated memory or mismatches between sensory and representational scales. We propose a multiscale architecture in which momentary sensory evidence, journey-scale updating and longer-duration memory remain analytically distinct but interacting. The framework does not assume a universal cue hierarchy, Bayesian integrator or conserved circuit. Its principal prediction is that navigation becomes vulnerable when the validity of information changes faster than sensory weighting, memory or action-selection processes can update.

Keywords: Insect navigation, Multisensory integration, Path integration, Central complex, Spatial scale, Navigational memory

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Introduction

Navigation is often described as if an insect extracts a direction or position from a stable set of environmental cues. Field and laboratory evidence instead shows that many insects can draw on several information sources whose contributions depend on ecology, sensory access and task demands [1]. This creates a problem of imperfect information: a cue may be detectable yet uninformative for the current goal, informative only over a restricted distance, or reliable at one moment and misleading at the next. The relevant problem is therefore not simply cue detection, but how an animal determines which information should influence behavior.

Path integration makes that problem explicit. Updating position from self-motion permits navigation when external references are unavailable, but accumulated noise means that an internally updated home vector can

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become increasingly uncertain [2]. Dung beetles provide a complementary example: straight-line orientation can depend on multiple celestial and environmental references whose usefulness varies with conditions [3]. At still larger scales, monarch migration requires persistent directional control across changing landscapes and times of day, illustrating that information adequate for a local homing decision need not be adequate for long-distance travel [4].

The framework developed here treats navigational information along four separate dimensions: availability, detectability, behavioral influence and validity. Availability asks whether a signal exists; detectability asks whether the insect can resolve it; influence asks whether it changes behavior; validity asks whether following it maintains alignment with the current navigational goal. These dimensions need not covary. A conspicuous signal can be readily detectable while degrading orientation, whereas internally generated information can remain influential after the environmental context that originally made it useful has changed.

The central contribution is a proposed multiscale architecture that links these distinctions without assuming that all insects solve navigation in the same way. It separates immediate sensory integration from memory-based updating, distinguishes physical distance from neural reference frame, and treats conflict, environmental corruption and strategy mismatch as different failure classes. Similarities among taxa constrain plausible organizing principles, but do not demonstrate one conserved circuit or one universal integration rule.

Theoretical methods

This article is a conceptual synthesis of behavioral, sensory, neurobiological, anatomical and computational evidence used to examine whether navigation under uncertain conditions can be organized around shared information-processing problems. The approach is comparative rather than meta-analytic: no pooled effect, new dataset or quantitative reliability index is constructed. Evidence is interpreted at the biological and analytical level at which it was generated, and cross-level claims are made only where the relationship is supportable.

Three inferential rules structure the synthesis. First, spatial geometry is treated as part of the navigational problem rather than as background context. Desert-ant research shows that path integration in three dimensions cannot automatically be reduced to a simple horizontal-displacement problem [5]. Second, methodological control is separated from ecological generalization. Naturalistic components of path-integration behavior can be elicited on an air-cushioned spherical treadmill [6], but reproducing homing components under controlled locomotion does not establish equivalence with free-ranging field navigation.

Third, computational and anatomical evidence establish feasibility rather than biological identity. A decentralized neural model can reproduce adaptive-looking integration of competing navigational strategies [7], while an anatomically constrained bee-brain model shows that known circuitry can support plausible path-integration computations [8]. Neither result demonstrates that the modeled operation is the mechanism used across insects. Behavioral evidence therefore anchors what animals demonstrably do, whereas models and neural architectures delimit possible implementations.

Sources of navigational information

Navigational information differs not only by sensory modality but also by persistence, spatial reach and relation to the animal's movement. Honeybees can use skyline structure for orientation, showing that panoramic terrestrial information can provide a directional reference beyond recognition of nearby objects [9]. Desert ants reveal a different relation between external and internal information: path integration and terrestrial visual cues interact during homing, altering route characteristics rather than behaving as mutually exclusive systems [10]. Their coexistence argues against treating “landmark navigation” and “path integration” as discrete behavioral categories.

External information is also not uniformly necessary. The dung beetle *Scarabaeus galenus* can path integrate without terrestrial landmarks [11], demonstrating that independence from landmarks in one task does not imply independence from environmental information in general. Conversely, sensory sources that are simultaneously available need not exert equal influence. During learning walks of *Cataglyphis fortis*, wind direction strongly affected behavioral organization under conditions in which novel visual information did not produce an equivalent effect [12]. Multisensory access therefore does not imply equal weighting.

Navigational sources are more usefully classified by informational function. Self-motion signals update displacement; panoramas and skyline structure can stabilize direction- or place-related behavior; celestial, magnetic and airflow-related signals can provide directional references; and remembered views or route outcomes

can modify later decisions. These categories can overlap in modality. Visual input, for example, may convey terrestrial panorama, optic flow, celestial polarization or skyline orientation depending on viewing geometry and task.

A functional classification also avoids unnecessary commitment to a unitary internal map. Comparative analysis indicates that much insect navigation can be accounted for by distributed or task-specific representations, although some observations remain difficult for minimal schemes [13]. The present framework therefore uses "representation" descriptively and does not infer a cognitive map whenever allocentric or memory-dependent information is observed.

Reliability and range of sensory cues

Cue reliability is often treated as intrinsic, yet experiments show that usefulness depends on environmental configuration. In nocturnal Bogong moths, agreement between magnetic and visual landmarks supports migratory orientation, whereas experimentally imposed conflict disrupts directional behavior [14]. This establishes behavioral sensitivity to cross-modal consistency but does not reveal a universal weighting algorithm.

Sensory range likewise has several meanings. In a diurnal dung beetle, spectral and brightness information contribute differently to orientation under manipulated illumination [15]. Physical visibility, sensory detectability and navigational usefulness therefore should not be collapsed into a single measure. A signal can be physically conspicuous but behaviorally unhelpful, whereas a weaker signal may suffice when alternatives are poor. Dung beetle compass behavior further demonstrates that relative cue influence can change with environmental conditions rather than following a fixed hierarchy [16].

Movement state can also change informational value. Honeybee flight control based on optic flow interacts with wind, so the behavioral consequence of visual motion depends partly on the air through which the bee moves [17]. Reliability is therefore action dependent in some contexts: identical visual structure can impose different control demands under different locomotor conditions. This does not establish that optic flow supplies a complete position estimate, but it shows that sensory usefulness can be inseparable from movement.

Environmental alteration can corrupt an information system without eliminating sensory input. Artificial light changes nocturnal dung beetle orientation behavior [18]. Such cases make the distinction between detectability and validity particularly important. A conspicuous signal may exert behavioral influence while being poorly aligned with the natural information structure of the task. Here, range therefore denotes not only the distance at which a signal can be detected, but the spatial and temporal domain across which using that signal remains appropriate.

Cross-modal integration

Cross-modal integration is better treated as a family of operations than as a single act of combining cues. Two signals may remain separate until action selection, or they may first be transformed into a compatible directional coordinate. Neurobehavioral work in *Drosophila* shows that airflow direction is represented by fan-shaped-body neurons and contributes to orientation [19]. This establishes a central representation for a nonvisual directional variable, but does not show that the same neurons integrate every navigational modality.

Computational work provides one route by which different directional streams could be coordinated within central-complex-like circuitry [20]. Its important implication is not that the modeled architecture is universal, but that cross-modal integration can occur after modality-specific preprocessing when signals are expressed in compatible formats. Anatomical evidence from the bumblebee central complex supports substantial cross-region routing capacity [21], while the *Drosophila* central-complex connectome contains recurrent motifs suitable for flexible navigation and context-dependent action selection [22]. Connectivity, however, establishes anatomical capacity rather than functional necessity.

Behavioral evidence supplies a complementary principle: integration may be conditional. Dung beetle compass experiments show that the relative influence of directional information changes with environmental conditions [16]. Accordingly, this framework distinguishes three operations. Cue weighting changes relative behavioral influence while retaining multiple sources. Conditional dominance allows one source to govern behavior in a particular state or context. Common-coordinate transformation converts different inputs into representations that can be compared with a goal, heading or other directional variable. These operations can coexist without requiring one neural locus or one universal optimization rule.

A fourth operation is proposed here: reliability-gated arbitration. The system need not assign an explicit numerical probability to every source. Instead, behavioral privilege could change when cue concordance, sensory access, locomotor state or recent experience changes. This is an organizational hypothesis rather than a demonstrated insect-wide mechanism.

Because these operations predict different observations, a prediction-and-test ledger resolves distinctions that would become cumbersome in prose. **Table 1** separates weighting, conditional dominance, coordinate transformation, anatomical convergence and the proposed arbitration process while preserving their evidential boundaries.

Table 1. Discriminating cross-modal operations when navigational information differs in validity and representational form

Multimodal input		Cross-modal computation	
Integration operation	**Navigation system and cue evidence**	**Output computation**	**Reliability challenge**
Cue weighting	Multicue compass behavior in dung beetles. Relative behavioral influence changes as cue conditions change	Multiple inputs remain available while influence is redistributed. Evidence supported.	Behavioral weighting does not identify the underlying neural algorithm. Manipulate cue quality independently while preserving access to both inputs
Conditional dominance	Orientation tasks in which one directional source becomes decisive in a particular context. Behavioral control shifts toward one available information source as conditions change	Integration may involve context-dependent switching rather than continuous averaging. Evidence supported as a behavioral pattern; mechanism unresolved.	Apparent dominance can reflect sensory masking or unequal detectability. Test whether control reverses when the environmental condition is restored
Common-coordinate transformation	Central directional representations and central-complex computation in flies. Modality-specific signals can be expressed in compatible directional coordinates	Different sources become comparable before action selection. Evidence supported for component transformations.	Laboratory neural representations do not establish field-scale generality. Record or perturb candidate representations during controlled cross-modal conflict
Anatomical convergence without functional proof	Bumblebee and fly central-complex circuitry. Projection architecture and recurrent connectivity permit information exchange	Circuit organization constrains plausible integration routes. Evidence supported as substrate only.	Connectivity alone cannot reveal the computation performed. Combine pathway-specific perturbation with simultaneous functional and behavioral testing
Reliability-gated arbitration	Cross-taxon synthesis proposed here. Predicted redistribution of behavioral privilege when concordance, movement state or recent experience changes	Selection among representations becomes state dependent without requiring explicit probabilistic weighting. Proposed synthesis.	No single study validates this rule across modalities, taxa and scales. Test cue conflict, state change, learning and recovery within the same individuals and task

The architecture underlying these distinctions is shown in **Figure 1** because cross-modal control is not adequately represented as a single convergence box: sensory acquisition, representational compatibility, anatomical capacity, uncertainty and action selection must remain analytically separable.

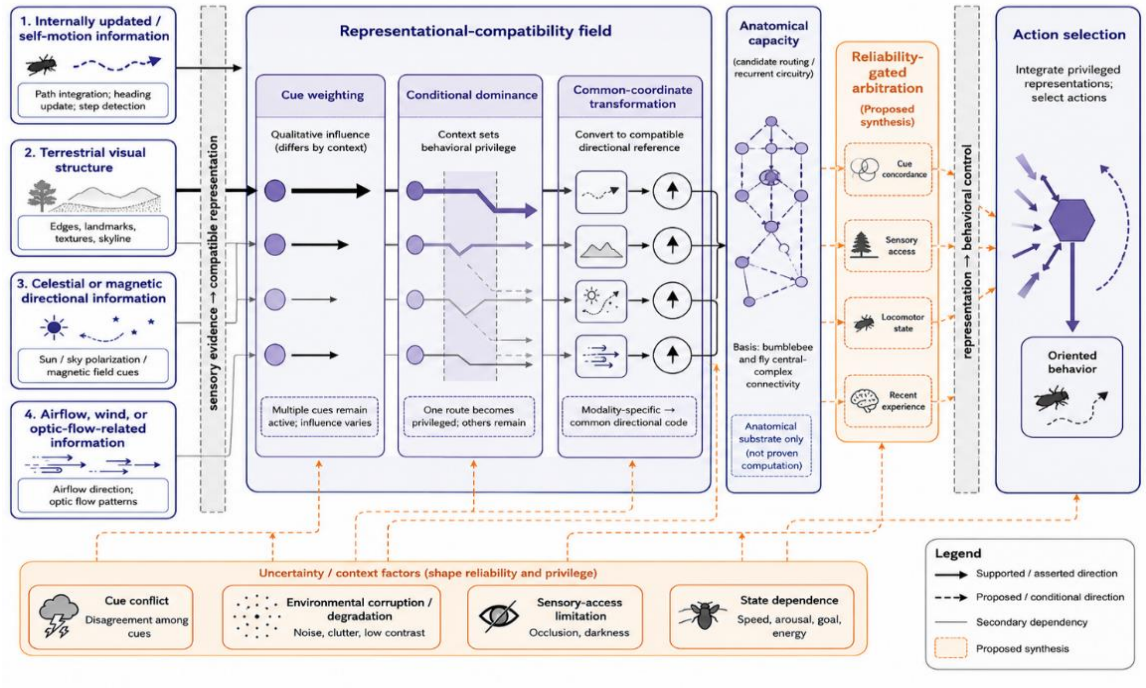


Figure 1. Cue validity and representational compatibility determine where multimodal navigational signals can converge

Memory and temporal updating

Navigation under imperfect information is not determined only by what is sensed at the present moment. Recent experience can change the value assigned to later observations. Desert ants rapidly learn aversive information associated with route errors, and that trace can modify subsequent navigation [23]. The important implication is not that learning necessarily improves performance, but that navigational control is history dependent: similar sensory input can generate different behavior before and after an informative event.

Path-integration memory also appears to contain partially dissociable components. In ants, anesthesia disrupted the distance component of the home vector more strongly than directional information [24]. A comparable asymmetry was observed after cold-induced anesthesia in the dung beetle *Scarabaeus galenus*, where distance-related path-integration memory was more vulnerable than direction [25]. These perturbations are physiologically broad and do not identify dedicated molecular stores, but they argue against treating "navigation memory" as one unitary state.

Temporal updating therefore occurs at multiple scales. Moment-to-moment self-motion contributes to an evolving displacement estimate; experience accumulated over a route can alter the later value of familiar views or actions; and longer-lived directional strategies can persist across behavioral episodes. Comparative analyses of ants and honeybees show that behavioral details constrain candidate path-integration mechanisms even when they do not uniquely identify one computation [26]. The time course of behavior is thus evidence about what information has to be retained, transformed or discarded.

The proposed framework consequently separates memory persistence from information validity. A representation can persist after its environmental basis has changed, whereas a short-lived trace may be unstable yet appropriate to the current route. Successful navigation requires retained information to remain both accessible and relevant to the current goal. Failure can arise when memory decays too rapidly, when obsolete information remains influential, or when updating occurs at a temporal scale mismatched to environmental change. These temporal mismatches become especially important when navigation crosses physical distances and neural reference frames, considered in the next section.

Spatial scale transitions

Physical distance and representational scale are related but not equivalent. In monarch butterflies, sun-compass neurons are tuned in relation to migratory orientation, providing a neural correlate of directional control at a life-history stage defined by long-distance movement [27]. Yet migratory heading is not simply a static sensory

readout. Active flight alters compass representation in the monarch heading network [28], indicating that behavioral state can modify how directional information is expressed.

At a much smaller physical scale, *Drosophila* circuitry demonstrates operations that are conceptually relevant to scale transitions without establishing migratory homology. Neural populations can construct an allocentric travelling-direction signal through vector computation [29], and movement representations can be transformed from body-centered into world-centered coordinates [30]. These findings show that a nervous system can convert momentary egocentric movement into a representation referenced to the external world. They do not show that the same computation supports kilometer-scale travel.

The proposed framework therefore separates three meanings of scale: physical extent, temporal horizon and representational frame. Local homing, repeated-route navigation and migration may differ in all three. A transition of scale occurs when information useful in one domain must be retained, transformed or replaced before it remains valid in another. This formulation avoids assuming that increasing travel distance simply adds more of the same computation.

This separation also clarifies why allocentric coding should not be treated as evidence for a unitary cognitive map. Representations adequate for immediate steering may be world referenced yet remain local, task specific or short lived. Conversely, migration can span large distances without requiring that every relevant variable be represented in one map-like format. Scale should therefore be inferred from the operation demonstrated, not from terminology applied to the representation.

Navigation failure under conflicting information

Conflict is only one route to navigational failure. In *Drosophila*, an internal heading estimate can be compared with a goal signal to guide oriented behavior [31]. Failure can therefore arise even when sensory detection is intact if the estimated current state, remembered goal or action mapping is mismatched. This distinction matters because an erroneous heading estimate, an obsolete goal and an inappropriate motor correction predict different behavioral signatures.

Strategy selection provides another failure point. Monarch butterflies can adopt different orientation strategies depending on stimulus conditions [32]. A behavioral switch is therefore not automatically evidence of successful reliability assessment: it may be appropriate, neutral or maladaptive depending on whether the newly privileged information remains valid for the task. Similarly, magnetic–visual conflict can disrupt Bogong moth orientation [14], artificial illumination can alter dung-beetle orientation [18], and recent aversive route experience can change subsequent ant navigation [23]. These cases represent different causal locations in the information chain.

We consequently propose four failure classes: cue discordance, environmental corruption, memory–environment mismatch and strategy–goal mismatch. They may co-occur, but should not be treated as interchangeable. The taxonomy/evidence decision matrix below separates what must be observed before assigning a failure to one class and identifies tests capable of discriminating competing interpretations.

Table 2. Distinguishing where conflicting or outdated information can derail insect navigation

	Trajectory disturbance			**Failure diagnosis**
Failure location	**Navigational context**	**Observable symptom**	**Navigation error**	**Alternative and discriminating manipulation**
Cue discordance	Multimodal orientation during simultaneous access to directional sources	Orientation degrades or changes when otherwise usable cues indicate incompatible directions	Conflict arises between concurrently available information streams	Apparent conflict may instead reflect unequal detectability or sensory masking. Manipulate cue agreement while holding visibility and stimulus strength as constant as practicable. Evidence-supported class.
Environmental corruption	Navigation in an anthropogenically altered cue field	Behavior changes when a conspicuous environmental signal no longer preserves the natural directional structure	Available information remains detectable but its navigational validity is altered	General stress or habitat change may contribute independently of cue interpretation. Restore the natural cue structure without changing the animal's internal state. Evidence-supported class.

Memory–environment mismatch	Repeated-route or path-integration behavior after learning or perturbation	Previously acquired information continues, disappears or changes in influence after environmental or internal-state change	Stored information and present conditions become temporally misaligned	Memory loss, retrieval failure and changed motivation can produce similar behavior. Cross environmental change with controlled retention or retrieval intervals. Proposed classification grounded in memory evidence.
Strategy–goal mismatch	Goal-directed orientation when stimulus configuration changes	The animal switches control strategy but movement no longer aligns with the experimentally defined goal	Action selection privileges information inappropriate for the current navigational objective	The goal representation itself may have changed. Manipulate information availability and goal state independently. Proposed classification.
Scale-transfer mismatch	Movement requiring information to remain useful across distances, durations or reference frames	A representation supports orientation in one domain but fails when task scale or coordinate requirement changes	Information valid at one scale is not automatically transferable to another	Performance loss may reflect sensory range or motor constraints instead. Test the same information source across explicitly separated physical, temporal and representational scales. Proposed synthesis.

Figure 2 shows that these failure classes are not a terminal checklist: they can emerge at different points along an evolving navigation trajectory, and feedback from error or experience can either restore or further destabilize information use.

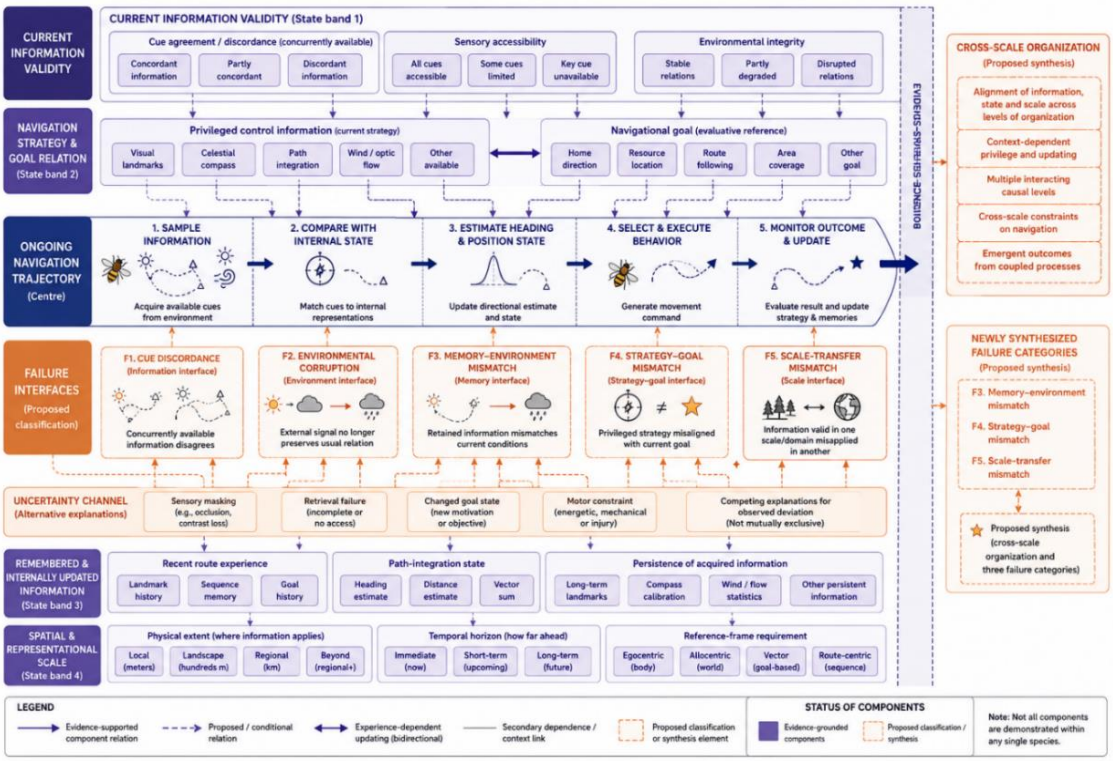


Figure 2. Navigational failure emerges when information validity, memory and strategy change on different trajectories

Multiscale navigation architecture

The proposed architecture treats navigation as interacting control processes with different update rates rather than as one decision made from one sensory snapshot. Control-theoretic analysis shows that orientation can involve oscillatory and feedback mechanisms with different functional roles [33]. This supports using multiple control relations as an organizing vocabulary, but not reducing insect navigation to a single servomechanism.

Three interacting levels are proposed. A fast level handles current sensory and self-motion information; an intermediate level retains journey-scale displacement, route experience and current goal relationships; a slower contextual level changes which information or strategy remains behaviorally privileged across episodes. Evidence that *Drosophila* reinforcement pathways represent movement differently across behavioral contexts [34] makes context-sensitive updating biologically plausible, but does not establish dopamine as a universal estimator of navigational reliability.

Cross-level exchange is essential. Fast sensory correction can update a journey representation, recent route experience can change later cue influence, and behavioral state can alter compass representation. Conversely, persistent memory can constrain immediate choices even after environmental validity changes. The central proposed rule is therefore relational: navigation is most vulnerable when the rate at which information validity changes exceeds the rate at which weighting, memory or strategy can be revised. This is a theoretical prediction, not a demonstrated general law.

Results and Discussion

The evidence considered here argues against treating insect navigation as either a hierarchy of fixed cues or an undifferentiated multisensory fusion problem. Multimodal behavior varies among taxa and tasks [1], and environmental conditions can redistribute cue influence [16]. Strategy switching in monarchs further shows that the form of control itself can depend on stimulus context [32]. Flexibility is therefore observable, but neither optimality nor a universal rule for achieving it follows from those observations.

A second implication is methodological. Computational models can establish sufficiency, neuroanatomy can identify plausible routing, and connectomics can reveal motifs compatible with flexible control, but those evidence classes do not by themselves demonstrate what a free-ranging insect uses. The central-complex model [20], bumblebee projectome [21] and *Drosophila* connectome [22] are strongest when interpreted as constraints on candidate mechanisms rather than as interchangeable proof of one conserved navigation circuit.

Temporal evidence similarly resists flattening. Rapid route learning [23], differential vulnerability of direction and distance memory [24], and state-dependent compass representation [28] demonstrate that information processing changes over different timescales. Their taxa and manipulations differ, so the synthesis should not imply that one species has been shown to implement every proposed level.

The framework consequently makes a testable organizational demand rather than a universal mechanistic claim. Strong validation would manipulate multiple information sources within the same taxon, separate detectability from behavioral influence, impose controlled cue agreement and conflict, follow repeated journeys, and test whether changes in physical scale or reference frame alter which information remains valid. Field transfer is especially important because laboratory precision can isolate component computations without establishing their ecological dominance.

Boundary conditions are equally important for interpreting apparent robustness. A navigator can remain oriented after one information source is removed because another source is sufficient, because memory temporarily bridges the loss, or because the experimental task does not demand the missing information. Conversely, degraded orientation does not reveal which computational stage failed. Future experiments should therefore combine behavioral trajectory analysis with manipulations that distinguish sensory access, coordinate transformation, memory state and goal comparison. Such designs would test the architecture at interfaces between levels rather than validating isolated components and then assuming their integration.

The main limitation is comparative patchwork. Ants, bees, dung beetles, monarchs, Bogong moths and *Drosophila* contribute different pieces, while many insect orders, immature stages and reproductive contexts remain poorly represented. Future work should therefore ask not whether insects possess “multisensory navigation” in general, but which integration operation is used, over what spatial and temporal domain, under which environmental conditions, and with what failure signature.

Conclusion

Insect navigation under imperfect information is best understood as a problem of maintaining correspondence between available signals, internal representations, remembered states and current goals. The proposed framework separates availability, detectability, influence and validity; distinguishes weighting, conditional dominance and

coordinate transformation; and identifies several non-equivalent failure states. Its multiscale architecture is intentionally mechanism-neutral where evidence is incomplete. The central implication is not that insects share one integration algorithm, but that reliable navigation depends on information remaining appropriate across changing sensory, temporal and spatial conditions.

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