Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

The self as part of the sensory ecology: how behavior affects sensation from the inside out

Kevin C Daly and Andrew Dacks

Insects exhibit remarkable sensory and motor capabilities to successfully navigate their environment. As insects move, they activate sensory afferents. Hence, insects are inextricably part of their sensory ecology. Insects must correctly attribute self- versus external sources of sensory activation to make adaptive behavioral choices. This is achieved via corollary discharge circuits (CDCs), motor-to-sensory neuronal pathways providing predictive motor signals to sensory networks to coordinate sensory processing within the context of ongoing behavior. While CDCs provide predictive motor signals, their underlying mechanisms of action and functional consequences are diverse. Here, we describe inferred CDCs and identified corollary discharge interneurons (CDIs) in insects, highlighting their anatomical commonalities and our limited understanding of their synaptic integration into the nervous system. By using connectomics information, we demonstrate that the complexity with which identified CDIs integrate into the central nervous system (CNS) can be revealed.

Address
West Virginia University, Morgantown, WV, USA

Corresponding author: Daly, Kevin C (KCDaly@mail.wvu.edu)

Current Opinion in Insect Science 2023, **58**:101053

This review comes from a themed issue on **Behavioural ecology**

Edited by **Natalie Hempel de Ibarra** and **Julie Mustard**

Available online xxxx

https://doi.org/10.1016/j.cois.2023.101053

2214–5745/Published by Elsevier Inc.

Introduction

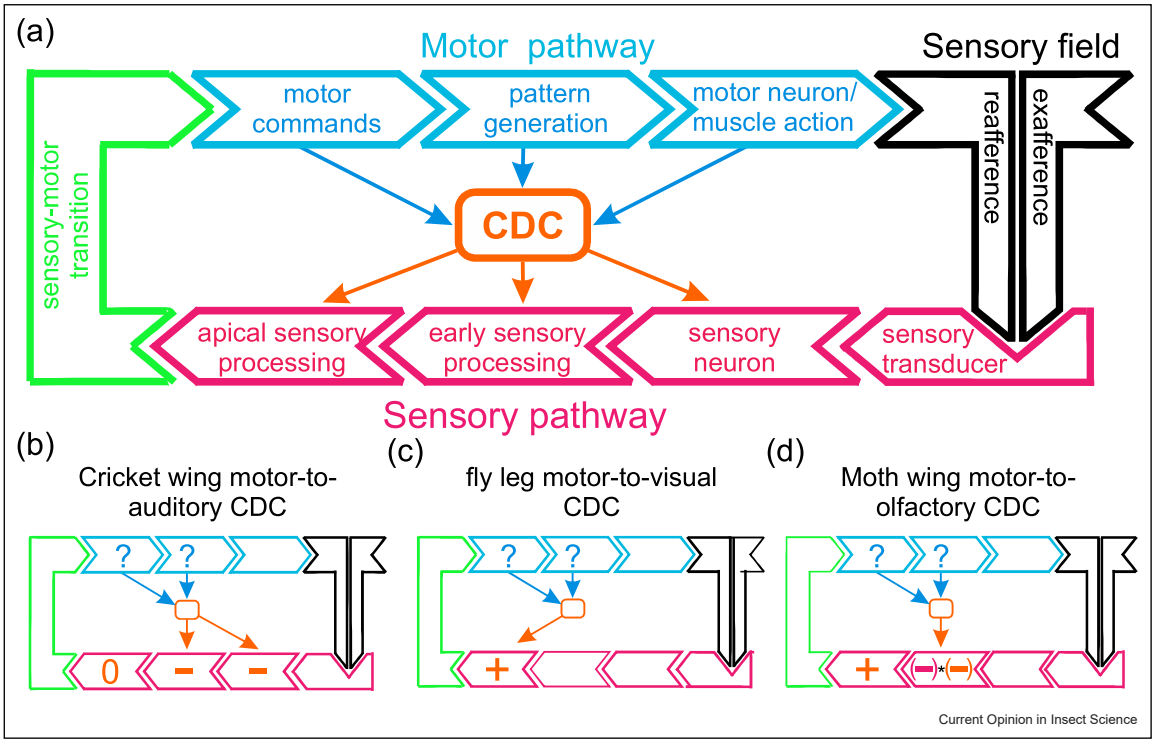
Animals including insects create elaborate and choreographed patterns of behavior. Consider the courtship behaviors of silkworm moths [1,2], pheromone plume-tracking in flighted insects [3,4], prey capture in dragon flies [5] and predator escape responses in fruit flies [6,7], or flight stabilization in bees [8]. All these behaviors require coordination of several muscle groups spanning the limbs, neck, and body. As behavior progresses, sensory systems must maintain active and accurate sensory processing to allow for modification of behavior based on existing goals and updated sensory information. However, all behaving animals are inextricably a part of their own sensory ecology. That is, as behaviors are committed, they necessarily activate sensory neurons, this is the effect of reafference. For example, visual saccades, rapid counterturning behavior in flying flies [9,10], create a behavior-induced panning visual scene that is similar to what is experienced by a gust of wind that pushes the fly about its horizontal axis. Sensory reafference was first described by von Holst and Mittelstaedt more than 70 years ago [11]. Reafference arises because motor acts activate sensory neurons, but they alone are unable to disambiguate the source of their activation, rather, they provide stimulus magnitude and timing information. Without intervention, sensory networks cannot attribute incoming signals to external sources such as wind gusts (exafference) or intentional saccades (reafference).

Reafference is accounted for in the nervous system through a broad class of neural circuits referred to as corollary discharge circuits (CDCs, Box 1). There are several excellent reviews of CDCs across broad taxa that highlight their universality and the diversity of their functional mechanisms of action [12–14]. We build on these discussions by exploring CDCs in insects, with examples that highlight how insect behaviors contribute to their own sensory ecology and how CDCs impact sensory function. All CDCs can be structurally and functionally defined as a neuron or neurons with dendritic processes in motor control networks that project to sensory and/or other motor networks to provide a predictive motor signal [13,15]. This internal representation of the motor plan, which CDCs provide, can function in a broad variety of ways to inhibit, excite, or otherwise modulate their downstream targets. Physiologically, the CDC must be reliably active in advance of and/or during implementation of the motor plan, which drives both behavior and reafference. That is, the activity of the CDC must faithfully correlate to motor output to be exploited downstream.

Inferred presence of corollary discharge circuits

The consequences of activating CDCs are often observed in behavioral assays, and/or, in physiological responses of neurons within sensory or motor pathways downstream of the CDC that reliably correlate to behavior. However, the neurons providing the CD signal

Box 1



Schematic representation of how CDCs are situated in the nervous system to shuttle information from motor pathways to sensory pathways. **(a)** As descending motor commands from the brain are patterned and implemented as muscle contractions (cyan), this drives changes in the sensory field (black), which are detected by sensory transduction mechanisms that convert physical energy from the environment into neural signals. Both reafferent and exafferent sensory information are passed through the sensory pathway (magenta), so to account for this, the CNS relies upon CDC interneuron/s, which receive signals from the motor pathway (orange). These motor signals correlate in some way to the motor action and are forwarded to affected sensory pathways. This information is used by the sensory pathway to modify sensory processing in one of several ways **(b–d)**. Note: all sensory-to-motor transitions are collectively represented (green). In insects, there are currently three identified CDC substrates, each represented by neuron pairs. **(b)** In the cricket, wing motor information arises from the VNC during stridulation (singing), which suppresses auditory afferents and second-order neurons within the VNC, resulting in no reafference arriving to auditory centers in the brain. **(c)** In the fruit fly, information about walking stride is received by a pair of ascending neurons in the VNC that forward walking information from the leg neuropil to higher-order visual processing neurons in the brain, which detect wide-field visual motion across the retina in the horizontal plane. In this case, the CDC neurons positively summate with walking-induced visual flow from the eye. **(d)** In the moth, information about wing beating during flight is forwarded from the VNC to the AL in the brain where they inhibit inhibitory local interneurons resulting in a net disinhibition of the AL network. In all three cases, the cellular basis for activation of the CDC interneurons remains unknown, however, EM-based CNS volume reconstructions promise to facilitate the identification of both up- and downstream synaptic targets of these CDCs.

are not always evident. For example, the cricket cercal sensory system consists of hundreds of wind-sensitive mechanosensory sensilla located on the cerci [16]. The cercal system detects airflow disturbances associated with approaching predators. When the sensory cells are activated, this drives reflexive escape behaviors [17] mediated by excitation of the bilaterally paired median giant interneuron (MGI) escape circuit [16,18,19]. However, male crickets also stridulate their wings (i.e. scissor) to produce acoustic communications for conspecifics to attract female mates and discourage male competitors. Stridulation displaces air proximal to the cerci and this drives responses in individual cercal sensory cells [20]. However, the male cricket's escape behaviors are not triggered by cercal sensory activation in this motor context, suggesting active mechanisms that help it discern airflow induced by predators versus his singing. Physiological recordings of MGI demonstrate that they are actively inhibited during fictive stridulation [20]. While the neurons representing the CDC substrate have not been identified, physiological results establish their presence and that they provide postsynaptic inhibition in MGI only during stridulation and not when the cricket is quiet.

Another example of an inferred CDC is found in the visual system of *Drosophila*. Flies experience rapid horizontal panning of the visual scene across their visual field when their flight path is disturbed by wind. This rapid visual panning drives a corrective optomotor

response to maintain visual stability in turbulence. However, flies also perform body saccades, an inflight behavior where the direction of flight is rapidly altered in the horizontal plane. This too causes a rapid horizontal panning of the visual scene across the fly's visual field, yet flies do not elicit a corrective optomotor response to spontaneous intentional saccades. By independently controlling the visual scene of the fly during actual body saccade behavior in restrained flies, Heisenberg and Wolf [9] demonstrated that optomotor responses to behaviorally induced visual panning must be suppressed, implying the presence of a CDC. Physiological evidence for suppression of visual responses to body saccade-induced optic flow has been observed in horizontal system (HS) cells [21]. HS cells are a subset of motion-sensitive lobula plate tangential cells, part of the visual flow processing system of the fly brain. When the nonspiking HS cells depolarize, they drive the optomotor response. However, HS cells are actively suppressed during both spontaneous body saccades [21,22] and saccades induced by a visual looming stimulus [23]. Thus, the visual system responds to a panning visual scene appropriately by driving an optomotor response when hit by a gust of wind but not when induced by reafference. Thus, while the CDC substrate has yet to be identified, the physiological and behavioral evidence implies a CDC that compensates for the induction of reafference by the fly's own behavior.

Anatomically identified corollary discharge interneurons

While the above examples infer the presence of a CDC, the underlying neuron or neurons providing the pathway for predictive motor signals have not been identified. Thus, determining how the circuit functions mechanistically is challenging. However, there are at least three examples in insects where corollary discharge interneurons (CDIs) have been identified and interrogated physiologically and/or behaviorally to gain a deeper cellular-level understanding of the mechanisms by which they modify sensory function and behavioral performance. Common to all are that the CD signal is carried by single bilateral pairs of identified CDIs [15]. Furthermore, all are ascending neurons originating within the ventral nerve cord (VNC), where they receive motor command information, and project it to sensory-processing neuropil in the VNC and/or brain. However, CDIs differ in their morphology, mechanisms of action, and functional consequences on sensory-motor coordination.

For example, crickets have ears located on the posterior side of the forelegs [24], which are tuned to transduce acoustic signals of conspecifics, and the neural circuitry for species-specific song recognition is well characterized [25]. Stridulation produces ~100-db reafferent acoustic signals to the ears, which could potentially desensitize the auditory pathway [15], or be misinterpreted by the singer as another nearby male. In either case, it is important for male crickets to disambiguate acoustic reafference within the auditory pathway. The neural circuitry underlying recognition of conspecific song, lacks a mechanism for disambiguating reafference from exafference [25], however, the auditory signals driven by stridulation-induced reafference specifically, are actively blocked [26]. This is accomplished by a bilateral pair of CDIs, which receive input from wing motor control centers of the mesothoracic neuromere, and reliably produce bursts of action potentials in precise temporal lockstep with stridulation behavior. The cricket CDIs ascend to the auditory pathway in the prothoracic neuromere of the VNC, where they provide presynaptic afferent depolarizing inhibition, which attenuates incoming auditory signaling by sensory afferents, and by directly inhibiting Omega neurons, which represent the first synaptic relay for auditory processing [15]. However, while CDIs clearly filter acoustic reafference attributable to stridulation early in auditory processing, they do not provide inhibition to the MGI escape circuit (described above) [20]. While the CDI neurons are identified, their overall morphology suggests that they likely receive more than wing motor information and affect more than auditory processing. That is, in addition to wing motor and auditory processing centers of the VNC, CDIs also project throughout the central nervous system (CNS), from the terminal abdominal ganglia, up to the brain [15]. The CDIs may integrate information about a variety of behaviors that also produce auditory reafference, or they may target sensorimotor networks that process auditory information in other contexts, but it is known that CDI is not the source of the inhibition of MGI [20]. Thus, as with visually guided flight in *Drosophila*, the CDIs cancel reafference before processing. However, without a comprehensive understanding of the connectivity of the CDIs, the totality of their function remains unclear.

As with visually guided flight, flies experience walking-dependent visual flow, which covaries with the fly's stride. Visual flow indicating a drifting trajectory during high-speed walking also depolarizes HS cells [27,28]. During walking, HS cells encode the fly's angular and forward velocities by integrating independent internal motor-related signals with incoming visual stimuli. These internal representations are predictive motor signals since they are present in the HS cells even in genetically blind flies or in no-light walking conditions and correlate to stride [27,29]. Targeted optogenetic activation of the left- or right-side HS cells causes

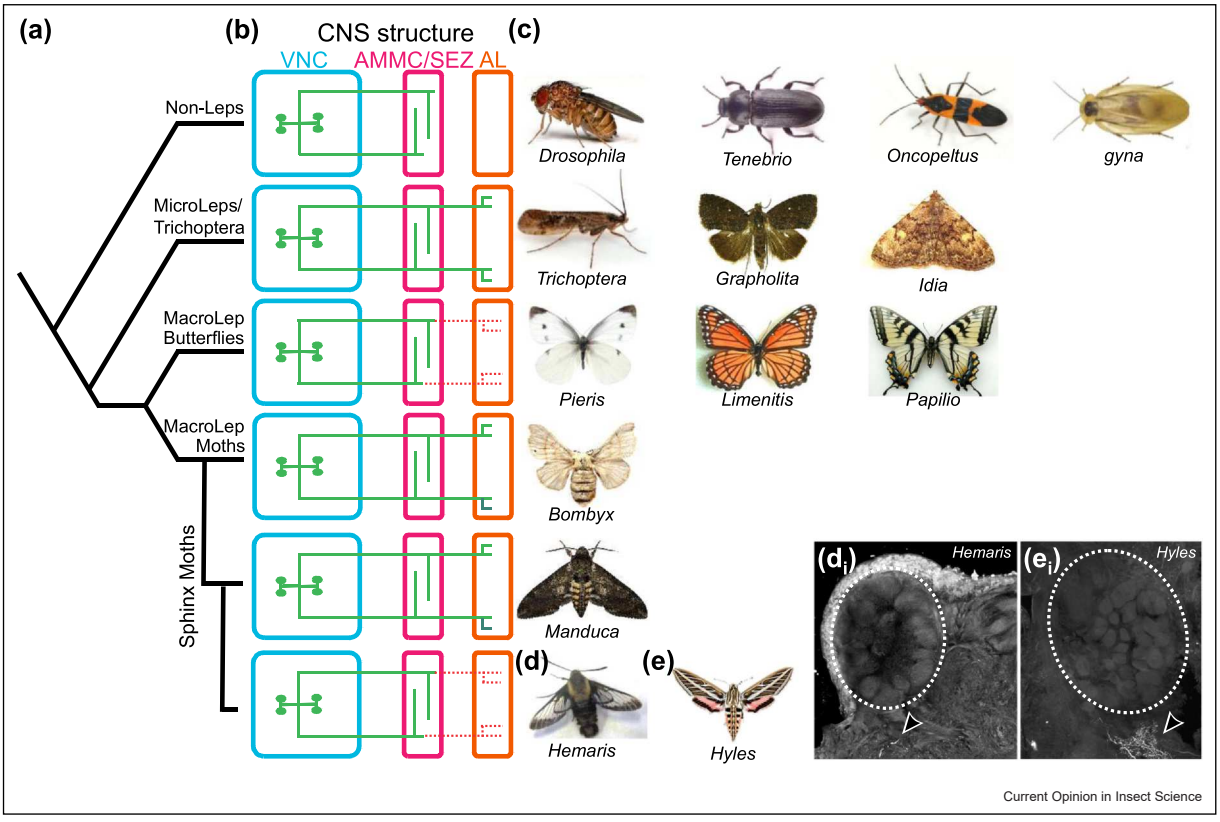
reflexive ipsilateral turning responses. Importantly, the HS cells integrate both a hyperpolarizing-predictive motor signal and walking-induced depolarization caused by visual flow information from the eye. These predictive motor signals are phase-locked with the fly's stride. At least one identified ascending neuron, LAL-PS-AN$_{contra}$, receives input from the front and middle leg neuropils within the VNC and projects contralaterally to the posterior slope of the brain [30], where the HS cells also project [27]. While LAL-PS-AN$_{contra}$ do not directly synapse upon HS cells, they nevertheless provide a predictive motor signal because optogenetic activation of LAL-PS-ANs$_{contra}$ depolarizes HS cells [27]. However, while the inactivation of the LAL-PS-AN$_{contra}$ reduced HS cell response, they did not significantly affect behavior, suggesting LAL-PS-AN$_{contra}$ is one of multiple CDC pathways forwarding motor context information.

Insect wing beating during flight can generate an oscillating inflow of air over the antennae that structures olfactory input [31–36]. Wing beat-induced oscillating airflows are necessary for odor plume-tracking [2] and periodically enhance odor penetration through the brush-like sensilla of the antennae [32]. Wing beating generally drives oscillating forces that act upon the antennae [37], causing both olfactory and mechanosensory-mediated reafference. In the hawkmoth *Manduca sexta*, odors pulsed to simulate wing beating are more easily detected [38] and produce more distinctive neural representations in the antennal lobe (AL) [39]. Principal output neurons (PNs) of the AL faithfully entrain to odor stimulus pulse trains to ~30 Hz, *Manduca*'s maximum wing beat frequency [35,40]. Their ALs each contain ~230 primarily GABAergic local interneurons (LNs, [41]). Broad pharmacological disruption of Gamma-aminobutyric acid (GABA) receptor function within the AL of *Manduca* abolishes the ability of PNs to represent the stimulus temporal structure of olfactory stimuli, indicating that GABA mediates this ability [40,42,43]. However, if the neck connective of Manduca is severed, PN's maximum entrainment drops to ~10 Hz [42,44], implying that ascending neurons from the VNC modulate the ability of PNs to represent the temporal structure of olfactory stimuli. Among neurons within the neck connective in *Manduca* are two pairs of ascending histamine-immunoreactive neurons (AHNs), which originate in the VNC and project to several brain neuropils including the AL [45,46]. Somata from one pair reside within the mesothoracic neuromere (MsAHNs), the other within the metathoracic neuromere (MtAHNs). Only the MsAHNs project to the AL and are the sole source of histamine therein. Severing the neck connective to axotomize the MsAHNs or pharmacological blockade of histamine receptors lowers the ability of AL PNs to track the temporal patterning of olfactory stimuli, whereas histamine receptor activation enhances this ability. Within the AL, 16 LNs express the histamine-gated ionotropic Cl^- channel HisCl1 [47], and project throughout all AL glomeruli [45], implying that suppression of this select group of LNs enhances the temporal fidelity with which the AL network tracks odor stimuli. Simultaneous recording from individual MsAHNs and a wing motor nerve, indicates that MsAHNs increase spiking rate with wing motor output [48] and hence reflect the wing motor state of the moth. As the moth flies, the MsAHNs polysynaptically enhance the ability of PNs to accurately represent the stimulus temporal structure. Thus, the MsAHNs do not filter or gate reafference, rather, they modulate the AL function in a way, which enhances behavioral measures of sensory acuity.

Importantly, AHNs have homologs in all insects thus far studied, suggesting an ancient origin. However, the sensory networks innervated by the AHNs differ based on ecological need [48] (Figure 1). For example, although MsAHN homologs innervate the ALs of caddisflies, silkworm moths, and nocturnal moths, they do not enter the ALs of other insects, including butterflies and other sphinx moths that are closely related to *Manduca* but are day-flying. This implies that the reliance on the olfactory system at night, for finding mates and food, has driven co-option of the MsAHN into an olfactory role, that was subsequently lost among diurnal moths and butterflies [49].

The AHN homologs innervate a variety of sensory structures within the brain, and several VNC neuropils. Thus, like the cricket CDI, AHN morphology suggests a more diverse and complex functional role in sensory-motor coordination [50]. One major gap in understanding of CDC function more broadly is the dearth of information about how CDIs, such as the three described herein, integrate wholistically throughout the CNS in terms of the information they receive and the downstream synaptic targets to which they forward this information. Electron microscopy (EM) volume reconstructions of the brain [51,52] and VNC [53] of *Drosophila melanogaster*, provide a unique and unbiased opportunity to identify and near-comprehensively map the connectivity of individual neurons of interest, to better understand the nature of their integration into the CNS. Connectomics analysis of the AHN homologs in *Drosophila* reveals that AHNs do in fact receive wing motor command signals from the brain and target this information to several sensory and motor networks throughout the CNS. Figure 2 displays the left MsAHN from the female adult nerve cord (FANC) EM volume, which is available to the scientific community [53]. The left MsAHN from this volume is displayed as an

Figure 1

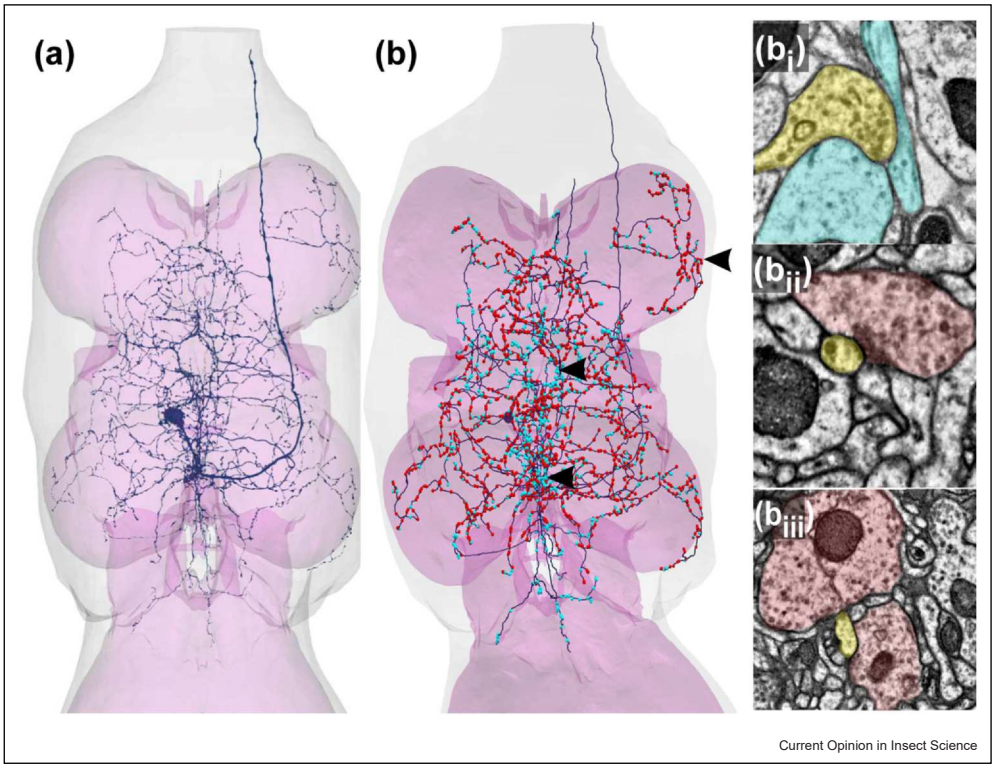


The differential co-option of AHNs to serve an olfactory function across insects. **(a)** Schematic representation of the evolutionary history of the AHNs. **(b)** Diagram of a generic insect CNS highlighting the major regions that the two pairs of AHNs (green) project. Red lines indicate presumed loss of AHNs to that region. **(c)** Individual insect species for which we evaluated histamine distribution in the CNS. Here, we show that the AHNs project into the subesophageal zone (SEZ) and antennal mechanosensory and motor area (AMMC) of all insects previously investigated [49]. **(d,e)** Two previously unreported sphinx moths, **(d)** the clear winged hummingbird moth *Hemaris* sp., and **(e)** the white-lined sphinx moth *Hyles* sp. Histamine immunolabeling for *Hemaris* (d_i) adapted from Ref. [58], and *Hyles* (e_i) indicates positive labeling for histamine (arrowheads) but no labeling in the AL (inset dashed ovals); protocols were the same as in Ref. [49]. In the last common ancestor of the Lepidoptera and Trichoptera, the AHNs were co-opted to innervate the ALs and serve an olfactory function. The innervation of the ALs was subsequently lost in butterflies and in the diurnal moths, but maintained in the night-flying, plume-tracking macrolepidopteran moth *Manduca*. *Copyright permissions for insect images pending.*

autosegmented subvolume (Figure 2a) and as a manually traced skeleton with coordinates of all observed pre- and postsynaptic surfaces (Figure 2b). By back-tracing from the AHNs, their synaptic partners can be identified, this represents a launch point for subsequent functional studies of their relationships. Publicly available tools that match morphologies across EM and light microscopy datasets, facilitate identification of driver lines [54–57], which can then be used in molecular genetic, physiological, and behavioral studies of their cellular mechanisms of function.

Connectomics holds the promise of providing a more comprehensive perspective of the structure of CDIs, leading to mechanistic studies of function. Ultimately, the careful study of insect CDIs will likely reveal that they integrate far more information to affect far more sensory and motor networks than previously thought. Furthermore, the FANC EM volume contains hundreds of pairs of ascending neurons from the VNC, which are ideally positioned to serve a CDC function. When considering the body-wide involvement in elaborate behaviors, it is likely that ensembles of these ascending neurons act in concert to create nuanced motor representations based on the specifics of the state of the sensory-motor ecology. Future studies of this ascending neuron population hold the promise of revealing conserved and complex features of network architectures that enable sensory-motor coordination across the nervous system.

Figure 2



EM resolution volume reconstruction of the Drosophila VNC provides an unbiased and near-comprehensive mapping of synaptic partners. **(a)** Three-D volumetric rendering of the VNC (gray) and the VNC neuropil (pink) from FANC [53]. Inset blue neuron is the left MsAHN, identified based on soma position. This neuron was reconstructed using automated approach described in Ref. [59] and then manually edited in neuroglancer (see Ref. [60]) to refine the final reconstruction. **(b)** A skeleton reconstruction of the left MsAHN based on manual reconstruction using CATMAID [61]. Overlaid are 1664 presynaptic (red dots) and 1086 postsynaptic sites (cyan dots) manually identified. Overlaid arrows point to specific synaptic sites. (b_i–b_{iii}) Three examples of presynaptic (red) and postsynaptic (cyan) contacts with the MsAHN (yellow). (b_i: top arrowhead) the MsAHN is presynaptic to two downstream partners (b_{ii}: middle arrowhead) the MsAHN is postsynaptic to an upstream partner. (b_{iii}: bottom arrowhead) MsAHN is postsynaptic to two upstream partners. Synapses identified in the raw EM volume were identified based on the presence of vesicle clouds, T-bars, synaptic cleft, and postsynaptic densities. Note: not all characteristics appear on a given z-plane.

Data Availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Jeffery Riffell for supplying the white-lined sphinx moths, Yasaman Etemadi and Phillip Chapman for conducting immunolabeling protocols shown in Figure 1, Jasper Phelps and Wei-Chung Allen Lee for generous access to the FANC EM volume reconstruction and rendering the image in Figure 2a, and Charlie T. Anderson for reviewing previous versions of this paper. This work was funded by Air Force Office of Scientific Research, USA, FA9550-17-1-0117 and National Science Foundation, USA, 2127379 to KCD and AMD, and a Howard Hughes Medical Institute Janelia Research Campus Visiting Scientist Program project to KCD, AMD, and Gwyneth M. Card.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Schneider D: **Insect antennae**. *Annu Rev Entomol* 1964, **9**:103-122.
2. Obara Y: **Bombyx mori mating dance: an essential in locating the female**. *Appl Entomol Zool* 1979, **14**:130-132.
3. Willis MA, Baker TC: **Effects of intermittent and continuous pheromone stimulation on the flight behavior of the oriental fruit moth, *Grapholita molesta***. *Physiol Entomol* 1984, **9**:341-358.
4. Baker TC, Willis MA, Phelan PL: **Optomotor anemotaxis polarizes self-steered zigzagging in flying moths**. *Physiol Entomol* 1984, **9**:365-376.
5. Olberg RM, Worthington AH, Venator KR: **Prey pursuit and interception in dragonflies**. *J Comp Physiol A* 2000, **186**:155-162.
6. Card GM: **Escape behaviors in insects**. *Curr Opin Neurobiol* 2012, **22**:180-186.
7. Card G, Dickinson M: **Performance trade-offs in the flight initiation of Drosophila**. *J Exp Biol* 2008, **211**:341-353.

8. Combes SA, Dudley R: **Turbulence-driven instabilities limit insect flight performance**. *Proc Natl Acad Sci* 2009, **106**:9105-9108.

9. Heisenberg M, Wolf R: **On the fine structure of yaw torque in visual flight orientation of *Drosophila melanogaster***. *J Comp Physiol* 1979, **130**:113-130.

10. Collett TS, Land MF: **Visual control of flight behaviour in the hoverfly *Syritta pipiens* L**. *J Comp Physiol* 1975, **99**:1-66.

11. von Holst E, Mittelstaedt H: **The principle of reafference: interactions between the central nervous system and the peripheral organs**. *Percept Process: Stimul Equiv Pattern Recognit* 1971, **37**:41-72.

12. Crapse TB, Sommer MA: **Corollary discharge across the animal kingdom**. *Nat Rev Neurosci* 2008, **9**:587-600.

13. Straka H, Simmers J, Chagnaud BP: **A new perspective on predictive motor signaling**. *Curr Biol* 2018, **28**:R232-R243.

14. Poulet JF, Hedwig B: **New insights into corollary discharges mediated by identified neural pathways**. *Trends Neurosci* 2007, **30**:14-21.

15. Poulet JF, Hedwig B: **The cellular basis of a corollary discharge**. *Science* 2006, **311**:518-522.

16. Edwards JS, Palka J: **The cerci and abdominal giant fibres of the house cricket, *Acheta domesticus*. I. Anatomy and physiology of normal adults**. *Proc R Soc Lond B Biol Sci* 1974, **185**:83-103.

17. Tauber E, Camhi J: **The wind-evoked escape behavior of the cricket *Gryllus bimaculatus*: integration of behavioral elements**. *J Exp Biol* 1995, **198**:1895-1907.

18. Miller JP, Jacobs GA, Theunissen FE: **Representation of sensory information in the cricket cercal sensory system. I. Response properties of the primary interneurons**. *J Neurophysiol* 1991, **66**:1680-1689.

19. Bodnar DA, Miller JP, Jacobs GA: **Anatomy and physiology of identified wind-sensitive local interneurons in the cricket cercal sensory system**. *J Comp Physiol A* 1991, **168**:553-564.

20. Schoneich S, Hedwig B: **Corollary discharge inhibition of wind-sensitive cercal giant interneurons in the singing field cricket**. *J Neurophysiol* 2015, **113**:390-399.

21. Kim AJ, Fitzgerald JK, Maimon G: **Cellular evidence for efference copy in Drosophila visuomotor processing**. *Nat Neurosci* 2015, **18**:1247-1255.

22. Kim AJ, *et al.*: **Quantitative predictions orchestrate visual signaling in Drosophila**. *Cell* 2017, **168**:280-294 e12.

23. •• Fenk LM, Kim AJ, Maimon G: **Suppression of motion vision during course-changing, but not course-stabilizing, navigational turns**. *Curr Biol* 2021, **31**:4608-4619 e3.

This study makes exquisite patch recordings of a subset of lobular plate tangential cells that detect visual flow in the horizontal (yaw) plane of the fly body axis. These recordings were performed while the tethered fruit flies make inflight turns under conditions: spontaneous turns, turns in response to visual looming stimuli, and counterturns to stabilize flight trajectory in response to wind gust stimuli. Using this approach, they demonstrate that these neurons are suppressed (i.e. do not induce a turning behavior) during looming stimuli and spontaneous turns but not in response to course corrections such as those induced by visual scene rotations induced by wind gusts.

24. Larsen ON, Michelsen A: **Biophysics of the ensiferan ear**. *J Comp Physiol* 1978, **123**:217-227.

25. Schoneich S, Kostarakos K, Hedwig B: **An auditory feature detection circuit for sound pattern recognition**. *Sci Adv* 2015, **1**:e1500325.

26. Poulet JFA, Hedwig B: **A corollary discharge maintains auditory sensitivity during sound production**. *Nature* 2002, **418**:872-876.

27. •• Fujiwara T, Brotas M, Chiappe ME: **Walking strides direct rapid and flexible recruitment of visual circuits for course control in Drosophila**. *Neuron* 2022, **110**:2124-2138 e8.

This study also investigates the role of the lobular plate tangential cells in steering, in this case, during walking. Here, the authors exploit patch-clamp recordings of these cells to show that they are coupled to walking strides. They show that a single pair of ascending neurons from the VNC carry information from the fore and middle leg neuropil on the contralateral side of the VNC to at least one intermediary neuron (that remains unidentified), which synapses on the lobular plate tangential cells. Unlike steering in flight, these neurons depolarize the contralateral visual system, in essence, providing confirming the visual flow during walking and does so across multiple timescales.

28. Chiappe ME, *et al.*: **Walking modulates speed sensitivity in Drosophila motion vision**. *Curr Biol* 2010, **20**:1470-1475.

29. Fujiwara T, *et al.*: **A faithful internal representation of walking movements in the Drosophila visual system**. *Nat Neurosci* 2017, **20**:72-81.

30. Ito K, *et al.*: **A systematic nomenclature for the insect brain**. *Neuron* 2014, **81**:755-765.

31. Koehl MAR: **The fluid mechanics of arthropod sniffing in turbulent odor plumes**. *Chem Senses* 2006, **31**:93-105.

32. Loudon C, Koehl MAR: **Sniffing by a silkworm moth: wing fanning enhances air penetration through and pheromone interception by antennae**. *J Exp Biol* 2000, **203**:2977-2990.

33. Li C, Dong H, Zhao K: **A balance between aerodynamic and olfactory performance during flight in Drosophila**. *Nat Commun* 2018, **9**:3215.

34. Li CY, Dong HB, Zhao K: **A balance between aerodynamic and olfactory performance during flight in Drosophila**. *Nat Commun* 2018, **9**:1-8.

35. Sane SP, Jacobson NP: **Induced airflow in flying insects II. Measurement of induced flow**. *J Exp Biol* 2006, **209**:43-56.

36. Sane SP: **Induced airflow in flying insects I. A theoretical model of the induced flow**. *J Exp Biol* 2006, **209**:32-42.

37. Sane SP, *et al.*: **Antennal mechanosensors mediate flight control in moths**. *Science* 2007, **315**:863-866.

38. Daly KC, *et al.*: **Odor detection in *Manduca sexta* is optimized when odor stimuli are pulsed at a frequency matching the wing beat during flight**. *PLoS One* 2013, **8**:e81863.

39. Houot B, *et al.*: **Antennal lobe representations are optimized when olfactory stimuli are periodically structured to simulate natural wing beat effects**. *Front Cell Neurosci* 2014, **8**:159.

40. Tripathy SJ, *et al.*: **Odors pulsed at wing beat frequencies are tracked by primary olfactory networks and enhance odor detection**. *Front Cell Neurosci* 2010, **4**:1.

41. Hoskins SG, *et al.*: **Immunocytochemistry of GABA in the antennal lobes of the sphinx moth *Manduca sexta***. *Cell Tissue Res* 1986, **244**:243-252.

42. Christensen TA, Waldrop BR, Hildebrand JG: **Multitasking in the olfactory system: context-dependent responses to odors reveal dual GABA-regulated coding mechanisms in single olfactory projection neurons**. *J Neurosci* 1998, **18**:5999-6008.

43. Waldrop B, Christensen TA, Hildebrand JG: **GABA-mediated synaptic inhibition of projection neurons in the antennal lobes of the Sphinx Moth, *Manduca-Sexta***. *J Comp Physiol A-Sens Neural Behav Physiol* 1987, **161**:23-32.

44. Heinbockel T, Christensen TA, Hildebrand JG: **Temporal tuning of odor responses in pheromone-responsive projection neurons in the brain of the sphinx moth *Manduca sexta***. *J Comp Neurol* 1999, **409**:1-12.

45. Bradley SP, *et al.*: **A flight sensory-motor to olfactory processing circuit in the moth *Manduca sexta***. *Front Neural Circuits* 2016, **10**:5.

46. Homberg U, Hildebrand JG: **Histamine-immunoreactive neurons in the midbrain and suboesophageal ganglion of sphinx moth *Manduca sexta***. *J Comp Neurol* 1991, **307**:647-657.

47. Hardie RC: **A histamine-activated chloride channel involved in neurotransmission at a photoreceptor synapse**. *Nature* 1989, **339**:704-706.

48. Chapman PD, *et al*.: **Flight motor networks modulate primary olfactory processing in the moth *Manduca sexta***. *Proc Natl Acad Sci USA* 2018, **115**:5588-5593.
•• This study uses intracellular electrophysiology to establish a correlation between wing motor output and activation of the MsAHNs in the hawkmoth *Manduca sexta*. It further demonstrates that histamine application increases and histamine receptor disruption decreases, the ability of recorded AL PNs to entrain to olfactory stimuli temporally structured to simulate the wing beat effect on airflow over the antennae disruption. Histamine receptor disruption also increases odor detection and discrimination thresholds in behavior pharmacological assays of olfactory sensitivity.

49. Chapman PD, *et al*.: **Co-option of a motor-to-sensory histaminergic circuit correlates with insect flight biomechanics**. *Proc Biol Sci* 2017, **284**:5588-5593.

50. Chapman PD, *et al*.: **Flight motor networks modulate primary olfactory processing in the moth *Manduca sexta***. *Proc Natl Acad Sci USA* 2018, **284**:1-8.

51. Zheng Z, *et al*.: **A complete electron microscopy volume of the brain of adult *Drosophila melanogaster***. *Cell* 2018, **174**:730-743 e22.

52. Scheffer LK, *et al*.: **A connectome and analysis of the adult Drosophila central brain**. *Elife* 2020, **9**:1-83.
• This article presents the 'Hemibrain' database based on a high-resolution (4 × 4 × 4 nm) partial reconstruction of a female adult fly brain. The Hemibrain database is relatively highly annotated and searchable, making it an excellent resource for neuroscientists to understand connectivity of brain neurons contained within that volume.

53. Phelps JS, *et al*.: **Reconstruction of motor control circuits in adult Drosophila using automated transmission electron microscopy**. *Cell* 2021, **184**:759-774 e18..
•• This paper describes the first female adult nerve cord EM reconstruction within the context of describing the motor circuitry of the VNC. What sets these data apart from previous work is the authors provide a crowd source-like effort to build a database of neurons based on both manual and autosegmented reconstructions, including annotation of synapse coordinates. The means to subsequently link these neurons with genetic reagents is also possible.

54. Meissner GW, *et al*.: **A searchable image resource of Drosophila GAL4 driver expression patterns with single neuron resolution**. *Elife* 2022, **12**:1-20 p. 2020.05.29.080473.

55. Meissner GW, *et al*.: **An image resource of subdivided Drosophila GAL4-driver expression patterns for neuron-level searches**. *BioRxiv* 2020, **5**.

56. Otsuna H, Ito M, Kawase T: **Color depth MIP mask search: a new tool to expedite Split-GAL4 creation**. *bioRxiv* (31) 2018, **1**:318006.

57. Clements J, *et al*.: **NeuronBridge: an intuitive web application for neuronal morphology search across large data sets**. *bioRxiv* 2022,1-24 p. 2022.07. 20.500311.
• This article presents a web application called NeuronBridge that allows a fast and easy way of identifying neurons based on morphological matching from large datasets of neurons imaged using primarily light microscopy. What is exciting about this application is that it allows searches through vast libraries of driver lines not only for a cell of interest but also for its synaptic partners. This manifoldly reduces the effort to find genetic reagents for experimental exploration of circuit function.

58. Chapman PD: **A Corrollary Discharge Circuit Modulates Olfactory Function During Flight *in Manduca sexta***. West Virginia University; 2018.

59. Lee K, *et al*.: **Learning and segmenting dense voxel embeddings for 3D neuron reconstruction**. *IEEE Trans Med Imaging* 2021, **40**:3801-3811.

60. Clements J, *et al*.: **NeuronBridge: an intuitive web application for neuronal morphology search across large data sets**. *BioRxiv* 2022,1-24 p. 2020.01. 16.909465.

61. Saalfeld S, *et al*.: **CATMAID: collaborative annotation toolkit for massive amounts of image data**. *Bioinformatics* 2009, **25**:1984-1986.