

COMMENTARY

Making sense of sparse data with neural encoding strategies

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The surface of the body is invested with populations of mechanosensory neurons and receptors which balance performance and efficiency to provide relevant input on stimuli such as touch and movement. While it might be biologically possible to generate dense arrays of sensors all over the body and take in vast amounts of information, the mechanosensory system has adapted with function, resulting in more sensors where they are needed and in sensors that extract key features of stimulus input. Such adaptations can be illustrated with touch sensation and the two-point discrimination test. In areas of the body that need fine discrimination ability—our fingertips, for example—two points touching the skin can be perceived as distinct at a very small separation distance due to a high number of mechanosensory neurons innervating the region. In areas of our skin that are not generally used to resolve fine surface features, such as the outer area of the upper arm, we may perceive similarly spaced touches as one stimulus due to lower numbers of mechanosensory neurons in the region. The touch stimulus itself is also filtered and coded as trains of action potentials that reflect relevant characteristics of the stimulus. Inspired by the biological instrumentation of mechanosensory surfaces, Mohren et al. (1) developed and implemented computational approaches that provide insight on the biology and engineering of sparse sensing from wings.

Engineered, sensation-enabled structures, like evolved biological ones, have sensory systems that strike a balance between performance and cost. The choice of density and placement of sensors, the type and resolution of information captured from them, and the extent of processing of those data will impact functionality and expense of the device. The ability to obtain the requisite information for function from the minimal number of sensors optimizes the efficiency of design without sacrificing performance.

To understand and innovate strategies for design of mechanosensory systems with sparse sensing, Mohren et al. (1) have looked to the wings of insects, where fast and controlled flight movements are informed, in part,

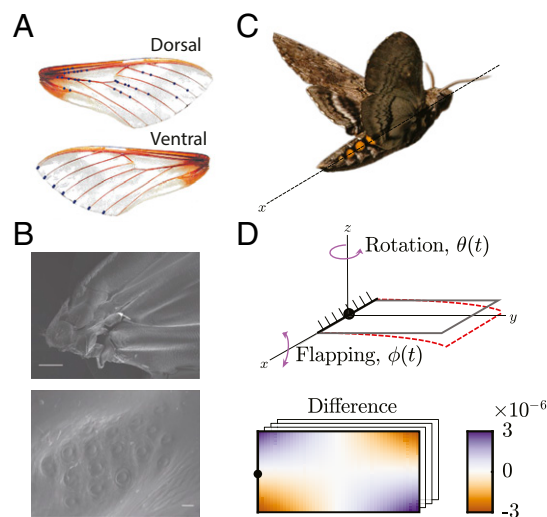


Fig. 1. Sensation and modeled mechanics in the hawkmoth (*Manduca sexta*) forewing. (A) Campaniform sensilla locations (blue circles) on the dorsal and ventral sides of the wing. (B) Dorsal sensilla near the base of the wing, indicated by arrow (Top; scale bar: 1 mm), and a close-up view on the ventral side (Bottom; scale bar: 10 μ m). (C) Hawkmoth showing axis of flapping (x). (D) Flapping and rotation in the model wing (Top). The difference in strain between flapping and flapping with rotation (Bottom). A and B are adapted with permission from ref. 7; C image courtesy of Armin J. Hinterwirth (photographer); and D is reprinted with permission from ref. 1.

by mechanosensory cells called campaniform sensilla located on the wings (Fig. 1 A and B). Early work on wing mechanosensation performed in flies showed that wing deflection causes the generation of action potentials by sensory neurons and described basic characterization of their properties (2–4), including heterogeneity in responses (e.g., refs. 2 and 5).

Mohren et al. (1) focus their work on the wings of the tobacco hawkmoth (*Manduca sexta*) (Fig. 1C), where recent physiology has described mechanosensory ability of the wings (6). Campaniform sensilla of the wings in general, and the of hawkmoth wing in particular, are

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sparse. Dickerson et al. (7) described the anatomy of sensilla on the hawkmoth forewing. They reported that the wing has around 250 sensilla that are organized into patches (Fig. 1B), varying in number and density per patch. The patches of sensilla are not evenly distributed across the wings but are located in wing veins and are clustered (Fig. 1A). On the dorsal surface, sensilla are mainly in the basal and middle part of the wing, with low representation near the tornal (distal) edge or the other wing edges, except for very basal placements. The ventral surface is quite different, with sensilla placement only along the tornal wing edge. Dickerson et al. (7) also explored whether sensilla can function in flight behavior by introducing pitch during flight. They found a reflexive response of the abdomen that corrected orientation, providing additional evidence that the wings are functioning as both sensors and propulsors. Ando et al. (8), working in another species of hawkmoth, the convolvuli hawkmoth (*Agrius convolvuli*), used anterograde neuron labeling to map the sensory nerve fibers from the forewings and hindwings of the moth. They found diverse projection patterns and convergence of inputs, suggesting complexity and multifunctionality in the sensory modulation of flight control.

The conclusion that wings have sensory and propulsive roles in flies and moths is consistent with observations across the animal kingdom showing that intrinsic limb sensation is important for generating normal movements (tetrapods, e.g. refs. 9–11; fish, e.g. ref. 12; and other insects, e.g. refs. 13–15). There is considerable diversity, however, in how mechanosensation is organized and likely used. In the propulsive forelimbs (pectoral fins) of fish, for example, mechanosensors on the membranous wing are distributed in a different pattern from hawkmoths, with fibers extending broadly across the span and length of the fin membranes (16). The universality of mechanosensory–motor integration in the control of limbs, with variation in basic elements of their organization, suggests value in examining these systems in diverse species as comparative work may illuminate general biological principles for the structure of such elements and how structure is related to function, which may also inform engineering choices.

Mohren et al. (1) focus on a particular context for their computational modeling: the moth's discernment of wing rotation, a subtle movement that must be detected in the context of high-amplitude wing beats and wind gusts. They trained classifiers to discriminate wing rotation in the context of flapping and with perturbation (Fig. 1 C and D). Recognizing that determining the placement of sensors to best capture information is intrinsically related to the information that needs to be captured, Mohren et al. (1) investigate the use of neurally encoded data as input to their classifier (e.g., ref. 17), as well as the raw strain data. They find that both neural encoding based on temporal filtering and nonlinear activation based on experimental data that link wing movement to neuron activity (e.g., ref. 6) were necessary for high-performance classification. Use of raw strain measurements led to poor classification due to difficulty in separating strain due to rotation from strain due to flapping.

Mohren et al. (1) then applied sparse sensor placement optimization for classification methods on the computational model of the wing. They aimed to determine efficient numbers and placement of sensors to optimize discrimination of rotation. They find that only a

small number of sensors is needed to classify rotation, even with strain perturbations mimicking wind gusts that also caused rotation. They determine that, for the most part, with just 10 well-placed sensors and using neural encoding for classification, they could match the performance of over 1,000 sensors distributed throughout the wing. They also find that multiple combinations of a sparse set of sensors could accomplish this classification task.

The modeling and method development of Mohren et al. provide important insights for the design of engineered mechanosensory-enabled wings.

Modeled sensor placement did not closely resemble the biological sensor organization on the wing, either in numbers of sensors or in placement of sensors, as acknowledged and discussed by the Mohren et al. (1). There are many more campaniform sensilla sensors on the wings of the hawkmoth, even if comparing groups of sensilla to individual sensors in the model. Optimized sensor placement in the model occurred in a distribution around the free edges of the modeled plate, perhaps not surprising, as these would be the points of greatest strain at any given distance from the anchored edge. In the hawkmoth, sensors are located on the tornal margin of the ventral surface but conspicuously absent from the other edges of the wing. The dorsal surface of the hawkmoth wing has no sensors at the edge (7).

The differences between sensor placement on the optimized model and sensor placement on the hawkmoth prompt a range of questions that could be explored to further characterize the neuromechanics of the wing. What is the range of sensory functions of the wing? There are likely multiple selective pressures on sensilla organization, and optimizing for rotation detection may contradict other needs. How do the wing sensors interact with sensors on other body elements? The forewing of a hawkmoth is not functioning in isolation as it is in the model; even considering just the wings, another forewing or the hindwings may experience and sense related wing rotation and contribute to the appropriate behavioral response. What are the constraints on building the wing as a sensory device? Perhaps sensor placement is constrained by the physical organization of the wing. On wings, nerve fibers and sensilla are associated with veins, which are stiffer than the surrounding membrane. If venation is required for the presence of afferent structures, for example, other roles for venation may limit options for sensor placement. Thickness of wing veins (18) and, relatedly, flexural stiffness of the wing decrease toward the tip (19–21), and increased bending could decrease the usefulness of sensors placed along the wing's margin or increase the likelihood of damage. The modeling and method development of Mohren et al. (1) provide important insights for the design of engineered mechanosensory-enabled wings. Just as biology inspired their modeling, their modeling is also inspiring new biological questions, in an iteratively advancing exchange of ideas and data.

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