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The neural basis of interspecies interactions in insects

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As insects move through the world, they continuously engage in behavioral interactions with other species. These interactions take on a spectrum of forms, from inconsequential encounters to predation, defense, and specialized symbiotic partnerships. All such interactions rely on sensorimotor pathways that carry out efficient categorization of different organisms and enact behaviors that cross species boundaries. Despite the universality of interspecies interactions, how insect brains perceive and process salient features of other species remains unexplored. Here, we present an overview of major questions concerning the neurobiology and evolution of behavioral interactions between species, providing a framework for future research on this critical role of the insect nervous system.

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Introduction

If you've ever sifted through leaf litter, examined a handful of soil, or observed an inflorescence attended by pollinators, it is strikingly apparent that within these microcosms exist complex social networks of insects that are constantly interacting with one another. It's hard to imagine living in such a world—one in which an organism must make rapid life-or-death decisions upon every encounter with another organism, evaluating if it's a potential mate, a food source, a predator, or just a benign animal crossing paths. Yet this is the living world through which insects must navigate, engaging in perpetual and dynamic interactions with diverse species, spanning predators, prey, parasites, hosts, and novel species never previously encountered. Behavioral responses during these frequent interactions have critical consequences for survival [1,2]. Yet, despite their ubiquity and importance, we know remarkably little about how insect nervous systems distinguish among different categories of organism and trigger the appropriate behavioral responses. Sensorimotor pathways that process information about other organisms are under selection to execute ecologically useful behaviors during interspecies encounters. In generalist, free-living taxa, these circuits underlie routine and often transient interactions with a diversity of other organisms, yielding behaviors such as generalized predation, predator and parasitoid evasion, physical or chemical defense maneuvers, or simply indifference. From this presumably ancestral condition, variation in sensorimotor circuitry has arisen, leading to widespread evolution of specialized interactions [3]. These include behaviors such as predation on specific prey species, mutualistic partnerships and parasitism in all of its forms. Here, we outline the challenges in understanding interspecies interactions from both neurobiological and evolutionary standpoints.

Interspecies interactions and their role in shaping sensorimotor pathways

Critical choices that insects make while interacting with other organisms arise from a sequence of computations that the nervous system performs to transform sensory input into motor output [4]. For instance, as a free-living, soil-dwelling insect, such as a rove beetle (Staphylinidae), moves through its environment, it detects other organisms via a repertoire of finely tuned receptors expressed within its sensory periphery that transduce chemical, visual, auditory and tactile cues (Figure 1). To filter relevant signals from a noisy background, sensory processing is distributed across peripheral and central circuits, and salient features within and across modalities are integrated, creating representations of valence (at the coarsest level, attractive, aversive or neutral), driving the selection of appropriate motor programs that coordinate muscle action, leading to behavior (Figure 1).

How does the nervous system process the deluge of sensory information from other species and select the right behavior? Computations performed by sensorimotor pathways must be robust to the breadth of interacting species an insect may encounter, but also flexible enough to compensate for both changes in environmental background stimuli and an organism's internal state.

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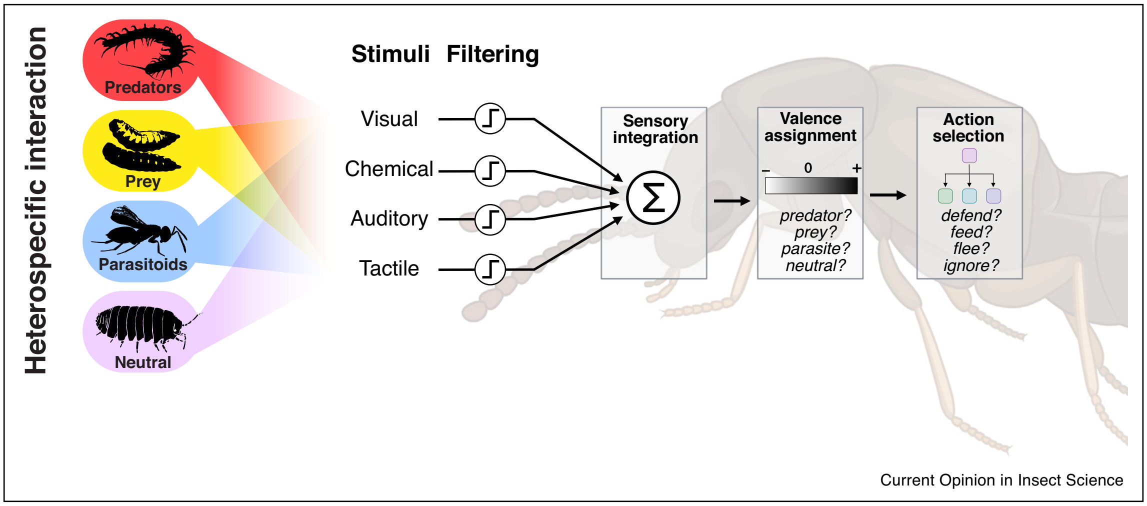
Figure 1



Sensorimotor computations that enable interspecies interactions.
Insects interact with a diversity of other species, here broadly categorized as predator, prey, parasite, or neutral. Upon encountering another species, an insect's peripheral sensory systems detect and begin filtering heterospecific sensory cues. These sensory cues are integrated across multiple modalities and assigned a valence, eliciting the selection of appropriate motor programs that determine how the insect behaviorally interacts with the heterospecific organism.

Evidently, these computations are also modifiable by evolution, enabling novel interactions to emerge. Prior studies on the evolution of insect sensorimotor processing have primarily explored circuits associated with goal-directed individual behaviors, such as chemosensory- or visually-guided navigation, or conspecific interactions such as courtship [e.g. Refs. 5–7,8••,9–11,12•,13]. Such behaviors have provided key insights and predictions into how neural circuits evolve; however, they represent a small fraction of the types of interactions that insects experience while navigating the living world. For example, identifying and catching a prey item, distinguishing predator cues and enacting defensive behavior, locating and interacting with the correct host species, or ignoring a non-threatening organism are routine behaviors that many insect species must perform with great frequency. How these pathways parse the diversity of other species, selecting from a spectrum of potential interactions to engage with or respond to other species in adaptive ways, remains largely unexplored.

Navigating through interspecies sensory space

Certain key insights into interspecies neural circuitry have come from the field of neuroethology. For instance, work on dragonfly prey capture has revealed how a set of visual neurons (small target motion detector neurons) are preferentially sensitive to movement of small prey-sized objects in a range of directions; these cells drive descending interneurons (target-selective descending neurons) that transmit target motion information to motor centers [14–16]. Extensive work on predation avoidance strategies in crickets and cockroaches [17] has revealed how a population of wind sensitive sensory neurons encode directional information resulting from an approaching predator, and relay this information to downstream interneurons (giant interneurons) and motor circuits that enable the animal to make a directed escape response [18–21]. In these and other examples, however, the emphasis has been on what these systems reveal about circuit properties, such as sensitivity and tuning, informing general principles of animal nervous systems. Less attention has been paid to how these circuits process multiple categories of organisms, and the neural transformations that enable categorization and discrimination of the breadth of species that insects typically encounter.

Regardless of lifestyle, fundamental mysteries apply to all insect species concerning how the brain processes information about other organisms coexisting in the environment. Below, we identify three major unanswered questions:

1) ***What computations does the brain perform to classify other species?***

Except for the most visually guided taxa, insects rely heavily on chemosensation for detecting and communicating with other species. Different insect species typically have a small molecule chemical signature encompassing cuticular hydrocarbons [22] as well as other exudates and volatiles such as aggregation and alarm pheromones or defensive compounds [23,24]. How this chemical information mediates behaviors between members of the same species is now comparatively well understood in many systems. In contrast, knowledge of how these compounds are used as 'allelochemicals'—governing communication between species—is more limited [25,26]. Multiple examples exist in which intraspecific cues have been co-opted as allelochemicals by specialized eavesdropping species. These include numerous cases of parasitoids and predators exploiting pheromones of hosts and prey [27–29], or myrmecophiles following chemical trails of their host ants [30,31]. Do such examples, in which a particular cue acts as a heterospecific identifier that triggers adaptive behavior, represent the norm? We suggest that for the majority of less specialized interactions between species, they do not. Given the potentially high number of species in an insect's local environment, it seems unlikely that natural selection would be sufficiently strong for most insect brains to evolve fine-grained, species-specific identification. Moreover, the success of thousands of species of introduced insects outside their native ranges, where they have been observed to adaptively interact with species of prey, predators, parasitoids and mutualists to which they were previously naïve, attests to a mechanism of heterospecific cue processing that is versatile and broadly tuned. Due to the exceptionally high stakes of a single instance of failure, the underlying mechanism is likely innate. To our knowledge, a general system of heterospecific perception has not been proposed for any insect species.

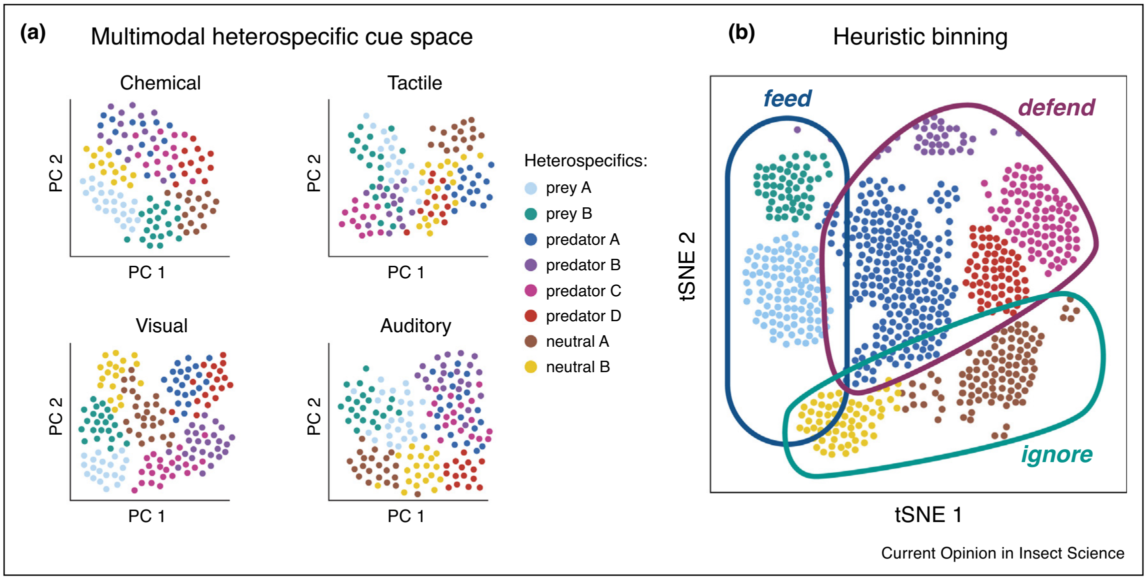
We hypothesize that the insect brain detects heterospecific chemosensory stimuli and applies a heuristic, computationally efficient classifier, enabling rapid, coarse-grained 'binning' of other species (Figure 2a,b). In its simplest form, such a heuristic algorithm may entail extraction of salient and invariant features of other organisms followed by classification based on valence—their attractiveness or aversiveness. Generalizing the representation of other organisms into positive, neutral, or negative valence is a potentially efficient approach that can enable rapid selection of the appropriate downstream motor response. A somewhat more granular heuristic algorithm might function by collapsing diverse chemosensory profiles of different species into a smaller number of dimensions representing major categories—threat, prey, benign, conspecific mate, conspecific competitor, and so on—eliciting distinct behaviors (Figure 2b). A precedent for such a system is found in the nestmate recognition systems of social insects, such as ants. Here, a colony-specific CHC profile is employed as a template for kin recognition. Divergence from the CHC template, even quantitatively slight, triggers aggression [32,33]. We speculate that this type of heuristic classification, in which divergence from conspecific chemistry elicits binning of other species into coarse-grained categories, may be universal, or at least phylogenetically primitive in insects.

We further suggest, however, that chemistry alone is unlikely to ensure robust classification of other species. Instead, additional sensory cues, including mechanosensory, auditory and thermosensory information, as well as visual input, may simultaneously be integrated to enable heterospecific classification [34,35]. Even in the case of ants, divergence from the colony CHC profile must be accompanied by further information that distinguishes a possible prey item from a predator—information critical for selecting the appropriate motor output of either prey capture behavior or predator defense behaviors (e.g. envenomation, release of alarm pheromone, and recruitment of a collective defense response). The information that ants use to perform this decision-making task is unknown. Intuitively, integration of other sensory modalities that enable determination of features such as organism size and kinematics seems likely.

2) *Where and how is classification of other species performed in the insect brain?*

The classification and valence assignment of other species begins at the sensory periphery. Here, the sensitivity and tuning of sensory neurons is the first stage of filtering salient features associated with other organisms, such as the presence of key pheromones or chemosensory signatures. Furthermore, recent work in *Drosophila* has demonstrated the existence of a valence map in the olfactory periphery, suggesting that sensory neurons may themselves comprise the first layer at which valence information is encoded [36••]. Next, local circuits within sensory brain regions such as the primary olfactory (antennal lobe, AL) or visual (optic lobe, OL) centers further filter key features representing other species, distilling species-specific information along key dimensions such as odor intensity and identity, and then integrating this information across sensory modalities. For instance, local inhibitory interneurons within the ALs may employ differential output onto different olfactory receptor neuron types. These differences in neural activity output in turn enable distinct odor representations at the AL level for aversive odor versus pheromone cues, contributing to distinct behavioral responses upon detection of each cue [37]. Furthermore, valence-specific mapping of insect-associated chemicals may occur at AL output projection neurons and further downstream in the mushroom body and lateral horn [38–40,41•,42]. Additionally, multisensory integration occurs in the mushroom bodies, and, for many insect species, even earlier in the ALs and OLs [43–46]. Ultimately, however, we simply do not yet know how the brain represents different categories of other species along sensorimotor pathways. This is especially true for multiple sensory modalities transduced by afferent inputs

Figure 2



Heuristic classification of heterospecific stimuli.
(a) Insects encounter diverse species of different categories, each species presenting a distinct multimodal sensory profile (represented here by PCA plots of each sensory modality). **(b)** To enact adaptive behaviors, salient heterospecific sensory features are integrated across modalities. The integrated profile is subjected to heuristic binning, whereby a rapid, course-grained classification based on weighting of different sensory components is applied. The outcome of heuristic binning is represented here as a t-SNE plot, with species becoming grouped together into classes based on valences (e.g. negative/positive/neutral) that correspond to different heterospecific categories (e.g. predator or prey). Valence assignment determines the subsequent behavioral response that the insect selects (e.g. defend versus feed). Regions of overlapping behavioral responses indicate plasticity in behavior, where the selected behavioral response is contingent on internal state or environment.

that operate along widely different temporal scales, such as touch and chemosensation.

3) ***How does the brain balance conflicting behavioral states?***

Insect behavior represents a constant balancing of motivations to satisfy adaptive internal and physiological needs such as satiety, hydration, reproduction and safety. Often, these persistent needs are in competition with each other. Thus, even as a predatory insect is hunting, it must balance perception of appetitive prey cues with detecting and responding to stimuli from its own predators. Upon encountering another species, how does the brain resolve such conflicting drives? One could imagine that for some species there is a 'default' innate setting that tends to prevail, and is contingent on perpetual needs within the insect's specific ecological context. For example, for insect species inhabiting hostile environments, such as ant-dominated litter and soil microhabitats, anti-predator vigilance may be an adaptive, default behavioral state to which the nervous system typically returns. In contrast, for a symbiotic species, the default drive may be to maintain a constant, intimate association with its host. In both of these examples, the nervous system would need to trade off these perpetual needs with potentially conflicting behaviors that arise more transiently, for example, when encountering conspecifics (e.g. courtship, mating, or male-male aggression), or prey species (prey capture and feeding).

Evolving new interactions

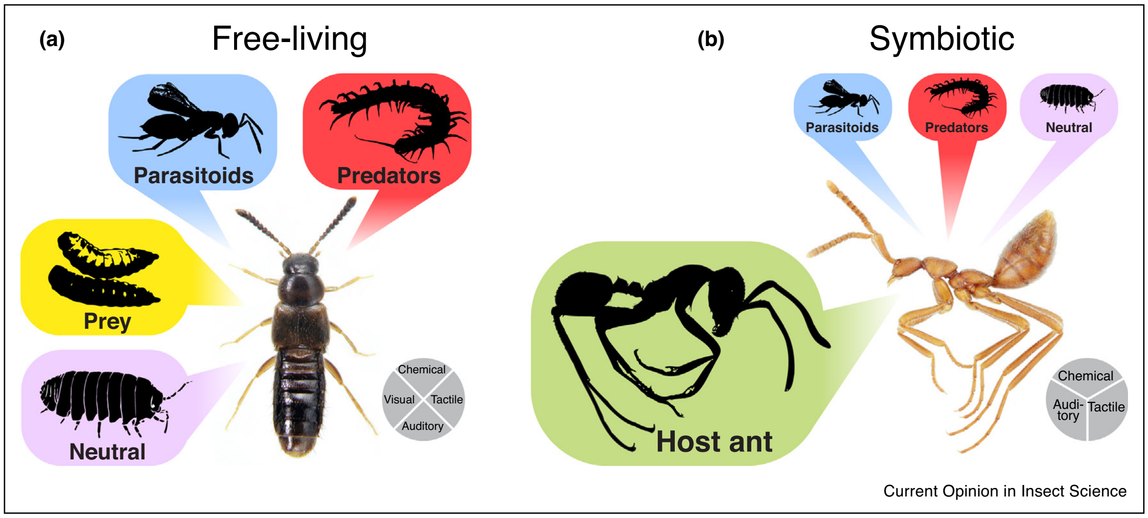
It is in these key areas—sensory cue reception, dimensionality reduction, valence assignment, and balancing of behavioral states—where evolution acts to shape novel interactions. The problem of explaining how relationships between species evolve is twofold. First, what factors cause nascent interactions to originate between previously non-interacting species? Second, what processes shape subsequent evolutionary specialization, leading to obligate and highly intricate relationships? A paradigm for understanding the evolution of interspecies relationships is provided by rove beetles of the subfamily Aleocharinae. Most members of this clade of ~17,000 species possess a benzoquinone-secreting chemical defense gland that functions as an potent ant deterrent [47,48]. From an ancestral free-living, predatory lifestyle, numerous aleocharine lineages have convergently evolved into symbiotic myrmecophiles that socially interact with specific host ant taxa [48,49,50••]. The evolutionary transition to myrmecophily typifies features seen in the emergence of many specialized interactions. First, there is a pronounced shift in interspecies sensory space such that a single or a narrow range of other species take precedence (Figure 3a,b). Presumably, defined combinations of chemosensory cues take on new salience, elevating them into allelochemicals; information from other sensory modalities likely becomes similarly elevated, eliciting multisensory partner detection. Second, there are dramatic changes in how the beetle behaves—in this case, engaging ants socially rather than defensively. How might these changes manifest in the brain?

At the sensory periphery, numerous examples exist of insects that exhibit modifications to sensory neuron number, sensitivity, and/or receptor tuning, which correlate with specialized ecological associations [51–53]. It is unclear, however, if changes in cue receptivity alone can account for the emergence of novel species interactions. Rather, we favor the view that nascent interactions are established when sensory information becomes reinterpreted—that is, via changes in valence. Valence assignment may be a mechanistically facile means of evolving new interactions: by modifying the behavioral output associated with previously detectable sensory inputs, what was once neutral or even aversive may become attractive (and vice versa). In the case of myrmecophile rove beetles, the valence of the beetle towards the host ant has seemingly fully reversed, so what was ancestrally perceived as a threat and met with defensive behavior is now treated as a social partner [48,49,54,55]. Analogous valence reversals may underlie the evolution of trophic mutualisms between ants and herbivorous insects. Here, ants solicit carbohydrate-rich honeydew from taxa including sap-sucking hemipteran bugs and lycaenid butterfly caterpillars, in return providing protection against predators and parasitoids [56,57]. In these systems, both partners exhibit diminished hostility towards each other, instead engaging in productive social behaviors. In still other interspecies contexts, a pre-existing positive valence may exist in a generalist ancestor but become exaggerated, such as genera of scydmaenine rove beetles that target specific mite taxa [58], or the many highly host-specific hymenopteran parasitoids [59].

Possible mechanisms of valence evolution

How do valence switches arise evolutionarily? Given its extreme importance, circuit motifs for valence processing can be innately hard-coded via labeled lines: parallel sensorimotor pathways for positive or negative stimuli that directly relay to motor circuits responsible for coordinating approach or avoidance behaviors [60,61]. Valence assignment can, however, be context dependent, such that animals can make adaptive decisions depending on their environment or internal state [62]. For instance, starved insects can suddenly be attracted to typically aversive stimuli, a reversal that may be advantageous in the pursuit of food [63]. Additionally, the foraging state of an insect can mediate whether certain chemosensory cues are attractive or aversive [64]. An indication

Figure 3



Specialized lifestyles alter interaction space and neural circuit evolution.
(a) The interaction space of a generalist. A free-living, soil-dwelling rove beetle (*Dalotia coriaria*), frequently encounters numerous species of different categories, employing multiple sensory modalities to distinguish them and behave adaptively. **(b)** The interaction space of a specialist. Extreme specialists such as the symbiotic rove beetle *Pseudomimeciton* are expected to interact predominantly with a single other species (in this case the host ant *Labidus praedator*), and less frequently with a much smaller range of species from other categories. Evolution of this symbiotic lifestyle is coupled to loss of the visual system. In (a) and (b), sizes of colored boxes correspond to the relative diversity and frequency of heterospecific encounters of each category for the two beetles. Pie charts symbolize the sensory modalities used by each beetle species.

of how changes in valence may be mediated evolutionarily comes from examination of courtship and mating behavior in *Drosophila* species. Studying the reproductive barrier between *Drosophila melanogaster* and *Drosophila simulans*, Seeholzer *et al.* identified a shift in the balance between excitation and inhibition relayed from conserved pheromone-sensitive sensory neurons onto a key node within courtship-promoting central circuitry, the P1 cells [8••]. Because of this shift, *D. simulans* exhibit aversion to *D. melanogaster* mating pheromone, thereby safeguarding against mating with heterospecifics. The P1 cells form a bottleneck, integrating inputs from multiple sensory pathways and propagating them to a range of cell types [65,66]. We hypothesize that analogous flexible nodes may be a hot spot for sensorimotor circuit changes that underlie interspecies interactions.

How underlying genetic changes impact the operation of such nodes is unknown. Although circuit remodeling may be responsible, mechanisms with a simpler underlying genetic architecture may account for how changes in valence can originate readily and spread within populations. One possibility is via changes in neuromodulation. Altered production of biogenic amines and their receptors is a known mechanism for synaptic re-weighting or gain modulation of neural activity. Neuromodulation can cause broad, distributed effects on entire sensorimotor pathways without structural circuit changes, and has been proposed as a mechanism conferring both plasticity and evolvability on sensorimotor circuits in a variety of animals, including insects [67–69]. Neuromodulators can reversibly tune neuronal excitability or strength to select between different functional circuit states [70]. For instance, internal state changes such as hunger or developmental changes in odor preference are mediated by neuromodulatory neurons that act on the sensory periphery and local neurons in the brain [71–73]. Because they often act in a distributed manner, receiving converging inputs and modulating output globally to multiple layers within sensorimotor circuits, neuromodulatory neurons may be strong targets for evolutionary modification. Moreover, multiple molecular mechanisms are known that enable neuromodulators to easily switch valence [71,74,75]. These features of neuromodulatory neurons imply that perhaps few genetic changes may be needed to modify their activity and elicit ecologically relevant changes in behavior.

It is also telling that host neuromodulatory systems are commonly targeted by symbiotic species. In the lycaenid butterfly, *Narathura japonica*, caterpillars secrete honeydew that leads to a reduction in dopamine levels in brains of attendant ants, restricting the ants' ability to move away from the caterpillar and leave it unprotected [76]. In parasitized *Manduca sexta*, the host brain undergoes changes in biogenic amines and the accumulation of neuropeptides, such as octopamine [77], while the emerald jewel wasp, *Ampulex compressa*, uses a venom of neuropeptides and neuromodulators that act within a central region of the cockroach brain to alter locomotory behavior [78•,79]. If neuromodulation is a common means of altering host behavior, it follows that evolutionary changes in neuromodulation may underlie the emergence of novel behaviors in the symbionts themselves, hence being causal in the emergence of novel interactions. Some neuromodulatory mechanisms confer behavioral plasticity, enabling valence to change within an individual's lifetime [80–82]. We speculate that these systems could be targets for evolutionary modification, the altered valence becoming canalized via genetic assimilation [83].

Cause and consequence in specialization

Following the establishment of a nascent interaction, subsequent nervous system modifications arise as species embark on the path of specialization. Intuitively, these could include peripheral changes in receptor and sensory neuron responsiveness to heterospecific cues; central brain modifications that heighten multisensory perception of and valence towards partner species; and the evolution of motor sequences that structure the kinematics of the interaction. The converse is also true, however, that the evolutionary process of specialization itself has ramifications for nervous system evolution. The range of potential species with which a specialist interacts is often smaller than that of a generalist (Figure 3a,b). This contraction in the diversity of encounters entails a weakening of selection on parts of sensorimotor circuits that enable generalist lifestyles. Specialization on another species may also involve building upon, or recalibrating, such ancestral circuits. By either means—circuit degeneration or modification—novel interactions may evolve at the expense of generalist behaviors, eventually rendering the interaction obligate. A corollary of our supposition above, that generalists employ broad-spectrum heuristic filtering of heterospecific cues, is that this ability can become diminished—perhaps ultimately forsaken—in specialists with highly constrained interactions. To our knowledge, such a tradeoff between specialist and generalist behaviors has not been investigated, nor has how it may stem from constraints within sensorimotor pathways for heterospecific cue processing.

There is potential for reciprocal reinforcement between evolution at the nervous system and behavioral levels, as modifications to the nervous system enable changes in ecology that in turn alter the selective environment acting on the nervous system. In such a scenario, the evolutionary trajectory may head irreversibly towards greater specialization ['runaway specialization', 84]. The consequences of departing a generalist, free-living lifestyle are perhaps most blatant in the reductive neural modifications exhibited by highly specialized insect symbionts. For instance, socially parasitic slave-making ants, which outsource brood care and foraging to host ants of other species, have lost approximately half of their gustatory receptors, and also display dramatic losses of olfactory receptors (ORs) [85••,86••], including 9-exon ORs thought to be critical for CHC-mediated interactions underlying eusociality [87]. Convergent losses of the same chemoreceptor orthologs in independent slave-making lineages implies that some of these losses may be adaptive. The convergent loss of eyes across lineages of myrmecophile rove beetles provides another striking example. Our own study of eyeless members of the rove beetle tribe Mimecitini (Figure 3b), associated with Neotropical *Labidus* army ants [49,88], has found that eye loss is correlated with a genomic absence of opsins, as well as losses of several other loci encoding visual system components (Kitchen, Yang and Parker, unpublished). Given that vision is likely of limited use to these nocturnal, subterranean symbionts, which are closely tied to a host ant that is itself blind, eye loss may be adaptive simply by virtue of the energetic cost of building eyes. Loss of visual input may, however, be even more beneficial in enhancing the reliance on other sensory modalities such as chemosensation and touch, which are vital for locating host workers with which these beetles interact constantly and intimately. The heightened valence of socially parasitic ants and myrmecophiles towards their hosts may thus arise not solely via strengthening of sensory inputs that transduce host stimuli, but also via the shedding of competing sensory inputs that have become ecologically obsolete.

We urge hesitancy, however, in interpreting the behavioral-level and circuit-level peculiarities of extreme specialists as unambiguous adaptive innovations. Coupled to specialization are changes in ecology that may restrict population size, with potential consequences for the nervous system. Specialists that are tied to single hosts, such as many obligate social parasites, endoparasites and ectoparasites, and parasitoids, are often amongst the rarest insects, seemingly naturally scarce with small effective population sizes [89–93]. The loss of flight in mimecitine rove beetles for example, combined with their obligate dependence on nomadic host colonies that reproduce by colony fission [94], implies that these beetles are vertically rather than horizontally transmitted between host colonies. In lineages such as these, which propagate as miniscule populations, pervasive genetic drift renders it plausible that some deleterious genetic changes could become fixed, potentially impacting nervous system function in non-adaptive ways [95]. Disentangling the population genetic forces that reconfigured the nervous systems of specialist taxa is therefore an additional challenge we foresee.

Outlook

Navigating interactions with other species is central to a metazoan existence. Yet, how the brains of insects and other animals perform this task remains largely mysterious. We have identified key unsolved problems, including how the brain classifies the diversity of species in the environment, assigns valence, and balances internal states relevant to other species. A mechanistic understanding of these phenomena will help uncover how evolutionary changes within sensorimotor pathways lead to nascent interactions and underlie subsequent specialization on other species. We suggest that a comparative approach—drawing inferences from taxa with specialized interactions and their closely related generalist relatives—offers a powerful way to uncover both the neurobiological mechanisms and evolution of species interactions [96].

Conflict of interest statement

Nothing declared.

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