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Functional diversity from generic encoding in insect campaniform sensilla

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Insect proprioception utilizes hundreds of campaniform sensilla embedded in the exoskeleton that sense strain. These sensilla are essential for many behaviors, especially flight control. Despite their role in diverse behaviors, campaniform sensilla share many neural properties. White noise analysis of campaniform sensilla on both lepidopteran wings and dipteran halteres shows selectivity to two stimulus features related by a derivative (derivative pair feature detection, DPFD), which are sufficient to explain spiking activity. DPFD is an inherent property of non-specialized Hodgkin-Huxley dynamics. Nonetheless, DPFD in campaniform sensilla enables simple control laws at multiple timescales. Campaniform sensilla specialization may derive more from stimulus prefiltering by receptor mechanics and anatomical arrangement, although neural specialization may also contribute for more complex, naturalistic stimuli. Evolution may tinker with the placement of these ubiquitous sensors and adapt them to different functions without the encumbrance of particular neural specialization, a strategy potentially useful for engineered walkers and fliers.

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Introduction

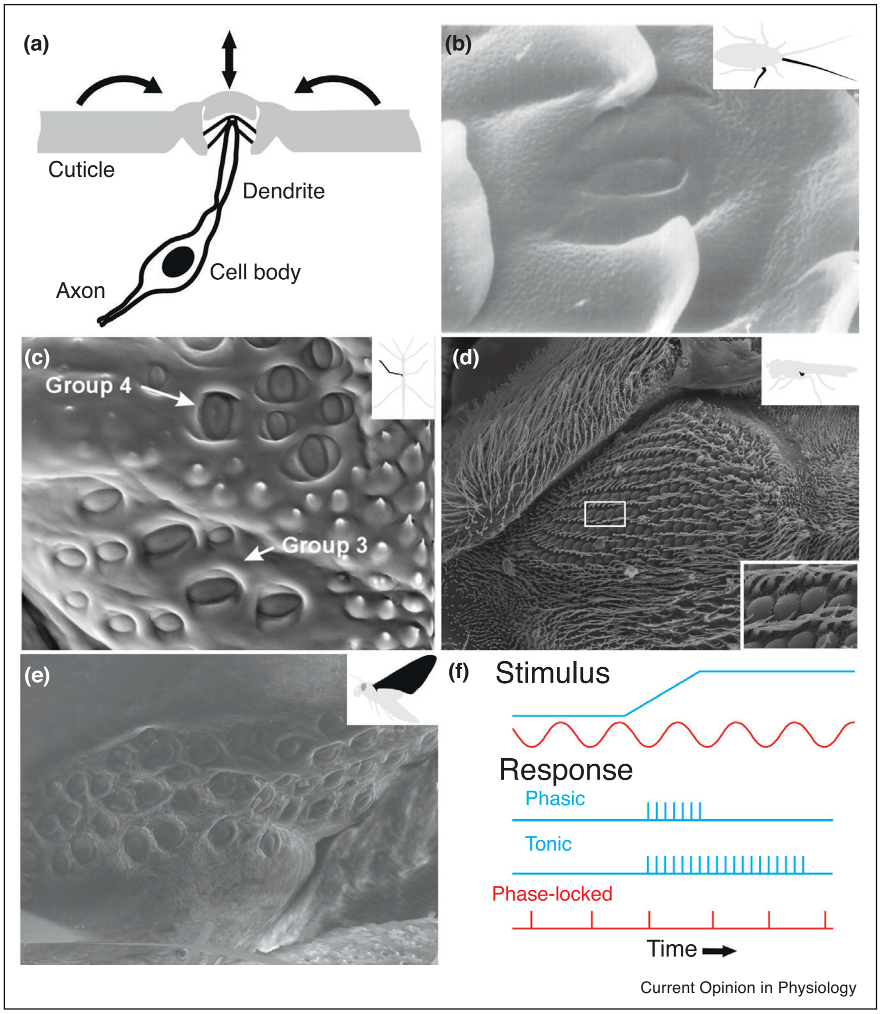
Agile locomotion requires a sense of the body's position and motion in space. Many vertebrates, especially mammals, combine a dedicated vestibular organ with specialized sensors in muscles and tendons that inform the nervous system about relative stretch, as well as cutaneous sensors that monitor deformation of the skin. Terrestrial and aerial arthropods lack a vestibular structure analogous to our inner ear, but still exhibit diverse locomotor repertoires. In these organisms, proprioception is accomplished primarily by three types of sensory cells [1,2]. First, internal stretch receptors, or chordotonal organs, connect segments or deformable regions of the exoskeleton to muscles, or form specialized clusters of neurons like in the antennal Johnston's organ of many insects [3]. Second, sensory hairs cover the surface of nearly all arthropods. While many are chemosensory, mechanosensitive hairs are arranged in specialized organs, like the prosternal hair plates that monitor the position of the head [4], or are found individually at various locations on the body [1]. Finally, campaniform sensilla (CS) are proprioceptors essential to many insect behaviors. CS are directly embedded in the exoskeleton itself and provide the animal with a sense of the deformations of its body [5].

The prevalence of CS suggests that their neural encoding may be specialized to serve many different proprioceptive roles. However, much of this specialization might arise through mechanical filtering of the stimulus and their placement on structures [3,5,6••,7]. Here we will discuss how their neural encoding is actually quite generic, suggesting that specialization may arise primarily through anatomical placement and mechanics, rather than necessarily requiring specialized neural computation and membrane dynamics. To explore this idea, we first survey some of the diversity of CS. We then examine in detail the examples where the stimulus selectivity of CS has been measured with methods drawn from computational neuroscience, specifically white noise analysis. Next, we relate how this selectivity is a natural consequence of Hodgkin and Huxley dynamics. We then connect the encoding properties of CS to the simple control laws for insect locomotion under more naturalistic stimuli. The use of many, fairly generic sensors that are specialized through placement and mechanics may decouple the evolution of new structures and behaviors from precise neural specialization. This is especially true in flight-related sensors, but may extend to leg CS as well. The proliferation and deployment of CS in specialized locations suggests a robust sensing strategy, in stark contrast to the few, highly specialized sensors we typically use when engineering motile robots [8].

The diverse morphology and mechanical properties of CS shape their stimulus response

Campaniform sensilla are dome-shaped sensory structures that detect local bending of the exoskeleton. These domes are embedded within a spongy tissue that is directly coupled to a single sensory neuron that lies

Figure 1



Diversity of campaniform sensilla.

(a) Campaniform sensilla act as strain sensors in the insect cuticle, transducing exoskeletal torsion and strain into spiking events. **(b)** Scanning electron micrograph (SEM) a campaniform on the antenna of the American cockroach, Periplanata americana, reproduced from Toh [28]. **(c)** SEM of the campaniform sensilla at the trochanter of the leg on the stick insect Carausius morosus, reproduced from Zill *et al.* [29]. **(d)** SEM of a field of campaniform at the base of the haltere (field dF2) on a robber fly. These sensors may detect out-of-plane bending due to gyroscopic forces or visually mediated steering commands. **(e)** SEM of a field of campaniforms found at the base of the forewing in the hawkmoth Manduca sexta. **(f)** The spikes elicited in campaniforms are stimulus-dependent. Static or ramp-and-hold stimuli result in spike trains that exhibit either rapid or slow adaptation. By contrast, periodic motion leads to phase-locking.

beneath [9] (Figure 1a). Fundamentally, CS are strain sensors: deformation of the cuticle cap applies mechanical strain to the dendrites of the sensory neuron where mechanosensitive ion channels from the TRP superfamily [10] transduce strain into depolarizing currents. CS are found wherever the cuticle experiences significant bending or torsion, including the legs, wings, and antennae (Figure 1b–e). Many are directionally sensitive, but this sensitivity seems to arise often from those with elliptical shapes, which creates anisotropy in their susceptibility to strain. For example, the American cockroach, *Periplanata americana*, possesses two groups of CS on the tibia of each leg that mediate different reflexes. These sensors detect both force and the rate of force arising from both external loads and internal stresses generated by muscles [11]. In one group, the proximal sensilla, the long axes of the CS are oriented perpendicular to the long axis of the tibia, whereas the distal sensilla are oriented parallel to the tibial long axis [12]. As a result, during walking or running, dorsal bending of the leg excites the proximal sensilla, while ventral bending excites the distal sensilla. Stimulating either the proximal or distal sensilla controls tibial flexion or extension, respectively [13]. While arrangement and morphology condition what stimuli the CS receive, the viscoelastic material properties of the receptor itself can act as a filter on its mechanotransduction [14•]

Similar directional selectivity of leg CS is also well-documented in the legs of stick insects and locusts [15,16] and while neural specialization cannot be ruled out, there is evidence that morphology likely shapes much of this specializaiton. Although the orientations of each of their four trochanteral CS groups differ, the CS within each group are parallel and electrophysiological evidence from trochanteral CS group 1 confirms their directional selectivity [15,17]. Notably, the directional selectivity of CS group 1 appears to be context-dependent: this group of campaniforms responds differently to *passive* horizontal deflections and *active* vertical displacements of the leg [17]. Moreover, CS groups 3 and 4, which are both located on the dorsal aspect of the trochanter but differ in their orientation by approximately 90 , encode leg loading in complementary directions (Figure 1c). The concentration of CS at the trochanter therefore provides stick insects with detailed information regarding their posture and walking. Even when the CS are round, directional selectivity can arise from the positioning of the dome within the cuticular collar surrounding the spongy tissue in which the dome is embedded [11].

Together, these elegant examples demonstrate how a limb or sensory structure's local mechanics can serve as a filter for mechanosensory transduction, without the need for specialization at the level of the individual neuron. It is unsurprising, then, that the insect body plan takes advantage of CS by either deploying them in precise patterns and orientations or increasing their number at locations that experience high stresses and strains.

Perhaps the clearest example of how both the precise patterning and CS density enable the encoding of crucial proprioceptive information is the haltere, the modified hindwing of flies. Like the hindwings of other insects, the halteres beat up and down during flight, and they provide essential mechanosensory feedback to the wing steering system on a stroke-by-stroke basis [18•]. Experiments conducted over 300 years ago demonstrated that flies cannot freely fly without these tiny organs [19]. Although commonly thought of as biological "gyroscopes" sensing body rotations [20,21], recent work in *Drosophila* has shown that the halteres also act as adjustable "metronomes," regulating the timing of the wing steering system with sub-millisecond precision [22••]. Thus, the haltere is a multifunctional sensory organ that allows flies to maintain aerial stability without sacrificing their unparalleled maneuverability.

The haltere's multifunctional capacity may rely on the directional selectivity of the CS embedded on it. The CS on the halteres are divided into five stereotyped groups along the haltere's dorsal and ventral aspects [23,24]. The CS found along the stalk, named fields dF3 and vF2, are grouped in a way that suggests that they detect in-plane beating for the metronomic function [20]. The CS embedded within field dF2 are oriented in a direction that suggests they are most sensitive to the shear strains that result from Coriolis forces during body rotations or visually mediated steering commands (Figure 1d) [20,22••].

Whether an insect is walking or flying, the resulting cuticular bending during locomotion will strongly influence the stimulus dynamics CS experience, and thus their elicited spike trains (Figure 1f) [7]. Indeed, static or ramp-and-hold deflections, which may approximate what insects experience during standing or walking, result in CS displaying either rapidly or slowly adapting responses [11,12,25]. Alternatively, periodic indentation of the dome, such as during the rapid flapping of the wings, causes the neuron to fire one or more action potentials that are phase-locked to the stimulus cycle [26•,27]. In the next section we will show that while some neural specialization may be present in a few cases, there is a common encoding strategy, especially amongst the wing and haltere CS of insects.

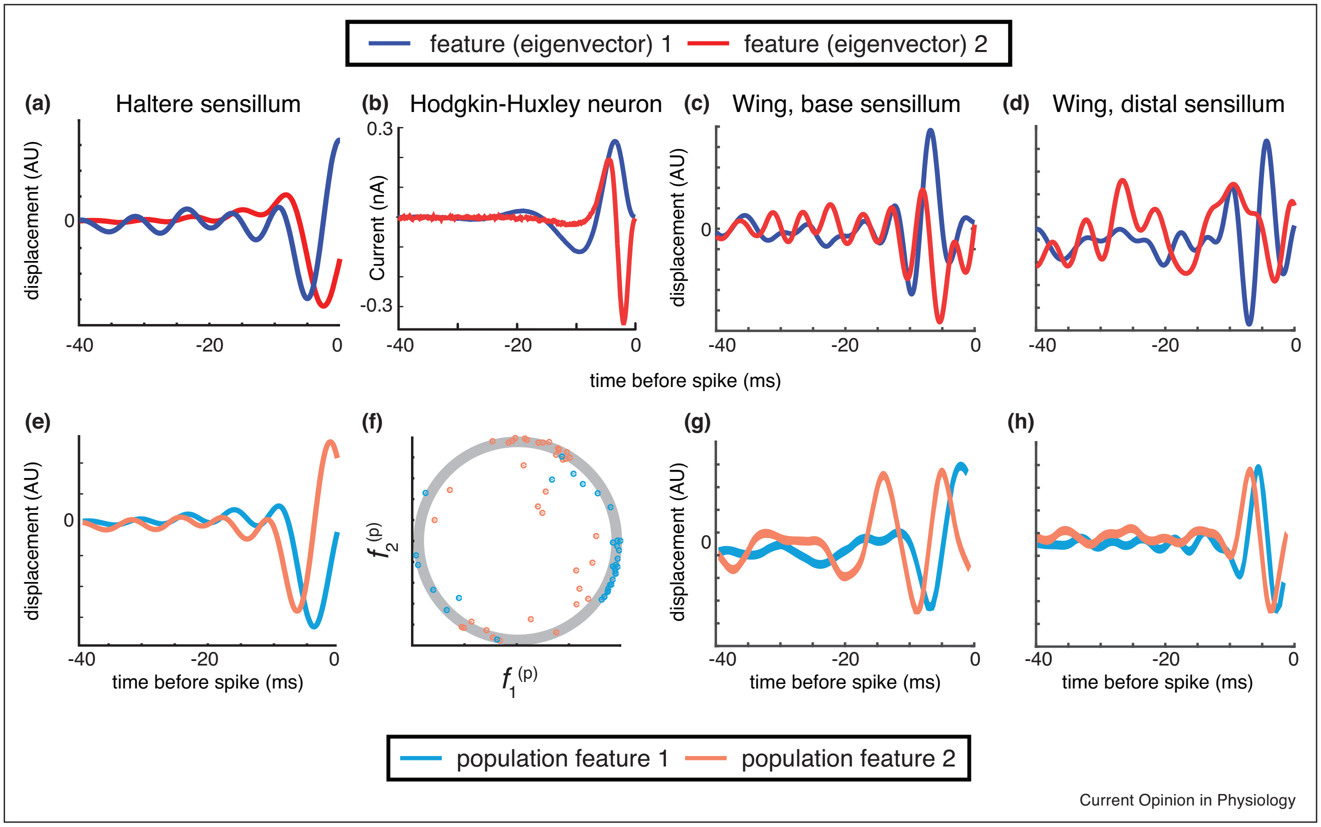
Derivative pair feature detection (DPFD) is a common encoding strategy in wing and haltere campaniform sensilla and Hodgkin-Huxley dynamics

Although spiking responses to simple static and periodic deflections are informative of a neuron's latency or frequency sensitivity, they do not provide a full description of the stimulus features to which the neuron responds. White noise analysis techniques stimulate neurons with a band limited gaussian noise (BLGN) stimulus that approximates a random presentation of all possible stimuli within a wide frequency range or "band" [30]. Spike triggered covariance analysis then takes the set of stimuli that precede each spike and reduces them to the small number of significant features (the dominant eigenvectors of the covariance matrix), that best elicit spiking [31••].

Mechanical BLGN stimulation of the haltere followed by spike-triggered covariance analysis shows that any haltere CS neuron, regardless of its location, can be described using only two features that approximate the derivative of each other (Figure 2a) [32••]. We refer to this mechanism of encoding as "derivative pair feature detection" (DPFD — see Box 1, Figure 2b). DPFD is not synonymous with phaso-tonic, which refers to the persistence of the spiking response to a change in stimulus amplitude. Some DPFD neurons encode the magnitude and velocity of the stimulus, but this is not necessarily the case, and we cannot simply interpret the two features as indicators of specific stimulus properties [33]. Rather, the derivative pair of features show the best linear set of features in a changing stimulus that elicit a spike.

Haltere CS are serially homologous to those on the forewing [24]. We may therefore hypothesize that the neurons associated with wing CS are not neurally distinct

Figure 2



DPFD is common in campaniform sensilla and is a property of Hodgkin-Huxley dynamics.

Derivative pair feature detection (DPFD) is a property of campaniforms belonging to crane fly (Tipula spp.) halteres **(a)**, a simulated Hodgkin and Huxley model neuron **(b)**, and those from the wing base **(c)** and wing tip **(d)** of Manduca sexta, all driven with BLGN excitatory input (mechanical deformation in (a), (c), and (d); current in (b)). **(e)** Single-value decomposition of the two dominant features for a population of 36 individual haltere sensilla results in a derivative pair of population features, showing that all the haltere units share a common basis. **(f)** Projection of any individual sensillum's features onto these population features, combined with a unique phase (position on the ring), describes the firing activity of a given neuron. The populations of features from the moth wing base sensilla **(g)** and wing distal sensilla **(h)** also map onto a derivative pair of population features. Haltere figures ((a), (e), & (f)) adapted from [32••]. Wing DPFD encoding was reanalyzed from the data from [34••] and panels ((g) & (h)) were replotted from that reference. Panel (b) adapted from [31••] with permission from MIT Press.

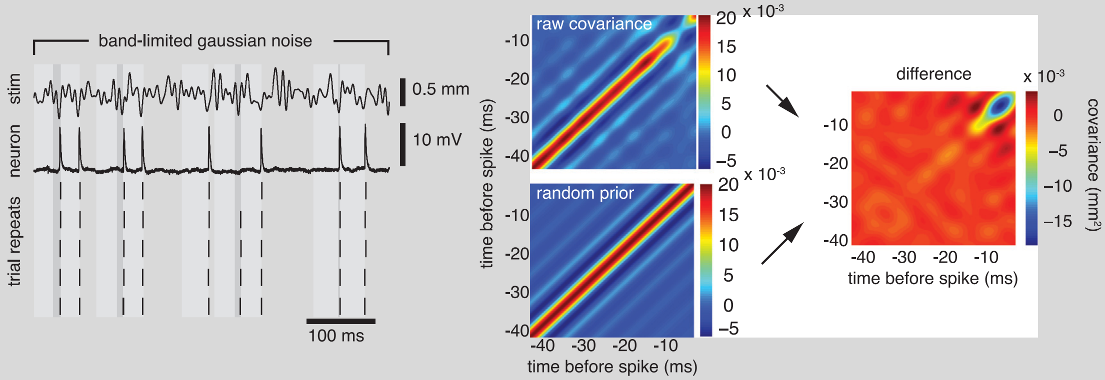
from those embedded in the haltere, although they could have evolved specialization [34••]. Pratt et al. captured extracellular recordings of spiking activity in the wing nerve of the hawkmoth *Manduca sexta* during stimulation of the wing tip with BLGN. We reanalyzed these data using the covariance analysis and found a pair of similar features in the wing CS [34••]. In the moth wing, the stimulus features that drive spiking in the CS at the wing base are nearly identical to those that drive spiking in haltere CS (Figure 2a, c). Moreover, in both wings and halteres, each individual campaniform could be well described by two features that were common to the whole population of sensilla, demonstrating the common features uniting the sensor array (Figure 2e–h) [32••,34••].

Does DPFD encoding in wings and halteres represent a particular specialization in these mechanoreceptors? To test this we can compare their BLGN responses to those of a model neuron and examine what kind of membrane properties may support their encoding characteristics. Simulations of a general Hodgkin-Huxley neuron demonstrate that the expected feature selectivity of an unspecialized neuron is the same as described above: a pair of features in which the second feature is the derivative of the first (Figure 2b) [31••,35]. These models show that the emergent pair of features is precisely what would be expected from the most generalized dynamics of a threshold crossing spiking neuron with excitatory currents directly proportional to stimulus magnitude.

Is the encoding of wing and haltere CS, and DPFD in general, simply capturing general properties common to all neurons? Covariance analysis of the spiking activity of diverse neurons suggests not. Though DPFD is common in sensory neurons, especially those that use precise spike timing to convey information (e.g. crab chordotonal

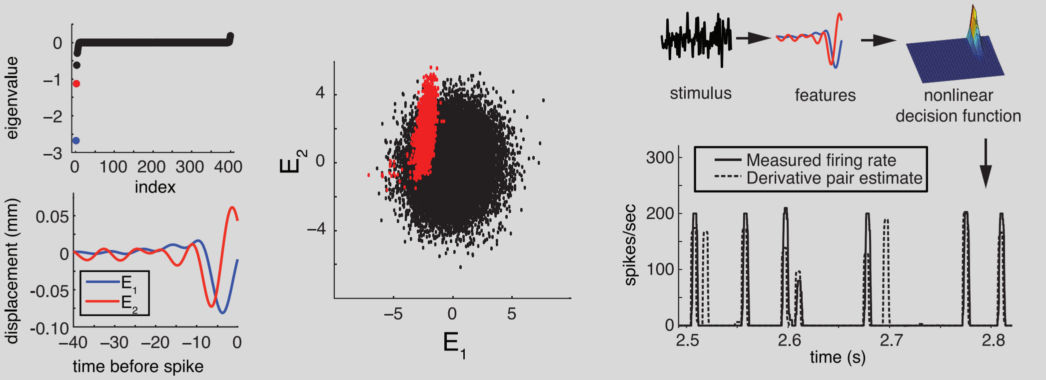
Box 1 Band limit Gaussian noise analysis methods and derivative pair feature detection (DPFD)

A random stimulus (BLGN) allows for a data-driven exploration of the features of stimulus encoded by a neuron. This assesses whether a neuron is consistent with DPFD or more specialized features. The dynamics of neurons are nonlinear and a spike-triggered average (STA) response would only capture a single dimension. However, the covariance analysis here will identify a number of linear features that approximate the system. The nonlinear decision function in step 4 is static (does not vary with time) and transforms the multidimensional filter into a spike train. The derivative pair of features should not be interpreted as a phaso-tonic response to held stimuli or a proportional, derivative, or integral signal which describes the control law. However, DPFD can be consistent with these responses. Figures adapted from Ref. [31••].



1. Stimulate with BLGN. Collect the stimuli proceeding each spike (”spike-triggering” stimuli).

2. Create covariance matrices of spike-triggering stimuli and randomly selected stimuli; find difference matrix.



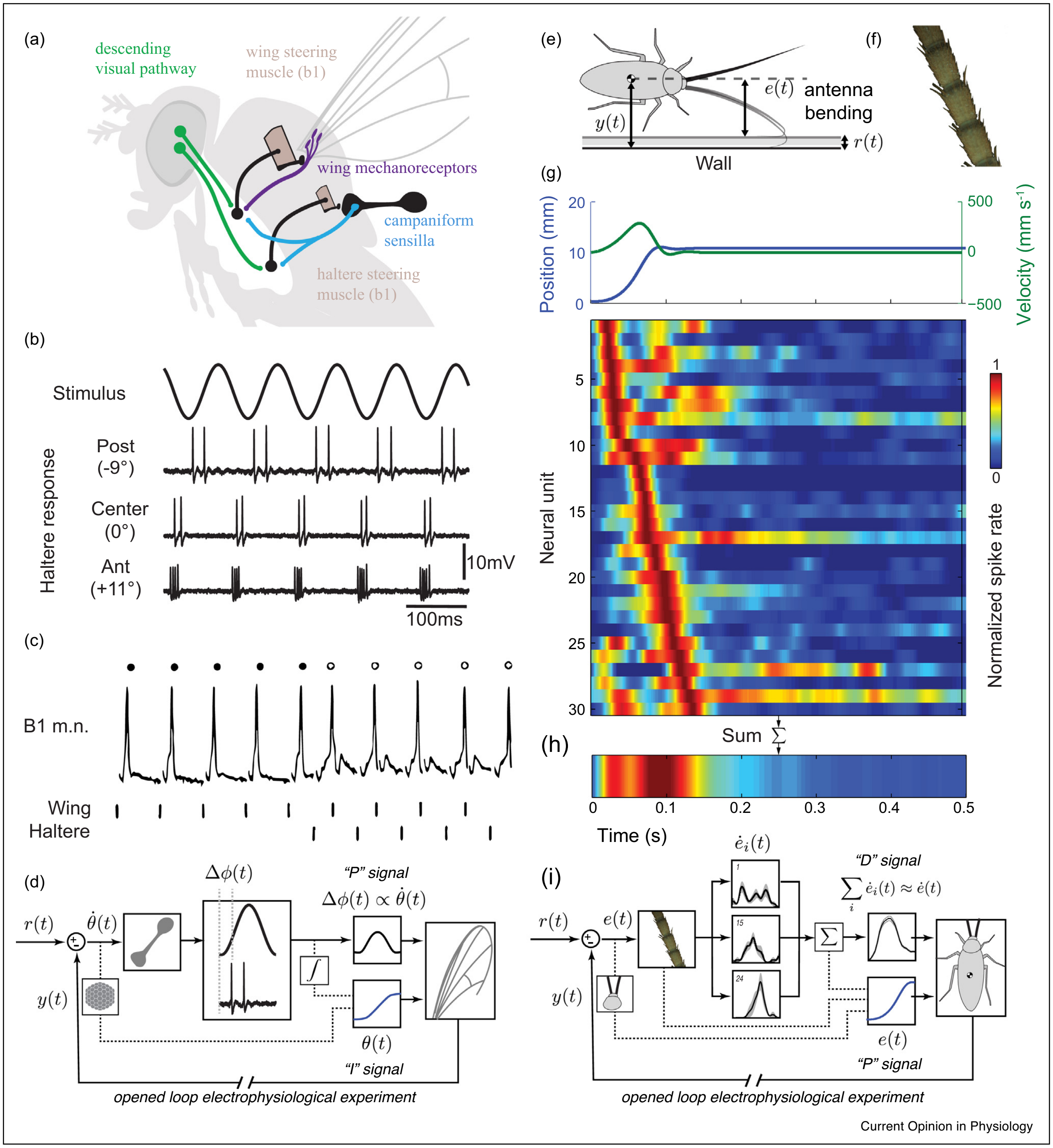
3. Two significant eigenvectors (E_1 and E_2) with a derivative relationship indicate derivative pair feature detection (DPFD). Projection onto the derivative pair shows stimulus selectivity.

4. Project stimulus onto derivative pair of features. Pass through a nonlinear decision function to predict spikes.

organs [36]; and sound localization neurons in auditory forebrain [37]), there are numerous neurons that do not deploy this encoding. Neurons selective for a single stimulus dimension are frequently found in the early sensory system, such as electric fish ampullary organs [38] or *Drosophila* olfactory receptors [39]. Neurons that are several synapses deep in the sensory pathway are occasionally selective for three or more stimulus features, endowing them with further complexity (salamander retinal ganglion cells [40]; primate visual cortex [41]). Though little is known about the specific conductances underlying feature detection beyond DPFD, experiments in diverse organisms suggest that fast potassium channels aid in speeding adaptation by increasing amplification and information processing and increasing selectivity by adding features ([42–44]). Thus, DPFD is not a necessary encoding strategy of all neurons, but is a general, and perhaps even default, encoding mechanism because it requires nothing beyond H-H dynamics. The potential advantage then is that CS may be neurally generic and hence easily modified for different purposes, while still providing specialized encoding of naturalistic stimuli via mechanical preconditioning.

There are many ways to characterize CS encoding. Relatively few campaniform sensilla studies use BLGN, but we do know that the most common encoding properties of CS is a phaso-tonic response. However, some neurons are exclusively phasic or exclusively tonic, such as the group 1 CS on the trochanter of the stick insect [17]. While

Figure 3



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Linking DPFD encoding to control laws for behavior.

(a) The wings and halteres provide sensory feedback on a wingbeat-to-wingbeat basis, structuring firing time of the wing muscles. Visual commands are sent to the haltere muscles, changing its motion, which recruits additional campaniform sensilla with different preferred firing times. This feedback alters the timing or activation of the wing steering muscles. The haltere's gyroscopic function may operate through a similar pathway. Redrawn from [22••]. **(b)** When halteres are deflected anteriorly or posteriorly, either from Coriolis forces or active movement, the firing phase of some campaniform sensilla can also shift [7,32••]. Adapted from [52••]. **(c)** Haltere campaniform sensilla from the field dF2 are electrotonically coupled with the first basalar (b1) wing steering muscle. Stimulation of the haltere at a certain phase offset relative to wing sensory inputs produces a corresponding advance or delay of the phase of activation of the b1 motor neuron. Reprinted from [53]. **(d)** The phase offset of the b1 spike is proportional to the rate of body rotation and therefore acts as the "P" signal in a PI control around angular velocity. The "I" signal much of the specialization in leg CS is likely attributable to mechanical features, we cannot rule out that neural specialization of membrane properties contributes to their selectivity, especially in neurons that lack obvious mechanical asymmetry like the distal wing CS of flies [45]. These CS are also exclusively phasic or exclusively tonic, but both types produce precise, phase-selective spiking under white noise analysis [26•]. Phase selectivity arises from DPFD (see next section) and so both phasic and tonic units are consistent with this encoding. In the moth, both wing base and wing tip CS both are DPFD (Figure 2c, d). Tuning of neurons to phasic or tonic responses could reflect a shift in the excitability of a neuron. Lacking BLGN studies in leg CS, we cannot be sure that DPFD extends to limb CS, and neural specializations could exist in some cases. Instead DPFD is a good null hypothesis for generic encoding in CS.

A white noise analysis does not fully describe the response of any nonlinear sensory system, and naturalistic stimuli can provide a different picture of a neuron's encoding, especially in modalities like audition where the frequency content of natural stimuli is highly structured [46]. White noise analysis is likely to be very appropriate for periodic natural motions like those of wing stokes, haltere oscillations, and periodic limb loading. However, the nonlinear encoding properties of jumping spider slit sensilla (close analogs of CS, but differing in morphology) result in different stimulus selectivity to white noise and complex naturalistic vibrations [47,48]. Thus, the identification of DPFD encoding should not be thought to describe every aspect of encoding, but rather as an assay of whether the dynamics of the sensory neuron are consistent with H-H model neurons or necessarily require specialization in the membrane dynamics. A BLGN analysis can demonstrate if neurons are consistent with the null hypothesis of DPFD derived from H-H model dynamics, but the functional implications for natural encoding and behavior are dependent on the type of stimuli. We next consider two examples that connect the responses of CS during naturalistic stimuli (oscillating wings and deflecting antennae) to emergent locomotor control laws.

From encoding to behavior: how generalized campaniform sensilla properties enable control strategies

Insects use CS to implement dynamics that are consistent with relatively simple control policies (e.g. linear, time-invariant). In *Drosophila*, flight stabilization to rotational perturbations is well described by a controller that detects signals proportional to, "P," and integrated from, "I," the angular velocity. In simulations and experiments, this "PI" control strategy is sufficient to stabilize fly flight and captures the response dynamics of freely flying *Drosophila* perturbed by a sudden torque caused by applying a magnetic field to a small metal pin attached to their backs [49,50,51•]. Even though "P" and "I" control responses to naturalistic stimuli are related by a derivative, they are not necessarily the same thing as the two features of DPFD which capture the response to BLGN.

The haltere-b1 motor neuron reflex shows how the phase selectivity of a DPFD neuron can encode the "P" signal of a control law when the animal senses a change in angular velocity. Body rotation produces spikes in haltere CS (Figure 3b) [52••], which phase shifts the once-per-wingstroke firing of the b1 via electrotonic coupling (Figure 3c) [18•,53]. The phase shift of b1 protracts the wing and changes wingbeat amplitude in proportion to the angular velocity perturbation [18•,51•,54•]. Could spikes from the haltere afferents also provide the "I" signal, which is the absolute position? This signal is necessary to account for the changes in body dynamics, but does not necessarily have to operate on such a rapid time course. It is possible that an integrated signal from the halteres could convey this information, but vision likely provides this signal. Indeed, recent physiological evidence from *Drosophila* hints that chemical synapses in wide-field visual interneurons provide a signal consistent with temporal integration [55].

Antennae are another location where insects use arrays of CS to implement simple control laws, but to much slower varying stimuli. Cockroaches are adept at navigating in low light and use their long antennae as tactile probes [56,57]. Mechanical properties of the antenna allow it to automatically conform into a "J" shape for tracking [58]. In addition to primarily chemoreceptive hairs, the antenna is covered in CS, and the closely related marginal sensilla at each segment of the flagellum [28]. The base of the antenna also has proprioceptors for object orientation and texture discrimination [56,59,60]. However, wall-following behavior is mediated by the flagellar receptors: the cockroach can no longer track a wall if the flagellum is severed and reattached [57].

As is the case in haltere-mediated reflexes, a pair of necessary control signals are required for antennal wall-

(Figure 3 Legend Continued) could come from several hypothesized pathways (dashed lines). **(e)** Cockroaches follow walls by regulating the distance of their body to the vertical surface (y(t)). When the reference position of the wall (r(t)) changes it produces a positional error signal (e(t)). **(f)** This signal is detected by campaniform and marginal sensilla on the antennal flagellum. **(g, h)** Each sensilla produces a phasic response to a ramp and hold stimulus that is much shorter than the overall behavior response (g), but the population sum is appropriately filtered because each unit has a different latency (h). **(i)** This population sum is consistent with the "D" signal in a PD controller around position with respect to the wall. The "P" likely comes from specific neurons in the population as well (see occasional tonic activity in (g), but might also be supplemented by vision. Plots in (e), (g) & (h) adapted from Ref. [6••].

following [61]. The cockroach responds to both the absolute position of the wall, termed proportional or "P" control, and its rate of change, termed derivative or "D" control [61,62]. A proportional derivative controller, "PD," around a *positional* error signal is very much like a proportional integral, PI, controller around a *velocity* error signal.

In response to deflections of the wall either during running or in a restrained preparation with a motorized wall (Figure 3e), the population of flagellar sensilla (Figure 3f) provides a well-resolved population code for encoding the wall's position [6••,62]. Mongeau et al. [6••] recorded from single mechanosensory neurons from the antennal nerve responding to an actuated wall that deflected the antenna. The response of each unit in the nerve to a transient deformation of 10 s of milliseconds is a phasic response of similar duration (Figure 3g). However, each unit responds with a different latency to the stimulus. The sum of the sensory activity provides a population low-pass filter, extending the transient response to 100 s of milliseconds in length but maintaining information about the rate of wall deflection, the "D" signal (Figure 3h,i) [6••,62]. The sensory signal proportional to wall position (the "P" signal) could come from small changes in the tonic firing of individual mechanoreceptors (Figure 3g), but might be provided by other cues, like vision or body contact. As in fly flight, many generic sensilla combined across a specific anatomical arrangement (the length of the antenna) likely shapes the sensory response necessary to control complex behavior. While the antennal CS have not been characterized with BLGN, they all show similar neural responses with appropriate mechanical prefiltering (changes in latency) to enable the necessary control (Figure 3g).

The versatility of proprioception through arrays of generic sensors

Mechanical filtering of sensory stimuli with generic encoding properties consistent with H-H dynamics may allow flexibility for arrays of campaniform sensilla to act in a variety of locomotor contexts. Yet a number of questions remain. While DPFD is an effective null hypothesis given that it arises from H-H dynamics, it has not been explicitly tested in a wide range of CS, especially on legs and antennae. Other arthropods that use strain receptors for prey detection or other kinds of behavior may be more specialized, as suggested for the slit sensilla of jumping spiders. We also do not yet know if mechanosensory hairs and chordotonal organs share similar encoding with CS. Finally, a major open question is how encoding of naturalistic stimuli by CS with DPFD and mechanical filtering is preserved through central processing and integrated with motor output.

During evolution, serial duplication of large arrays of generalized sensors may not require specialized tuning of individual neurons, potentially reducing constraints on the contexts in which they can be effective. Furthermore, deploying multiple sensors with similar properties might enable multifunctionality that is robust to damage and insensitive to stochasticity in individual sensory channels. Nonetheless, many biological systems seem to produce behaviors that are well-described by simple control laws [63]. Neuromorphic, or event-based, engineered sensors have growing applicability in machine vision in robots, but arrays of mechanosensory neuromorphic sensors may be advantageous for sensing and control especially on soft and deformable structures. Tuning their placement could maximize information encoding [64]. Using many localized proprioceptors with generic encoding properties simplifies the need for neural specialization, enhances robustness, and facilitates control.

Conflict of interest statement

Nothing declared.

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