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### Spatial distribution of campaniform sensilla mechanosensors on wings: form, function, and phylogeny

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Insect wings serve two crucial functions in flight: propulsion and sensing. During flapping flight, complex spatiotemporal patterns of strain on the wing reflect mechanics, kinematics, and external perturbations; sensing wing deformation provides feedback necessary for flight control. Campaniform sensilla distributed across the wing transduce local strain fluctuations into neural signals, so their placement on the wing determines sensory information available to the insect. Thus, understanding the significance of these sensor locations will also reveal how sensing and wing movement are coupled. Here, we identify trends in wing campaniform sensilla placement across flying insects from the literature. We then discuss how these patterns can influence sensory encoding by wing mechanosensors. Finally, we propose combining a comparative approach on model insect clades with computational modeling, leveraging the spectacular natural diversity in wings to uncover biological principles of mechanosensory feedback in flight control.

#### Addresses

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#### Introduction

The locomotor appendages of animals serve as both sensors and propulsors [1,2]. Mechanosensory signals from the limbs provide crucial information about the animal's own motion and the external world, and rapid feedback is critical for robust and flexible locomotor performance [3,4<sup>••</sup>]. In flying insects, complex spatiotemporal patterns of wing strain are shaped by actuation, fluid-structure interactions, body accelerations, external perturbations (e.g. wind, collisions), and several aspects of wing morphology, including size, shape, venation pattern, and material properties. These patterns are detected by a population of strain sensors called *campaniform sensilla* (CS) embedded in the wing's external cuticle, which encode fluctuations in local strain on the wing [2,5,6] (Figure 1a,b). CS at different locations experience unique local strains varying in both space and time, so the spatial distribution of CS directly determines the sensory information available to the organism (Figure 1c).

Flying insects are exceedingly diverse, with shared, convergent, or exceptional performance demands that are reflected in their wing morphologies and life histories. This diversity presents an opportunity to reveal principles of mechanosensory feedback and their role in flight control. Here we describe likely evolutionary patterns in CS placement (Section 'Mechanosensor features and placement in insect wings') and discuss their implications for neural encoding (Section 'Potential impacts of CS placement on neural encoding'). The spatial distribution of wing CS likely reflects a complex set of objectives and competing demands, including non-neural constraints (Section 'Non-neural constraints on sensor placement'). Finally, we suggest that a comparative approach (Section 'Combining comparative methods and computational models'), particularly one grounded explicitly in the phylogenetic patterns of CS placement and integrated tightly with neuromechanical computational models, could drive a new understanding of mechanosensation in flight.

# Mechanosensor features and placement in insect wings

CS detect wing deformation, so we expect sensor placement to vary with interspecific differences in wing anatomy, mechanics, and movement across Insecta. Even so, many features of insect wing morphology are conserved and can be compared across species. Thus, we also expect that CS distribution exhibits general trends, despite interspecific variation. Here we briefly review CS physiology and then review trends in CS distribution across Insecta.





Strain sensors on the wing surface called *campaniform sensilla* (CS) provide crucial information about wing bending for flight control. (a) The insect flight control system consists of the wing structure, actuators at the base of the wing, and mechanosensors (including CS) distributed across the wing. (b) *Left:* Fields of CS on the wing base (highlighted in blue dashed oval and arrows (Images modified from [2]). *Center:* TEM sections of two different morphologies of CS on fly halteres (Images modified from [27]). *Right:* Schematic of a CS (based on [28]). (c) Neural responses depend on interactions between wing morphology & mechanics, motor output, CS placement, and neural encoding properties. Wing morphology, mechanics, and motor trajectories determine wing deformations. Local strain activates individual CS, and the timing of CS activation depends on CS placement on the wing. Wing morphology & mechanics, motor output, sensor placement, and neural properties can be tuned by evolutionary processes.

#### Morphology & response properties

The insect flight system comprises a flexible wing blade that is actuated both indirectly and directly by muscles in the thorax. Sensory feedback is provided by mechanosensors (including but not restricted to CS) distributed across the wing surface (Figure 1a). An individual CS is a mechanosensitive neuron suspended within a cuticular depression under a dome (Figure 1b); because of this structure, local compressive or tensile forces cause the dome to deform and elicit action potentials [7,8]. CS are often clustered in dense, distinct fields on the wings, although they can also be present as individual, isolated sensors. Typically elliptical in shape, many CS are thought to confer directional selectivity as they vary in their orientation relative to the axis of the wing [3,9–16]. However, round CS also exist and are often found as isolated sensors [11,12,14].

The response properties of CS neurons may be slowly adapting, rapidly adapting, or a combination thereof [17–19]. Slowly adapting CS respond throughout the duration of a stimulus, while rapidly adapting CS respond to stimulus onset and/or offset; however, both slowly and rapidly adapting CS respond to periodic stimuli, such as wing flapping, with phase-locked spikes [5,2,18–20] (Figure 1c). Individual CS likely respond at different phases of the wingbeat, and modifications or perturbations to rhythmic flapping motion result in phaseadvanced or phase-delayed responses [20,21°,22°]. In this way, changes in the firing phase of a given CS, or

Trait	Species	Known exceptions
1. CS are found on wing veins.	True for all species examined.	Single CS are also found in the inter-veinal membranes in <i>Melanoplus sanguinipes</i> (Orthoptera) [11] and <i>Periplaneta americana</i> (Blattodea) as referenced by [14]
<ol> <li>Proximal wing CS are concentrated towards the leading edge of the wing.</li> <li>More CS are found on the proximal wing in comparison to the distal wing.</li> </ol>	Melanoplus sanguinipes (hindwing; Orthoptera) [11], Schistocerca gregaria (Orthoptera) [3], Trichogramma minutum (Hymenoptera) [13], Drosophila melanogaster (forewing; Diptera) [12], Calliphora vicina (forewing; Diptera) [14], 150 spp. of flies (haltere; Diptera) [35**], 112 spp. of beetles (Coleoptera) [16], Xenos vesparum (haltere; Strepsiptera) [15], Hemianax papuensis (Odonata) [36], Perithemis tenera (Odonata) [31**]	The forewing of <i>Melanoplus sanguinipes</i> (Orthoptera) [11]
4. Proximal CS are found in groups or fields and are elliptical in shape.	Drosophila melanogaster (Diptera) [12], Calliphora vicina (Diptera) [14], Melanoplus sanguinipes (Orthoptera) [11], Schistocerca gregaria (Orthoptera) [3], Hemianax papuensis (Odonata) [36], Perithemis tenera (Odonata) [31**]	Proximal CS can also occur as single, isolated sensors and be round [12,14,11,69].
5. The forewing contains more CS than the hindwing.	Apis mellifera (Hymenoptera) [39], Blattella germanica (Blattodea) [37], Chorthippus biguttulus (Orthoptera) [38], Manduca sexta (Lepidoptera) [30], Schistocerca gregaria (Orthoptera) [3], Trichogramma minutum (Hymenoptera) [13]	Anabolia laevis (Trichoptera) [42], Aphrophora alni (Hemiptera) [41], Chloroperla tripunctata (Plecoptera) [40], and Panorpa communis (Mecoptera) [45]. Specialized wings: dipteran halteres [14,12], elytra of beetles [32].
6. CS are found on both wing surfaces.	All examined species of Diptera [12,14,35**,43,44], Strepsiptera (haltere) [15], and Odonata [31**,36]. <i>Aphrophora alni</i> (Hemiptera) [41], <i>Apis mellifera</i> (Hymenoptera) [39], <i>Anabolia laevis</i> (Trichoptera) [42], <i>Chloroperla tripunctata</i> (Plecoptera) [40], <i>Manduca sexta</i> (Lepidoptera) [30], <i>Panorpa communis</i> (Mecoptera) [45], <i>Tettigonia cantans</i> (Orthoptera) [46], <i>Acheta domesticus</i> (Orthoptera) [47], <i>Chorthippus biguttulus</i> (Orthoptera) [38].	Schistocerca gregaria (ventral only; Orthoptera) [3], <i>Trichogramma minutum</i> (forewing ventral only; Hymenoptera) [13], <i>Dytiscus marginalis</i> (elytra dorsal only; Coleoptera) [32]
7. CS count is correlated with wing size.	The elytra (forewings) of beetles (Coleoptera) [16]. The halteres of flies (Diptera) [35 <sup>••</sup> ]. 14 spp. of dragonflies & damselflies (Odonata) [31 <sup>••</sup> ].	No correlation between CS count and wing size across species belonging to different orders.

relative phase differences between CS, could be used to encode features of wing deformation, and thus, body and wing dynamics. Because local deformations on the wing vary in both space and time during natural flight, CS placement critically determines the available sensory information. Furthermore, the population of CS samples strain at a limited set of locations on the wing. Even for species with wings that have many CS or a high density of CS, this sampling is mathematically sparse (i.e. far more locations remain unsampled than sampled), and placement is therefore particularly important for determining what subset of the full strain profile is encoded as sensory information [23–26].

### Trends in campaniform sensilla placement across Insecta

Wing morphology has diversified extensively across Insecta, and along with behavior and physiology, has enabled insects to invade a multitude of aeroecological niches. Despite this large interspecific variation, we have identified general trends in CS distribution that may help reveal the principles of mechanosensory feedback for flight control (Table 1). In assembling these trends, we note that they rely on currently reported CS placement in a limited number of species. Given methodological differences between studies, some reported sensor distributions could be biased or incomplete. While future work may strengthen or challenge the trends catalogued here, the following features of CS placement are useful aspects of variation for understanding CS function and motivating functional hypotheses (Section 'Potential impacts of CS placement on neural encoding').

The described trends rely on the following definitions. Historically, clusters of CS have been defined as 'groups' when at least three (3) CS of identical morphology are found within 20 microns of each other and as 'fields' when multiple rows of CS exist within less than a micron of each other [14]. Here, we maintain these definitions of group and field. Further, we define 'proximal' as the most proximal third of the wing blade and 'distal' as the distal two thirds of the wing blade, as this reflects a natural division in sensor placement trends that generally holds true across species. In some cases, we describe CS placement on specialized wings, specifically, the elytra of beetles (hardened forewings that protect the body) and the halteres of Diptera and Strepsiptera (sensory organs that are evolutionarily derived from wings [10]). Unless otherwise noted, trends refer to placement on unspecialized wings.

#### Proximal CS are more abundant than distal CS and are found in groups located on the leading half of the wing

Across catalogued species and wings (both forewings and hindwings) that have CS, the total number of CS located near the proximal wing base is generally greater than the number of CS located distally. Proximal wing CS are typically found in groups or fields [3,12–16,29,35°,36], although some species examined also have a few isolated proximal CS [11,12,14]. CS are reliably found near the wing base on veins towards the leading edge. In both dipteran and strepsipteran halteres, numerous CS are found on the proximal third of the haltere, while none are found distally [15,35°].

One notable exception to these trends across both specialized and nonspecialized wings is the proximal CS arrangement and count on the dorsal forewing of a grasshopper (*Melanoplus sanguinipes*, Orthoptera, Figure 2). The dorsal forewing of *M. sanguinipes* contains more distal CS than proximal CS. The proximal CS are arranged as a small cluster of four CS located towards the trailing edge and a few other isolated CS occur along the wing veins [11].

#### Isolated CS are sparsely distributed across the distal wing

Distal CS typically occur as isolated sensors, distributed across the wing blade. The specific arrangement of isolated CS on the distal regions of a wing varies widely across species. Like proximal CS, distal CS are typically located on wing veins, but they have also been found in the inter-veinal membranes in a grasshopper (*M. sangui-nipes*, Orthoptera) [11] and a cockroach (*Periplaneta amer-icana*, Blattodea) (as referenced by Gnatzy *et al.* [14]). In addition to isolated CS, the distal forewing of *M. sangui-nipes* has several CS in close proximity to each other, especially along the distal trailing edge [11]. No distal CS have been reported in beetle elytra or dipteran or strepsipteran halteres [12, 14–16,35<sup>••</sup>].

### Unspecialized forewings contain more CS than unspecialized hindwings

The forewing generally has a greater number of CS than the hindwing [3,10,13,30,37,38]. For example, the ratio of forewing to hindwing CS is nearly 2 in the western honey bee (*Apis mellifera*, Hymenoptera [39]). However, the ratio is approximately equal in other species (e.g. a stonefly *Chloroperla tripunctata*, Plecoptera [40] and a froghopper *Aphrophora alni*, Hemiptera [41]). The hindwing can also have more CS than the forewing (e.g. the caddisfly *Anaboilia laevis*, Trichoptera [42]). The relative number of sensors on unspecialized forewings and hindwings might be strongly impacted by how ipsilateral wings are actuated. For instance, the dragonfly actuates the ipsilateral wing pair independently, whereas wing pairs of the hawkmoth are physically coupled, and the forewing overlaps with the hindwing to form a single functional surface during flight. In physically coupled wing pairs, the relative number of CS on a given wing may be less important than the overall distribution across the combined wing surface.

In insects where one set of wings has evolved specializations not directly tied to propulsion, the hindwing often has more CS than the forewing. The halteres of flies (Diptera) have nearly double the number of CS as the forewing [12,14]. In beetles (Coleoptera), the hindwings have many more CS than their modified forewings, the elytra [32].

#### CS are found on both surfaces of the wing

In most of the species described in the literature, CS are found on both the dorsal and ventral wing surfaces (Diptera [12,14,35<sup>••</sup>,43,44], Hemiptera [41], Lepidoptera [30], Odonata [31<sup>••</sup>,36], Plecoptera [40], Strepsiptera haltere [15], Trichoptera [42], Mecoptera [45]). Although at least one species of Hymenoptera (A. mellifica [39]) has CS on both surfaces of both the forewings and hindwings, in Trichogramma minutum, CS are only reported on the ventral side of the forewing [13]. In beetles (Coleoptera), CS are reported to only occupy the dorsal surface of the elytra but are found on both the dorsal and ventral surfaces of the hindwing [32,16]. Finally, in orthopterans, CS are reported to be restricted to the ventral wing surface in the desert locust (Schistocerca gregaria [3]) but are found on both wing surfaces in two cricket species (Tettigonia cantans and Acheta domesticus; formerly Locusta cantans and Gryllus domesticus [46,47]) and a grasshopper (Chorthippus biguttulus [38]).

## CS count is correlated with intraspecific and intraordinal variation in wing size

Significant relationships between CS count and wing size exist within a species (Coleoptera [16]) and across species of a single order (Diptera, Coleoptera, Odonata [16,31<sup>••</sup>,35<sup>••</sup>]). However, our review of the literature revealed no broader-scale, interordinal correlation between wing size and CS count. For instance, the dorsal side of the large forewings of the grasshopper (*M. sanguinipes*, Orthoptera) has ~54 CS [11] while the large forewings of the cockroach (*B. germanica*, Blattodea) have only ~15 CS, respectively (estimate by Pringle [10] based on [37]). The smaller forewings of the blowfly (*Calliphora vicina*, Diptera) and western honey bee (*A. mellifera*, Hymenoptera) contain ~130 ([14]) and ~750 CS, respectively (estimate by Pringle [10] based on [39]).





Campaniform sensilla (CS) placement varies across wings of Insecta, but some trends in placement can be discerned. All images and the relative orientations of forewings and hindwings are for diagrammatic purposes. Individual, relatively isolated CS are depicted as dots, and fields of CS are hatch shaded ellipses (i.e. the CS within fields are not each depicted separately). Red and blue color indicate dorsal and ventral CS, respectively. Dotted box outlines indicate that, to our knowledge, the CS have not yet been fully mapped. Only the dorsal CS were mapped for *Melanoplus sanguinipes* [11], and only the joints (i.e. the wing bases) were examined for *Cicadella viridis* [29]. References for CS placement for the other taxa are as follows: *Manduca sexta* [30], *Drosophila melanogaster* [12,17], *Perithemis tenera* [31\*\*], *Dytiscus marginalis* [32], *Trichogramma minutum* [13]. Note that *T. minutum* does not have distal venation like the other species. Center phylogeny from [33,34] is pruned to the insect orders, and colored branches indicate the pictured taxa.

## Potential impacts of CS placement on neural encoding

The trends in CS placement across Insecta summarized in the previous section have implications for how strain information is encoded by the nervous system to support flight control. In this section, we discuss possible relationships between placement and neural encoding.

#### **Proximal CS arrangement**

A conserved feature across many orders of insects is the high concentration of CS at the wing base. In both wings and halteres, these proximal fields of CS likely serve a similar role in sensing body rotations [19,6,5,48], with fields of CS at different locations differing in their sensitivity to different axes of rotation [9]. For example, simulations of halteres show that the position of CS along the circumference of the haltere determines their sensitivity to body rotations in an axis orthogonal to the plane of haltere motion. In particular, CS located dorsally and ventrally exhibit little change in spike timing with the addition of body rotation, whereas CS rostrally and caudally show changes in spike timing large enough to be detectable [21<sup>••</sup>]. Therefore, multiple fields of CS at different locations, along with directional selectivity of individual CS, may combine to produce a representation of body rotation in all axes [9,49]. The presumed role of these CS fields in detecting inertial forces induced by body rotations does not preclude the possibility that they may also detect aerodynamic forces.

It remains unclear why there are so many CS in each proximal field, but there are several plausible hypotheses. These high-density CS groups might provide redundant information in order to counteract ambiguities introduced by noise; however, the high reliability of CS responses suggests that redundancy may be unnecessary. When presented with repeats of an identical stimulus, CS responses typically have a spike timing jitter (standard deviation) of only approximately 0.5 ms, below the timing differences expected to be produced by body rotations  $[6,5,1^{\bullet\bullet},50]$ .

The high density of proximal CS fields may instead serve other functions. The small differences in location of CS within a field may result in subtle but detectable differences in the strain experienced by those CS, such that the population can provide detailed spatial information about local bending over the area covered by the field. CS within a field may also have somewhat different response properties, allowing them to convey distinct information even if the strain experienced by CS within a field is functionally identical. Although CS seem to respond to similar temporal patterns of strain [5,20], they may have different selectivity for this feature. Different thresholds, for example, could result in CS that respond to different magnitudes or preferentially at different phases of the wingstroke. This population encoding might facilitate lower-latency detection of perturbations, as the insect would not be restricted to detection, via spike timing advance or delay, at one particular phase of the wingstroke. Additionally, CS at differing orientations provide selectivity to different directions of strain [9]. A large population of CS may thus be useful not simply for reducing noise but for providing distinct information over the course of the wingstroke.

#### **Distal CS arrangement**

In contrast to the conserved aspects of proximal CS arrangement, there is little consistency in distal CS density or placement across insect orders. This disparity likely reflects the large differences in wing shape and wingstroke kinematics across orders, which presumably result in vastly different spatiotemporal patterns of wing strain. Distal CS may be important for detecting external perturbations, such as wing collisions with external objects, or for producing a more complete internal wing representation. Reconstruction of wing deformation based on limited local strain measurements is an active area of research in aerospace engineering [51–53]. The relatively small number of distal CS in flying insects might be sufficient to identify behaviorally relevant modes of wing bending and inform flight control [54,26]. Additionally, under certain conditions, CS located distally provide more information for sensing wing deformations induced by body rotations than proximal CS groups do [25,55,56\*\*].

#### Forewing versus hindwing

Across insect orders, CS are generally found on both the forewing and hindwing, and it appears that sensory feedback from both wings is critical for flight control, regardless of which wing is primarily responsible for force production during flight. In a locust (S. gregaria, Orthoptera), the forewing sensory feedback modulates the central pattern generator driving wing actuation [57], whereas the hindwing sensory feedback plays a role in regulating forewing kinematics such as twisting [3]. In a hawkmoth (Manduca sexta, Lepidoptera), forewing bending elicits stabilizing body reflexes [6]. In insects of Diptera and Strepsiptera, one set of wings (the halteres) no longer generate force and serve instead primarily as sensory organs [9,15]. In Diptera, the halteres are associated with controlling forewing kinematics, head rotations, and several other key aspects of flight control [9,5,20].

Although sensory feedback from wings is essential for flight control across all insects, how sensory information is processed downstream and used for modulating motor output likely varies depending on how the wings are actuated. Variation in wing actuation includes muscle architecture (e.g. direct flight muscles of dragonfly versus indirect flight muscles of flies), muscle physiology (e.g. synchronous flight muscles of flies), and how the wings are coupled (e.g. independently actuated wings of dragonfly versus the physically coupled forewing and hindwing of a moth). Thus, how CS input modulates motor patterns could vary with the diversity of muscle anatomy and function across insects. As future studies map CS placement, it will be interesting to determine whether the motor and actuation systems are correlated with CS placement and feedback strategies across different species.

#### CS count and wing size

Although intraspecific and intraordinal relationships between the number of CS and wing size have been found, there does not appear to be a significant relationship on the interordinal taxonomic level (i.e. across Insecta). The absence of an interordinal relationship could be because other factors vary strongly between orders, such as behavioral strategies or highly modified morphologies (such as halteres). For example, insects known to have maneuverable flight like flies (Diptera) have relatively smaller wings with more than 6 times the number of wing CS than cockroaches (Blattodea) and grasshoppers (Orthoptera), which have a relatively reduced flight capacity [37,11,12,14]. The significant relationships found at lower taxonomic levels may indicate that more CS are required as wing size increases to maintain controlled flight, provided other wing characteristics remain similar. In addition, large interspecific variation in wing size (e.g. comparing *M. sexta* to *T. minutum*) impacts the Revnolds number. the ratio of inertial to viscous forces, which could also have significant implications for sensor distribution because of influences on different mechanisms of aerodynamic force production and aeroelastic wing deformation. Ultimately, the relationship between wing morphology and CS count would be augmented by a strong foundation in the biomechanics of flapping flight; we hope that the preliminary trends catalogued in this section will inspire future work in this area.

#### Non-neural constraints on sensor placement

Mechanosensor placement is not entirely dictated by their functional role within the flight control system. Indeed, other wing functions can impact sensor placement, as well as developmental or physiological constraints and the evolutionary history of a particular taxon. For instance, in all insects studied thus far, CS are closely associated with wing veins. Venation pattern directly impacts the distribution of wing stiffness [58] and how the wing bends under loading [59–61]. At the same time, veins are also responsible for innervation, circulation, and gas exchange throughout the wing, ensuring proper tissue maintenance [62,63]. Consequently, homeostatic regulatory requirements may restrict possible CS locations by constraining the placement of the vein network. In addition, CS could primarily serve non-locomotor functions in winged insects that do not regularly fly. For example, in a species of flightless cricket (Gryllus campestris, Orthoptera), one field of CS only found in males helps produce attractive calls [64], suggesting that sexual selection also

plays a role in the evolution of CS placement. The complex interplay among these various constraints on CS placement has yet to be thoroughly explored.

## Combining comparative methods and computational models

Many interacting pressures drive wing evolution, so an integrative approach is a compelling path forward to understand patterns and significance of wing CS placement. In particular, we suggest leveraging interspecific diversity in wing morphology and kinematics along with computational modeling to explore the functional consequences of wing CS. A number of outstanding questions will benefit from this perspective, including: How correlated is the evolution of wing size, shape, venation pattern, and CS distribution? What are the functional roles of sparsely distributed distal wing CS? Do hypotheses of optimal placement, encoding, and control capture the diverse behavioral demands of different flying insects?

Answering these questions will require testing wellscoped hypotheses, some of which can be framed within lower taxonomic levels. Indeed, interpreting differences in wing mechanosensor distribution among flying insect taxa (Section 'Mechanosensor features and placement in insect wings') is complicated by the extreme differences in wing morphology and behavior across insect orders. Therefore, focusing on lower taxonomic levels (e.g. examining interspecific differences in an Insecta subclade at the family or subfamily level) and incorporating new methods for quantifying wing morphology [65<sup>•</sup>] might provide clearer links between particular features of wing morphology and CS placement. Indeed, many orders and even families - within Insecta exhibit the morphological and behavioral diversity necessary to test how CS placement might relate to wing morphology and flight style [66<sup>••</sup>], and different groups may reveal different principles. Establishing some clades of Insecta as 'model clades' for neuroscience [67<sup>•</sup>] would allow the insect neuroscience community to more readily test hypotheses about the correlated evolution of morphology, kinematics, CS placement, and CS function.

When applied in conjunction with comparative phylogenetics, computational modeling is a powerful approach to test hypotheses of functional significance. Computational tools, such as finite element methods (FEM), allow us to model spatiotemporal patterns of strain for arbitrary wing morphologies and actuation patterns [31<sup>••</sup>,68]. Aerodynamic models, such as quasi-steady and computational fluid dynamics models, may be combined with FEM, immersed boundary methods (IBM), or lattice Boltzmann methods (LBM) to incorporate the effects of fluid-structure interaction into predicted strain. Encoding this strain data in a population of model neurons (e.g. integrate-and-fire neurons or generalized linear models) allows us to then identify effective and robust sensor placement strategies. Using methods like sensor placement optimization and observability metrics, we can directly test functional hypotheses of CS placement [25,55,56<sup>••</sup>].

The proposed computational framework is a challenging one. Accurately characterizing spatiotemporal patterns of wing strain depends on details of wing shape, venation pattern, material properties such as cuticle stiffness, and actuation pattern. Further, neural encoding properties are not fully understood and may vary from species to species, or for different CS locations within a given species. Nevertheless, such models may provide insight by allowing us to probe specific, targeted manipulations of individual features (e.g. altering wing size) while holding others constant and observing the effects. The use of model insect clades, combined with computational approaches, may therefore be particularly valuable, as this would facilitate comparison between species where a considerable amount of variation in features has been reduced. Intriguingly, computational methods also allow us to explore combinations of features that are not observed in nature, such as assessing how particular modifications to a given species' venation pattern or wingstroke may affect sensing performance. We anticipate that the integration of comparative methods and computational models will lead to more complete understanding of the wing as both a sensor and a propulsor.

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#### Conflict of interest statement

Nothing declared.

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#### References and recommended reading

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

- of special interest
- •• of outstanding interest
- Aiello BR, Westneat MW, Hale ME: Mechanosensation is evolutionarily tuned to locomotor mechanics. Proc Natl Acad Sci U S A 2017, 14:4459-4464 http://dx.doi.org/10.1073/ pnas.1616839114.

- Pratt B, Deora T, Mohren T, Daniel T: Neural evidence supports a dual sensory-motor role for insect wings. Proc Biol Sci 2017, 284 http://dx.doi.org/10.1098/rspb.2017.0969.
- 3. Gettrup E: Sensory regulation of wing twisting in locusts. *J Exp Biol* 1966, 44:1-16 <Go to ISI>://WOS:A19667486400001.
- Aiello BR, Olsen AM, Mathis CE, Westneat MW, Hale ME: Pectoral
   fin kinematics and motor patterns are shaped by fin ray mechanosensation during steady swimming in scarus quoyi. J Exp Biol 2020, 223 http://dx.doi.org/10.1242/jeb.211466

The shape and size of insect wings evolve to meet the functional demands of a given species, leading to a wide diversity of wing morphology across orders. In highly diverse sister families — the hawkmoths and wild silkmoths — which diverge in both life history and flight behavior, wing morphology has also strongly diverged between and within families, demonstrating the correlated evolution of flight behavior and wing morphology.

- Fox JL, Fairhall AL, Daniel TL: Encoding properties of haltere neurons enable motion feature detection in a biological gyroscope. Proc Natl Acad Sci U S A 2010, 107:3840-3845 http:// dx.doi.org/10.1073/pnas.0912548107.
- Dickerson BH, Aldworth ZN, Daniel TL: Control of moth flight posture is mediated by wing mechanosensory feedback. *J Exp Biol* 2014, 217:2301-2308 http://dx.doi.org/10.1242/jeb.103770.
- Zill SN, Moran DT: The exoskeleton and insect proprioception.
   Responses of tibial campaniform sensilla to external and muscle-generated forces in the american cockroach, *Periplaneta Americana*. J Exp Biol 1981, 91:1-24.
- Spinola S, Chapman K: Proprioceptive indentation of the campaniform sensilla of cockroach legs. J Comp Physiol 1975, 96:257-272.
- Pringle JWS: The gyroscopic mechanism of the halteres of diptera. Philos Trans R Soc Lond Ser B Biol Sci 1948, 233:347-384.
- 10. Pringle J: Insect Flight. Cambridge: Cambridge University Press; 1957.
- 11. Albert PJ, Zacharuk RY, Wong L: **Structure, innervation, and distribution of sensilla on wings of a grasshopper**. *Can J Zool* [[*Revue Canadienne De Zoologie*]] 1976, **54**:1542-1553 http://dx. doi.org/10.1139/Z76-178.
- 12. Cole ES, Palka J: The pattern of campaniform sensilla on the wing and haltere of drosophila-melanogaster and several of its homeotic mutants. *J Embryol Exp Morphol* 1982, **71**:41-61 <Go to ISI>://WOS:A1982PR39400004.
- Schmidt JM, Smith JJB: The ultrastructure of the wings and the external sensory morphology of the thorax in female trichogramma-minutum riley (hymenoptera, chalcidoidea, trichogrammatidae). Proc R Soc Ser B Biol Sci 1985, 224:287 http://dx.doi.org/10.1098/rspb.1985.0033.
- Gnatzy W, Grunert U, Bender M: Campaniform sensilla of calliphora-vicina (insecta, diptera). 1. Topography. Zoomorphology 1987, 106:312-319 http://dx.doi.org/10.1007/ Bf00312005.
- Pix W, Nalbach G, Zeil J: Strepsipteran forewings are halterelike organs of equilibrium. *Naturwissenschaften* 1993, 80:371-374 http://dx.doi.org/10.1007/Bf01138795.
- Frantsevich L, Gorb S, Radchenko V, Gladun D, Polilov A: Lehr's fields of campaniform sensilla in beetles (coleoptera): functional morphology. I. General part and allometry. *Arthropod Struct Dev* 2014, 43:523-535 http://dx.doi.org/10.1016/ j.asd.2014.09.001.
- Dickinson MH, Palka J: Physiological properties, time of development, and central projection are correlated in the wing mechanoreceptors of drosophila. *J Neurosci* 1987, 7:4201-4208.
- Dickinson MH: Linear and nonlinear encoding properties of an identified mechanoreceptor on the fly wing measured with mechanical noise stimulation. J Exp Biol 1990, 151:219-244.
- Dickinson MH: Comparison of the encoding properties of campaniform sensilla on the fly wing. J Exp Biol 1990, 151:245-261.

- 20. Dickerson BH, Fox JL, Sponberg S: Functional diversity from generic encoding in insect campaniform sensilla. *Curr Opin Physiol* 2020.
- 21. Mohren T, Daniel T, Eberle A, Reinhall P, Fox J: Coriolis and • centrifugal forces drive haltere deformations and influence

**spike timing.** J R Soc Interface 2019, **16**:20190035 Using computational methods, the authors show that the size, shape, and mass distribution of dipteran halteres strongly influence the magnitude and spatiotemporal patterns of strain produced from haltere oscillation. Moreover, CS located at different circumferential positions on a haltere exhibit differential sensitivity in spike timing to body rotations.

 Yarger AM, Fox JL: Single mechanosensory neurons encode
 lateral displacements using precise spike timing and thresholds. Proc R Soc B: Biol Sci 2018, 285:20181759

Individual CS on the haltere base shift the timing of their phase-locked response as the halteres are laterally displaced.

- 23. Ganguli S, Sompolinsky H: Compressed sensing, sparsity, and dimensionality in neuronal information processing and data analysis. *Annu Rev Neurosci* 2012, **35**:485-508.
- 24. Manohar K, Brunton SL, Kutz JN: Environment identification in flight using sparse approximation of wing strain. *J Fluids Struct* 2017, **70**:162-180.
- 25. Mohren TL, Daniel TL, Brunton SL, Brunton BW: Neural-inspired sensors enable sparse, efficient classification of spatiotemporal data. *Proc Natl Acad Sci U S A* 2018, **115**:10564-10569.
- Johns W, Davis L, Jankauski M: Reconstructing full-field flapping wing dynamics from sparse measurements. *Bioinsp Biomimet* 2020, 16:016005.
- Sun L, Gao Y, He J, Cui L, Meissner J, Verbavatz J-M, Li B, Feng X, Liang X: Ultrastructural organization of nompc in the mechanoreceptive organelle of drosophila campaniform mechanoreceptors. Proc Natl Acad Sci U S A 2019, 116:7343-7352.
- Keil TA: Functional morphology of insect mechanoreceptors. Microsc Res Techn 1997, 39:506-531.
- Durso V, Ippolito S: Proprioceptor organs in cicadella-viridis (I) (homoptera, cicadellidae). Int J Insect Morphol Embryol 1988, 17:381-391 http://dx.doi.org/10.1016/0020-7322(88)90018-9.
- Dombrowski UJ: Untersuchungen zur funktionellen Organisation des Flugsystems von Manduca sexta. Germany: Cologne University; 1991. (Dissertation).
- 31. Fabian J, Siwanowicz I, Uhrhan M, Maeda M, Bomphrey R, Lin H-
- T: Complete neuroanatomy and sensor maps of odonata wings for fly-by-feel flight control. *bioRxiv* 2021 http://dx.doi. org/10.1101/2021.04.11.439336

Mechanosensory structures are mapped on odonate wings, revealing different sensor morphologies and the locations of hundreds of sensors per wing. Sensor count on major veins is correlated with wing size across odonate species, and computational modeling shows that areas of high CS density overlap with areas of the wing that experience large fluctuations in strain.

- 32. Lehr R: The sensory organ of both elytra on dytiscus maginalis. Zeit Wissensch Zool 1914, 110:87-150 <Go to ISI>:// WOS:000202676500004.
- Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG et al.: Phylogenomics resolves the timing and pattern of insect evolution. Science 2014, 346:763-767.
- Tong KJ, Duchêne S, Ho SY, Lo N: Comment on "phylogenomics resolves the timing and pattern of insect evolution". Science 2015, 349:487.
- 35. Agrawal S, Grimaldi D, Fox JL: Haltere morphology and
- campaniform sensilla arrangement across diptera. Arthropod Struct Dev 2017, 46:215-229

The authors use scanning electron microscopy to map the number, distribution, and orientation of haltere CS across all the diverse Diptera infraorders. Across species, CS mapping reveals diversity in CS shape, size, and distribution, as well as a previously undocumented correlation between CS count and haltere size

- Simmons PJ: Crevice organs sensory structures on wings of dragonflies (insecta, odonata). Zoomorphologie 1978, 89:251-255 http://dx.doi.org/10.1007/Bf00993951.
- Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel von schabe phyllodromia germanica. Bull Int Acad Cracovie (Acad Pol Sci) B II 1934:89-104.
- **38.** Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel der feldheuschrecke stauroderus biguttulus. Bull Int Acad Cracovie (Acad Pol Sci) B 1934, II:187-196.
- 39. Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel der honigbiene (apis mellifica). Bull Int Acad Cracovie (Acad Pol Sci) B 1933, II:275-289.
- Zacwilichowski J: Über die innervierung und sinnesorgane der flügel der afterfrühlingsfliege isopteryx tripunctata scop. (plecoptera). Bull Int Acad Cracovie (Acad Pol Sci) B 1936, II:267-284.
- 41. Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel von aphrophora alni fall (rhynchota-homoptera). Bull Int Acad Cracovie (Acad Pol Sci) B 1936, II:85-99.
- 42. Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel von kocherfliegen (tichoptera). Bull Int Acad Cracovie (Acad Pol Sci) B 1933, II:305-319.
- **43.** Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel der lausfliege oxypterum leach. (diptera, pupipara). Bull Int Acad Cracovie (Acad Pol Sci) B 1934, II:251-257.
- 44. Zacwilichowski J: Über die innervvierung und die sinnesorgane des flügel der schnake tipula paludosa meig. Bull Int Acad Cracovie (Acad Pol Sci) B 1934, II:375-383.
- 45. Zacwilichowski J: Über die innervvierung und die sinnesorgane der flügel von schnabelfliegen (panorpa). Bull Int Acad Cracovie (Acad Pol Sci) B 1933, II:109-124.
- Fudalewicz-Niemczyk W: The innervation and sense organs in the wings of the grasshopper locusta cantans. Füssl Pol Pismo Ent 1955, 25:127-160.
- Fudalewicz-Niemczyk W, Rosciszewska M: Innervation and sense organs of wings of gryllus-domesticus I (orthoptera). Acta Biol Cracoviensia Ser Zool 1972, 15:35-51 <Go to ISI>:// WOS:A1972O104100006.
- Eberle AL, Dickerson BH, Reinhall PG, Daniel TL: A new twist on gyroscopic sensing: body rotations lead to torsion in flapping, flexing insect wings. J R Soc Interface 2015, 12 http://dx.doi.org/ 10.1098/Rsif.2014.1088.
- Chan WP, Dickinson MH: Position-specific central projections of mechanosensory neurons on the haltere of the blow fly, *Calliphora vicina*. J Comp Neurol 1996, 369:405-418.
- Fox J, Daniel T: A neural basis for gyroscopic force measurement in the halteres of holorusia. J Comp Physiol A 2008, 194:887-897.
- 51. Pak CG: Wing shape sensing from measured strain. AIAA J 2016, 54:1064-1073 http://dx.doi.org/10.2514/1.J053986.
- Gherlone M, Cerracchio P, Mattone M: Shape sensing methods: Review and experimental comparison on a wing-shaped plate. Prog Aerosp Sci 2018, 99:14-26 http://dx.doi.org/10.1016/j. paerosci.2018.04.001.
- Zhao Y, Du J, Bao H, Xu Q: Optimal sensor placement based on eigenvalues analysis for sensing deformation of wing frame using iFEM. Sensors (Switzerland) 2018, 18 http://dx.doi.org/ 10.3390/s18082424.
- Taylor GK, Krapp HG: Sensory systems and flight stability: what do insects measure and why? Adv Insect Physiol 2007, 34:231-316.
- 55. Boyacioglu B, Morgansen KA: Bioinspired observability analysis tools for deterministic systems with memory in flight applications. AIAA Scitech 2021 Forum 2021:1679.
- 56. Weber AI, Daniel TL, Brunton BW: Wing structure and neural
   encoding jointly determine sensing strategies in insect flight. bioRxiv 2021 http://dx.doi.org/10.1101/2021.02.09.430476

The optimal sensor distribution on a wing is determined by both wing structure and CS encoding properties, with a small number of sensors sufficient for accurate detection of body rotations. Dynamic signals necessary for flight control can therefore be extracted from a sparse set of sensors when tuned to wing structure.

- 57. Wendler G: The influence of proprioceptive feedback on locust flight co-ordination. J Comp Physiol 1974, 88:173-200.
- Combes SA, Daniel TL: Flexural stiffness in insect wings. I. Scaling and the influence of wing venation. J Exp Biol 2003, 206:2979-2987 http://dx.doi.org/10.1242/jeb.00523.
- 59. Rees CJ: Aerodynamic properties of an insect wing section and a smooth aerofoil compared. *Nature* 1975, 258:141-142.
- 60. Jongerius S, Lentink D: Structural analysis of a dragonfly wing. *Exp Mech* 2010, **50**:1323-1334.
- 61. Bomphrey RJ, Nakata T, Henningsson P, Lin HT: Flight of the dragonflies and damselflies. *Philos Trans R Soc B: Biol Sci* 2016, 371 http://dx.doi.org/10.1098/rstb.2015.0389.
- Salcedo MK, Socha JJ: Circulation in insect wings. Integr Comp Biol 2020, 60:1208-1220.
- Tsai C-C, Childers RA, Shi NN, Ren C, Pelaez JN, Bernard GD, Pierce NE, Yu N: Physical and behavioral adaptations to prevent overheating of the living wings of butterflies. Nat Commun 2020, 11:1-14.
- 64. Schäffner K-H, Koch UT: A new field of wing campaniform sensilla essential for the production of the attractive calling song in crickets. *J Exp Biol* 1987, **129**:1-23.

- 65. Salcedo MK, Hoffmann J, Donoughe S, Mahadevan L:
- Computational analysis of size, shape and structure of insect wings. Biol Open 2019, 8:1-9 http://dx.doi.org/10.1242/ bio.040774

A new method for quantifying variation in wing morphology, including venation pattern, is established and can be used for future studies investigating the correlated evolution of wing morphology and sensor placement.

- 66. Aiello BR, Sikandar UB, Minoguchi H, Kimball K, Hamilton CA,
- Kawahara AY, Sponberg S: Wing shape evolution in bombycoid moths reveals two distinct strategies for maneuverable flight. bioRxiv 2020

The shape and size of insect wings evolve to meet the functional demands of a given species, leading to a wide diversity of wing morphology across orders. In highly diverse sister families — the hawkmoths and wild silk-moths — which diverge in both life history and flight behavior, wing morphology has also strongly diverged between and within families, demonstrating the correlated evolution of flight behavior and wing morphology.

#### 67. Jourjine N, Hoekstra HE: Expanding evolutionary neuroscience:

• **insights from comparing variation in behavior**. *Neuron* 2021 The authors advocate for the development of model clades, analogous to model organisms, where phylogenetic approaches can be integrated with neural and behavioral experimentation to leverage natural variation to answer questions in neurobiology.

- Krishna S, Cho M, Wehmann H-N, Engels T, Lehmann F-O: Wing design in flies: properties and aerodynamic function. *Insects* 2020, 11:466.
- 69. Gettrup E, Wilson DM: The lift-control reaction of flying locusts. *J Exp Biol* 1964, **41**:183-190.