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INVITED REVIEW

Inertial Sensing and Encoding of Self-Motion: Structural and Functional Similarities across Metazoan Taxa

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Synopsis To properly orient and navigate, moving animals must obtain information about the position and motion of their bodies. Animals detect inertial signals resulting from body accelerations and rotations using a variety of sensory systems. In this review, we briefly summarize current knowledge on inertial sensing across widely disparate animal taxa with an emphasis on neuronal coding and sensory transduction. We outline systems built around mechanosensory hair cells, including the chordate vestibular complex and the statocysts seen in many marine invertebrates. We next compare these to schemes employed by flying insects for managing inherently unstable aspects of flapping flight, built around comparable mechanosensory cells but taking unique advantage of the physics of rotating systems to facilitate motion encoding. Finally, we highlight fundamental similarities across taxa with respect to the partnering of inertial senses with visual senses and conclude with a discussion of the functional utility of maintaining a multiplicity of encoding schemes for self-motion information.

Introduction

Moving animals use a variety of sensory systems to navigate the complex three-dimensional environments in which they live. While exteroreceptive senses like touch, hearing, vision, and olfaction provide detailed information about the animal's environment, none of the cues they provide are useful in the absence of context regarding the body's position and movement in space. In many animal taxa, inertial senses (together with the visual system) provide this essential context that permits stability and control for goal-directed movement. Inertial senses are broadly thought of as belonging to one of two categories: graviception and rotation-sensing. Senses belonging to the former category are sensitive to linear or translational acceleration and orient the animal relative to the earth's gravity field, whereas senses in the latter division are sensitive to changes in angular or rotational accelerations. Both types of inertial senses are built around mechanosensory systems, facilitating control over locomotor reflexes on rapid timescales.

With this review, we provide a brief overview of major inertial sensory systems across diverse animal taxa, with two major points of focal interest. First, we describe the vertebrate vestibular complex as well as invertebrate statocysts, and contrast these with functionally similar schemes for inertial self-motion sensing employed by flying insects. Second, for each of these systems, we outline how nervous system elements encode motion information, both at the level of primary sensation and (where known) at higher centers. We illustrate how various mechanisms, both structural and neuronal, measure orientation and motion to guide behavioral control of animal bodies.

Hair cell systems

The best-described inertial sensory systems, including vertebrate vestibular systems, transduce mechanical stimuli using hair cells, so named for their ciliated mechanosensory "hairs." In chordate hair cells (Fig. 1A) in both the vestibular and auditory systems, these "hairs" are known as stereocillia and are interconnected by tip-linking proteins through which all the stereocilia are ultimately linked to a single, elongated apical process known as the kinocilium (rev Fritzsch and Beisel 2004). The kinocilium defines the hair cell's measuring axis: motion of each stereocilium activates mechanically-gated ion channels, with movements toward and away from the kinocilium producing depolarizing and hyperpolarizing graded potentials, respectively (Howard and Hudspeth 1988; Assad et al. 1991). This axis can be thought of as a unit vector, with another vector modeling possible directions of hair deflection. The dot-product of the two vectors produces a tuning curve taking the shape of a cosine function, with the hair cell responding at the highest magnitude when the stimulus is aligned with the preferred axis.

This cosine-shaped directional tuning curve (Fig. 1B) is the canonical encoding found in chordate vestibular hair cell afferents (Blanks and Precht 1976; Fernández and Goldberg 1976a, 1976b, 1976c; Angelaki and Dickman 2000; Haque et al. 2004; Laurens et al. 2017). It exemplifies rate coding, in which information about the stimulus is conveyed via changes in the firing frequency of the neuron. While an individual spike may be correlated with some phase of the driving mechanical stimulus, by definition the phase relationships of individual spikes provides little or no information in this mechanism of encoding. This contrasts with time-precision coding (Fig. 1C), in which the phase relationship is the primary means by which information about the stimulus is represented. Such units are said to be "phase-locked" to the stimulus, and this form of encoding is common in auditory hair cells and their afferents (Palmer and Russell 1986). Standardized definitions of both of these encoding strategies can be found in Theunissen and Miller (1995).

Invertebrate statocysts

Many marine invertebrates possess inertial-sensing organs known as statocysts. These are typically fluid- or gel-filled sacs of tissue lined with hair cells and containing one or more small calcified masses called statoliths (Fig. 2A). The statolithic weight is subject to gravity and produces responses in the underlying hair cells by compressing the suspensory medium (or by laying on top of them) and bending the stereocilia, resulting in specific hair cells becoming active in specific body orientations (Markl 1974). This is an example of a population code, where the aggregate firing of a collection of sensory cells produces a more precise estimate of the input stimulus—in this case the animal's body orientation (Fig. 2B)—than the firing of any individual constitutive cell (Georgopoulos et al. 1983, 1986). Population codes are widely observed in nervous systems, likely as a result of this increased precision as well as their ability to represent multiple stimulus parameters concurrently (Dayan and Abbott 2005).

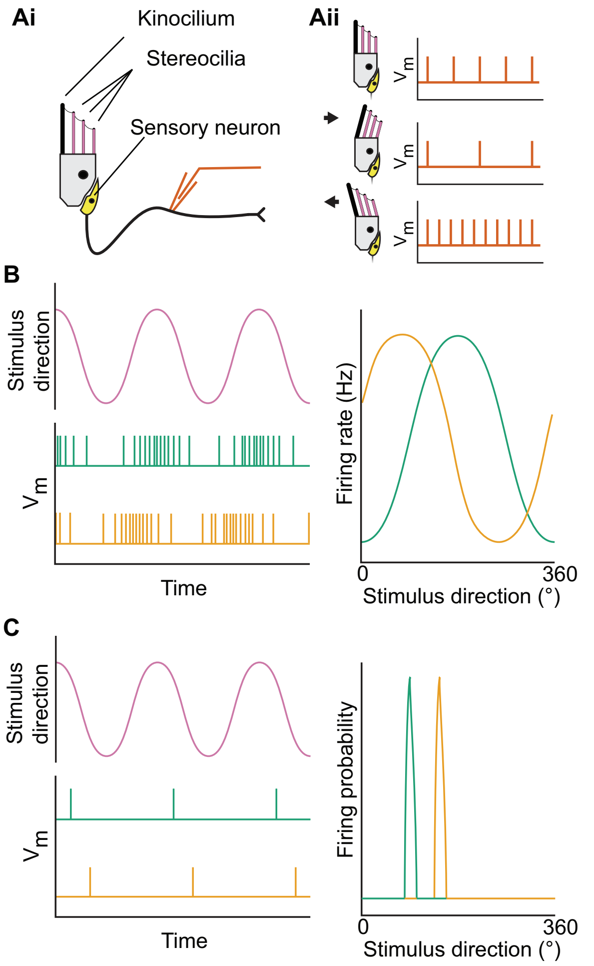

Fig. 1 Firing properties of hair cell afferents and encoding schemes used by mechanosensory elements of animal inertial senses. (**A**) Schematic view of chordate hair cell. (i) Chordate hair cells possess mechanosensory stereocilia, a large apical kinocilium, and synapse with a neuronal afferent. (ii) Directional response and firing properties of hair cell afferents. Top: With no mechanical stimulus, hair cell afferents fire with a particular baseline firing rate. Middle: when a mechanical stimulus (black arrow) deflects the stereocilia away from the kinocilium, this hyperpolarizes the afferent and lowers the firing rate. Bottom: when the stereocilia are deflected toward the kinocilium, this depolarizes the afferent and increases the firing rate. (**B**) In rate-coded units, information about the stimulus is transmitted by variation in firing rate. The top (green) and bottom (orange) units exhibit similar tuning curves, but with different preferred stimulus directions (right). For sensory cells with a defined measuring axis, like hair cells, this relationship is described by a cosine-shaped directional tuning curve, which emerges from the degree to which the stimulation direction is aligned with the measuring axis defined by the kinocilium. (**C**) Time-coded units fire reliably at a specific phase of a periodic directional stimulus (purple), and are thus said to be phase-locked. The top (green) and bottom (orange) units exhibit similar degrees of temporally precise firing with relation to the stimulus, but at different phases.

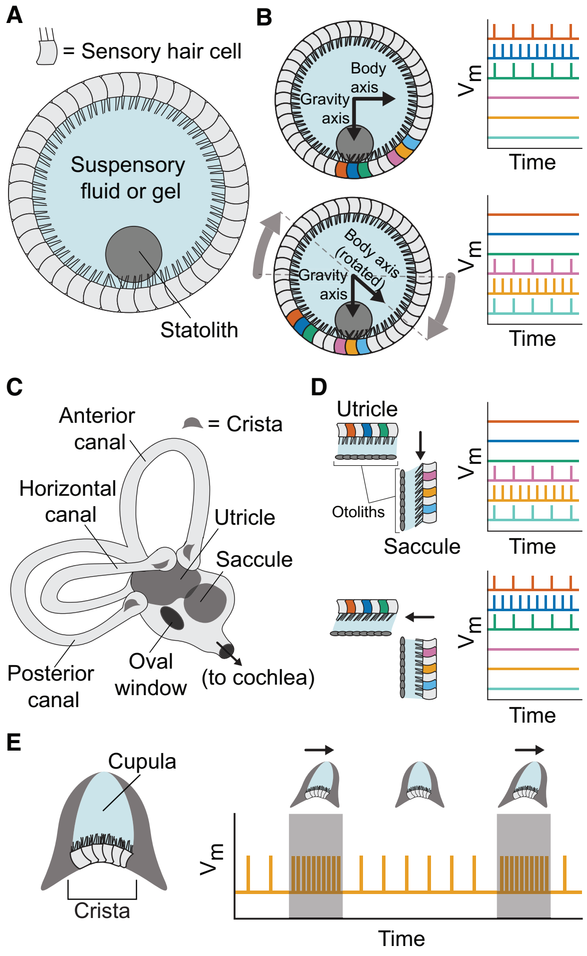

Fig 2 Hair cell organs. Invertebrate statocysts and vertebrate labyrinth. (**A**) Schematic crosssectional view of a generalized statocyst, showing mechanosensory hair cells and statolith in suspensory medium. Although morphology of invertebrate statocysts and physiology of invertebrate hair cells varies considerably, this diagrammatic view is a representative of well-characterized crustacean and molluscan systems (Markl 1974). (**B**) Population coding of body orientation using a statocyst. Top: at a given body orientation, the statolithic mass aligns with the gravity axis, and activates a particular ensemble of hair cells. Bottom: When the animal's body orientation changes, the statolithic mass remains aligned with the gravity axis, and now activates a different ensemble of hair cells. (**C**) Schematic view of generalized mammalian vestibular complex, showing the utricle and saccule (shaded, labeled) and semicircular canals (labeled) with cristae (shaded). Elements of the mammalian auditory system, the oval window and passage to the auditory cochlea, are shown in black for context. (**D**) Linear acceleration sensing via otolithic organs. The two otolithic chambers (utricle and saccule) are positioned orthogonally to one another. Fields of hair cells in each organ are anchored to calcified otoliths (dark gray) by a suspensory gel. As in the statocyst, the hair cells are deflected via alignment of the otolithic mass with the gravity field. Vertical accelerations are sensed with the saccule (top), and horizontal accelerations sensed with the utricle (bottom). (**E**) Angular acceleration sensing via semicircular canals. Left: Each canal's crista contains an array of hair cells embedded in a gelatinous mass known as the cupula. Right: Head rotations produce motion of the endolymph fluid through the canal, actuating the hair cells through movement of the cupula. The directional sensitivity of these hair cells is predominately determined by the orientation of the canal in which they are embedded.

As they are found over disparate metazoan taxa, including but not limited to crustaceans, mollusks, and coelenterates, the specific encoding properties of statocyst hair cells and their higher-order targets across this wide diversity are still mostly unknown (Markl 1974; Fritzsch and Beisel 2004; Duncan and Fritzsch 2012). Similarly, while invertebrate hair cells often feature a kinocilium or other directionally-polarized cellular morphology (Fritzsch and Straka 2014), whether this also confers directional preference to hair cell responses in a given taxa remains incompletely surveyed. Hair cells in gastropod mollusks have been shown to demonstrate cosine-shaped directional tuning to varying body orientations (Balaban et al. 2011; Popova and Boyle 2015). Cephalopod statocysts are often considerably elaborated: in *Octopus* and many other coleoids, distinct macula and crista systems sense linear and angular accelerations, respectively, and feature fields of hair cells polarized with kinocilia (Young 1960; Markl 1974; Williamson 1995). These are functionally analogous to the divisions of the vertebrate vestibular system (see below). Functional divisions are also observed in some crustaceans, as in the mud crab *Scylla* where spatially segregated afferents encode pitch and yaw body rotations (Silvey et al. 1976). Higher-order targets of crustacean statocysts mediate an equilibrium reflex akin to the vertebrate vestibulo-ocular response, stabilizing the eyestalks against body rotations (Markl 1974; Silvey and Sandeman 1976; Nalbach 1990; Fujisawa and Takahata 2007). Similarly, leg proprioceptors and statocyst inputs assort to complementary targets in the crayfish brain, guiding postural control responses (Takahata et al. 1981; Hama and Takahata 2005).

The vertebrate labyrinth

Although the evolutionary history of the vertebrate vestibular complex has been addressed from developmental (Beisel et al. 2005) and sensory transduction perspectives (Duncan and Fritzsch 2012; Fritzsch and Straka 2014), a cursory discussion of this organ's complex three-dimensional topology illustrates how a simple system such as the statocyst can specialize into dedicated regions measuring angular and linear accelerations. It is likely that the common ancestor of vertebrates and invertebrates had a sensor similar to statocysts (Markl 1974; O'Brien and Degnan 2002; Duncan and Fritzsch 2012). Basal chordates; hagfish and lampreys (Cyclostomata) have a single statocyst-like structure, the macula. It is an oblate, unpaired, median structure in which floats a "raft" of calcified otoconia (Fritzsch et al. 2014). In jawed fish and their descendants (*Gnathostomata*), the organ is elaborated into a paired structure subdivided into two chambers, the utricle and saccule (Fig. 2C). These are oriented orthogonally to one other, and this morphology, along with the orientation of hair cells within them, tunes them to linear accelerations along specific translational motion vectors (Fig. 2D). As in the invertebrate statocyst, hair cells in these structures are activated principally by calcified mass elements (otoliths) and signal acceleration with respect to the gravity field.

The most prominent departure from an ancestral statocyst-like structure in chordates is the fluid-filled semicircular canals (Fig. 2C). These are rudimentary in the cyclostomes, but in gnathostomes they are arranged on either side of the animal into a triplet of bony arches (Fritzsch et al. 2014), each orthogonal to the other two and located in the plane of one of the principal rotational motion vectors (yaw, pitch, roll). Hair cells are oriented along the plane of each canal and contained within specialized regions known as cristae (Fig. 2E). The canals lack the calcified masses found in the otolithic organs. Instead, endolymph fluid moves through the canals and deflects the hair cells via the action of an overlying gelatinous mass known as the cupula (Hillman and McLaren 1979). Transient movements of the fluid accompany body rotations due to the fluid's inertia, driving hair cells in the semicircular canals to signal angular accelerations roughly (though not precisely) in correspondence with the canal's plane of orientation (Haque et al. 2004).

Vestibular hair cell afferents and their higher-order targets

Postsynaptically to the hair cells, populations of distinct "regular" and "irregular" vestibular hair cell afferents send information to the brain (Kalluri et al. 2010; Eatock and Songer 2011). As their names suggest, regular afferents fire with little variation in their interspike intervals, and irregular afferents fire with wider variation. The canonical cosine tuning (described above and illustrated in Fig. 1A, B) for stimuli with respect to the hair cell's preferred measuring axis explains motion encoding by both types of units. Although regular afferents were long thought to convey more information through time-coding than irregular afferents (Sadeghi et al. 2007; Cullen 2012), recent information theoretic approaches support the opposite view, showing that irregular afferents encode information principally through precise spike timing. A single model was able to recapitulate the respective spiking patterns of both types of affererent by varying sensitivity and variability, suggesting that these two properties can account for the differences in their encoding strategies (Jamali et al. 2016). Afferents send output to the vestibular nucleus, and from there to a variety of brainstem nuclei, subcortical, and cortical targets, serving a variety of functions such as gaze-stabilizing vestibulo-ocular reflexes, balance and postural control, and spatial navigation (Angelaki 2004; Cullen 2012, 2014; Jacob et al. 2014; Besnard et al. 2015). A recent analysis of vestibular system projections in the primate brain demonstrates that, in response to identical motion stimuli, encoding schemes vary considerably among higher-order centers and are not aligned within a common coordinate framework (Laurens et al. 2017). This underscores open questions about the diversity of encoding patterns observed in vestibular afferents, a discussion we will continue below under the heading "Parallel encoding mechanisms: similarities across taxa."

Insect solutions to the challenge of body-rotation sensing

Here we describe inertial sensory mechanisms in flying insects. Notably absent from this discussion are statocysts. While their crustacean ancestors almost certainly had statocysts, virtually all insects, except for a few hymenopteran taxa, lack them (Markl 1974; Ishay et al. 1983, 2008). In both aerial and terrestrial locomotion, insects make use of a variety of sensory strategies for graviception (summarized by Markl [1974] and Bender and Frye [2009]). We therefore limit our discussion of insect inertial senses to the context of body rotation sensing. Rotation sensing is especially important for flying insects, as flapping flight is inherently unstable at the time-scale of individual wingbeats, and requires corrective reflexes with high speed and precision (Taylor and Krapp 2007; Liang and Sun 2013). We describe three organs used by insects to detect inertial forces associated with body rotations. Each is built around specialized mechanosensory cells which, like hair cells, are directionally tuned to mechanical forces acting on the body arising from motion. Unlike hair cell-based organs, however, each of these sensory mechanisms takes advantage of the physics of rotating systems to facilitate active sensing of body rotations.

Dipteran halteres

In true flies (order *Diptera*), the hind wings of their four-winged ancestors have evolved into small, club-shaped organs known as halteres (Fig. 3A, top). Known for centuries to be necessary for flight (Derham 1714), halteres remain the best-described insect inertial sensory system. Several works (Taylor and Krapp 2007; Yarger and Fox 2016) elaborate more thoroughly on the topics in the following discussion. During flight, the aerodynamically-inert halteres beat in coordination with the wings. A rotating mass (in this case the flapping haltere with its relatively massive bulb) will develop an angular momentum (Fig. 3B). Due to this momentum, the haltere will resist movement when the animal rotates its body. This results in Coriolis forces acting at the haltere base, which create strain on the campaniform sensilla (Fig. 3C). Models of haltere kinematics show that motion of the animal along all three principal rotational motion vectors (roll, pitch, and yaw) produces unique profiles of Coriolis and other inertial forces (Pringle 1948; Nalbach 1993; Thompson et al. 2009). These models also suggest that these forces cause the haltere to deviate slightly from its natural beat-plane, though these deflections are predicted to be very small and have not been empirically measured.

Coriolis and other inertial forces associated with body rotation are exerted maximally at the haltere bases (Nalbach 1993; Thompson et al. 2009), at which lie several fields of campaniform sensilla. Found in many locations on insect bodies, campaniform sensilla are strain sensors embedded in the cuticle and are comprised of a mechanosensory neuron embedded in a deformable cuticular dome (Fig. 3D). Approximately 1200 campaniform sensilla are found on the blowfly, roughly half of which are localized to the haltere bases (Gnatzy et al. 1987). Firing properties of campaniform sensilla have been characterized extensively in the context of insect locomotion (Zill and Moran 1981; Ridgel et al. 1999; Akay et al. 2004). Each sensillum fires preferentially in response to forces acting along a particular vector, and this tuning is generally thought to be imparted by the shape of the dome and its orientation in the cuticle (Pringle 1948; Zill and Moran 1981). Tuthill and Wilson (2016) more thoroughly review encoding properties of campaniform sensilla in a recent publication.

Haltere campaniform sensilla and their higher-order targets

Pringle (1948) predicted many features of campaniform sensilla encoding using mechanical models, and made the first physiological recordings from the haltere nerve. More recently, encoding properties of individual haltere campaniform afferents have been characterized via intracellular recordings. Individual sensilla fire at every cycle of the haltere's oscillation with extraordinarily precise phase locking (Fig. 1C), having both low latency and low jitter. In the crane fly *Tipula*, this tuning persists even when the haltere is experimentally driven to over four times the frequency observed during natural flight (Fox and Daniel 2008).

Many questions remain about the processing of haltere information beyond primary afferent neurons. Of the haltere campaniform fields, the basal plate (also termed dF2; Fig. 3A, top) is the only one for which synaptic targets have been unambiguously identified. In a series of ablation experiments in *Calliphora*, basal plate afferents were found to be the sole inputs from the haltere nerve onto the motoneuron commanding the first basalare, a wing-steering muscle (Fayyazuddin and Dickinson 1996). This motoneuron also receives input from terminals of wing campaniform afferents, and experimentally stimulating both haltere and wing nerves illustrates a scheme by which precise spike timing might relay motion information during flight (Fayyazuddin and Dickinson 1999). Similarly, neck motoneurons directing the head (and thus gaze, since flies cannot make eye movements independent of the head) receive parallel inputs from haltere primary afferents and the fly's motion vision system (Strausfeld and Seyan 1985; Milde et al. 1987). Behavioral experiments in blowflies demonstrate that these two modalities can jointly or independently mediate gaze-stabilizing reflexes (Hengstenberg 1988, 1993). In the blowfly, some neck motoneurons require excitatory drive from haltere afferents in order to fire (Huston and Krapp 2009), and recent work in *Drosophila* shows that intact halteres are required even for reflexes driven entirely by vision (Mureli et al. 2017). The integration of haltere input with vision is considered in more detail below under the heading "Ubiquity of Optokinetic Reflexes."

Lepidopteran wings

Dipteran halteres evolved from wings, and other insects likely use their wings to obtain similar information during flight. Like halteres, wings experience Coriolis forces during body rotations and feature

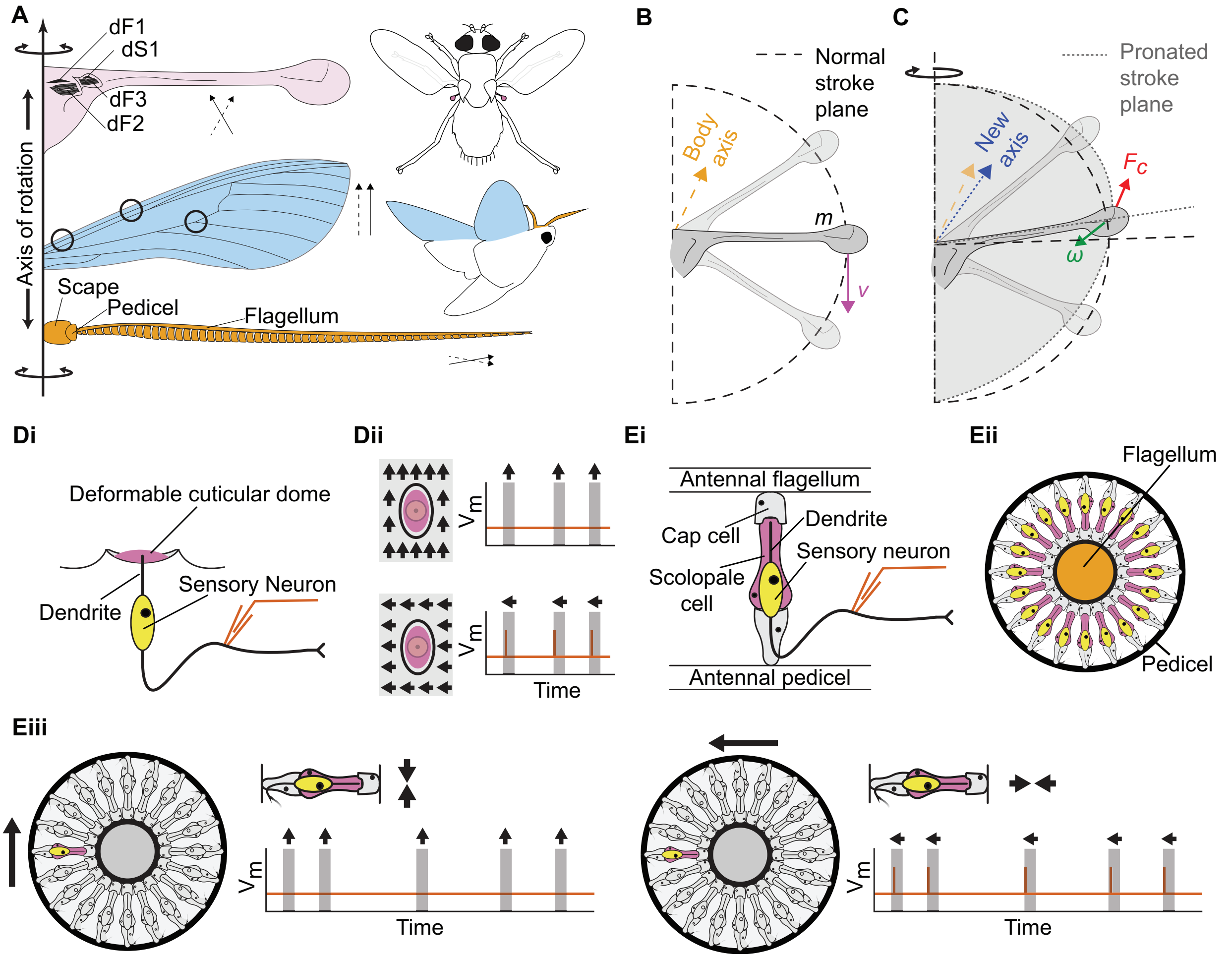

Fig. 3 Insect inertial sense organs. (**A**) Schematic view of inertial sense organs arranged along their axes of rotation, showing right-side dipteran haltere (top), lepidopteran forewing (middle), and lepidopteran antenna (bottom). Each organ is viewed from the dorsal surface, with the approximate relative direction of the body axis being shown adjacent to each organ (solid arrow for right organ, dashed arrow for left organ). Top: dorsal fields of campaniform sensilla are labeled (after Gnatzy et al. 1987) and shown in black. Middle: Hawkmoth forewing. Circles identify locations of campaniform fields (Pratt et al. 2017). Bottom: Hawkmoth antenna. (**B**) Predicted forces acting on a haltere during normal oscillation (after Bender and Frye 2009). The mass (*m*) and velocity (*v*, magenta arrow in the image plane) of the haltere bulb (black dashed line in the image plane) confer momentum (*mv*). Orange dashed arrow shows the body axis, drawn projecting into the image. (**C**) Predicted forces change in a yaw turn. Body orientation changes to the new axis defined (blue dotted arrow). This imparts angular velocity (ω, green arrow projecting out of the image) onto the bulb, producing a Coriolis force (F_C, red arrow projecting into the image) orthogonal to the beat plane. The force moves the haltere out of its normal stroke plane into a pronated stroke plane (gray dotted line, projecting into the image), inducing strain on the base which can be sensed by campaniform sensilla. Wings and antennae experience similar forces during rotations, but with respect to different coordinate frames owing to their different points of articulation. Wings also experience confounding aerodynamic forces, which are negligible for halteres. (**D**) Schematic view of insect campaniform sensillum. (i) The dendrite of a bipolar neuron is embedded within a deformable cuticular dome. (ii) Directional response is determined by the ovoid shape of the dome. Cuticular strain forces (black arrows) acting along the major axis of the oval (top) do not trigger an action potential, whereas forces acting along the minor axis (bottom) do. Gray bars illustrate stimulus epochs, illustrating the temporal precision of campaniform sensilla. (**E**) Schematic view of insect JO scolopidium. (i) A stretch-sensitive JON is embedded within a deformable scolopale cell anchored to a cap cell. (ii) The scolopidia circumferentially bridge the second (pedicel) and third (flagellum) antennal segments, shown in cross-section (after Sanes and Hildebrand 1976). (iii) Antennal flexion (black arrow) does not reliably trigger action potentials in the highlighted scolopidium (left) unless it is aligned with the scolopale's long axis (right). As above, gray bars illustrate stimulus epochs for the antenna flexions.

fields of campaniform sensilla. Because wings also experience aerodynamic loading during flapping flight, characterizing the changing forces acting across the wing surface becomes more complicated than in the aerodynamically inert haltere. Accordingly, wing campaniforms are distributed across the wing surface rather than concentrated at the base as in the haltere. As in understanding the wing's primary role in producing lift and thrust, rigorous biomechanical modeling is essential for understanding its role as a sensor. In recent years, a number of researchers have laid the groundwork for such an analysis, focusing on the tobacco hornworm moth (*Manduca sexta*).

A diversity of methods has been employed to study the role of wing-sensing in flight control. Mathematical modeling work suggests that wing Coriolis forces have their major effect in twisting of the wing plane, and are most likely sensed via the accompanying shearing forces (Hinson and Morgansen 2015). Robotic models of deformable surfaces have shown that inertial torques during flapping flight may be crucial to steering and maneuverability for larger insects such as *Manduca*, as the small wingstroke deviations that result in inertial torques can have disproportionate consequences for flight control (Eberle et al. 2015; Jankauski et al. 2017). Finally, tethered flight experiments demonstrate that the moth's behavior is indeed influenced by inertial sensory cues from the wings. By attaching small magnets to the wing and rotating an energized pair of Helmholtz coils around the animal, a torsional strain along a continuum of force vectors was induced as the magnets aligned with the magnetic field. The moth's abdomen followed the movement of the magnetic field (and thus the induced torsional strain) with close fidelity, suggesting inertial signals from the wings take part in an abdominal elevator reflex that stabilizes pitch during flight (Dickerson et al. 2014).

While these behavioral and theoretical works clearly outline a role for wings in inertial sensing, neurophysiological data about the firing properties of individual wing campaniforms have been scant. However, a recent work used novel extracellular recording technique to record from the afferent neurons in the wings of *Manduca* (Pratt et al. 2017). Firing properties of campaniform sensilla can be modulated by temperature, and the distribution of campaniform fields across the wing surface enables them to be selectively targeted with an infrared laser. By using the laser in conjunction with multielectrode recording, individual spiking units in the wing nerve could be traced back to their associated campaniform sensillum on the wing surface (Fig. 3A, middle). Information theoretical analysis was then used in conjunction with a mechanical model of the wing surface to estimate the forces acting on a particular campaniform field and characterize firing properties in response to wing movements. While this approach showcases many advantages of the moth as a model organism by combining rigorous quantitative mechanical models with robust neurophysiological methods, the interpretation of these findings nonetheless remains limited pending more detailed analysis of higher-order targets of wing campaniforms or the functional role of particular campaniform fields during behavior.

The Johnston's organ in moths and flies

The Johnston's organ (JO) of the antenna is present in many insects and has been extensively characterized in moths, flies, bees, and other insects in diverse roles such as windspeed sensing, graviception, and a band-limited sense of hearing for courtship and predation avoidance (Bennet-Clark and Ewing 1969; Gewecke 1974; Kamikouchi et al. 2009; Yorozu et al. 2009; Krishnan et al. 2012; Lapshin and Vorontsov 2013; Fuller et al. 2014; Khurana and Sane 2016). In the hawkmoth *Manduca*, the antennae comprise a mechanical system with some similarities to the dipteran halteres, and the JO can act as an inertial rotation sensor. As the moth beats its wings, it induces passive oscillations in the elongated antennal flagella, causing Coriolis forces when the animal rotates. In another similarity to the haltere system, antennal flagella are required for stable flight: when the flagella are amputated leaving the JO intact, the moth cannot control its trajectory, and flight returns to normal when the amputated flagella are reattached (Sane et al. 2007).

Mechanical stimuli are transduced in the JO via an array of scolopidia (Taylor and Krapp 2007), complexes centered around stretch-sensitive cells that monitor the relative movement of the pedicel (second segment) and flagellum (third and terminal segment) of the antennae (Fig. 3A, bottom). Like hair cells and campaniform sensilla, scolopidia are innervated with a spiking neuron which fires in response to mechanical deformation (Fig. 3E). Intracellular recordings of Johnston's organ neurons (JONs) reveal a high degree of phase-locking with respect to their driving mechanical stimuli, similar to haltere primary afferents (Dieudonne et al. 2014). Many of these units were responsive over a range spanning from 0 up to 100 Hz—covering the frequency ranges where induced Coriolis forces would be expected to occur given the moth's typical wingbeat frequency (Sane et al. 2007; Dieudonne et al. 2014). Taken together, these findings illustrate the sensitivity of JONs and their suitability for encoding Coriolis forces acting on the antennae, but as in wing-borne mechanosensation, a more comprehensive analysis of motion encoding by this organ would require knowledge of encoding in higher-order regions.

Toward this end, the genetic tools available in *Drosophila* have facilitated a better understanding of the cellular physiology of JO scolopidial neurons and their downstream synaptic targets. Firing properties of two identified classes of cells receiving direct inputs from distinct classes of JONs in the antennae have recently been characterized (Azevedo and Wilson 2017). Fruit fly JON afferents follow five distinct branches (A–E) into the brain, and postsynaptic cells A2 and B1 are named for the branches from which one or potentially more JONs supply them with input (Kamikouchi et al. 2009; Lai et al. 2012; Matsuo et al. 2016; Azevedo and Wilson 2017). A2 cells act as envelope followers for antennal vibrational inputs: they perform a nonlinear transformation integrating both frequency and amplitude components of the mechanical stimulus. As a result of this transformation, their firing phase is decoupled from that of the stimulus. B1-cell membrane responses, by contrast, remain phase-locked to their upstream JON. The B1 cells are further subdivided into distinct clusters, each tuned to a restricted band of frequencies. This allows them to act as "biological band-pass filters" to emphasize particular frequency ranges, further narrowing the range-fractionation of their supplying JON afferents.

The fly is known to make use of this sensory system as part of its repertoire of flight-control reflexes. Passive oscillations at wingbeat frequency are observed in the fly's antennae, which are interpreted to be the result of wing-induced airflow (Mamiya et al. 2011). This enables the antennae to respond to changes in the wing power and steering effort, and several antenna-wing reflexes are identified, including one where antennal movements feed back onto the muscles controlling the contralateral wing's downstroke power. Wild-type flies with ablated or immobilized antennal flagella (and thus silenced JOs) show deficits in these behaviors, reproducing effects caused by genetic ablation of the JONs (Mamiya et al. 2011; Mamiya and Dickinson 2015). Aerodynamic coupling between the wing and antennae might therefore implement a kind of indirect proprioception monitoring wing kinematic parameters, but whether or not fly JONs also constitute an inertial sense is unclear. Although the JONs have an appropriate range of input to detect Coriolis forces, it is not resolved whether the higher order pathways make use of such information, or whether they are representative of the JO sensory pathway in other insects like the moth. Likewise, though the antennae oscillate at wingbeat frequency during flight, the club-type *Drosophila* antennae might not have appropriate mechanical characteristics for making induced Coriolis or other inertial forces salient to the JO. Mechanical characterization and kinematic modeling in conjunction with further characterization of the JO sensory pathway in flies might help resolve this ambiguity.

General considerations

Ubiquity of optokinetic reflexes

The vertebrate and crustacean gaze-following and vestibulo-ocular responses, *Drosophila* head and wing compensatory responses, and moth abdominal elevator response all exemplify reflexive behaviors that can be mediated by both inertial and visual senses. A recent review explores this topic across a similar taxonomic diversity as we consider here, with a focus on how the strengths of each sensory modality complement shortcomings of the other (Hardcastle and Krapp 2016). Inertial senses respond quickly, but are susceptible to drift in the represented coordinate frame. Vision can orient the animal in terms of absolute landmarks, but signal transduction is comparatively slow and thereby susceptible to motion blur. Because it operates at a faster time-scale than vision, the inertial system is well-suited to stabilizing the animal's motion and increasing the visual system's effectiveness for guiding active behavior.

Because information from the inertial and vestibular senses must be brought into register with each other to control common motor targets, studying such systems can grant insight into sensory encoding strategies. In vertebrates, motion-sensitive cells in the mouse retina have recently been shown to encode along distinct axes that nonetheless differ from those observed in the vestibular system, implying that the two are brought into registration further along in signal processing in order to execute gaze-stabilizing vestibulo-ocular reflexes (Sabbah et al. 2017). As with mammals, insects must coordinate input from each sensory modality in downstream targets. In the fly, the neck motoneurons driving compensatory gaze reflexes are directly targeted by both haltere afferents and motion-sensitive visual cells in the lobula plate tangential cell network (Strausfeld and Seyan 1985; Milde et al. 1987). These motoneurons are preferentially tuned to visual motion inputs in their relevant direction of control, achieved by a series of "matched filters" implemented sequentially throughout the visual system (Huston and Krapp 2008). The neck motoneurons therefore define a terminal control point in the system architecture, and it is thus likely that the haltere system assorts in a complementary manner at this level of signal processing. Regardless of how this is accomplished, the insect system illustrates how the computational demands of performing coordinate transformations among different sense modalities can be made tractable to individual neurons.

Parallel encoding mechanisms: similarities across taxa

The diversity in encoding schemes employed by vertebrate vestibular afferents underscores a broader observation about the different roles inertial systems occupy in mediating behavior. This is illustrated by a proposed functional division of the vertebrate otolith afferents into a "sustained" system that accurately represents the orientation of the body in space, and a "transient" system that operates at rapid timescales for guiding postural and locomotor reflexes (Curthoys et al. 2017). The sustained system is supplied by rate-coding regular units, whereas the transient system uses spike-timing information from irregular units. A hardware model of the vertebrate vestibular system was considered successful when it recapitulated the spike activities of both classes of primary afferent and reconstructed the stimulus from them (Corradi et al. 2014).

The utility of precise spike time encoding for fast postural adjustments is demonstrated by insect systems, as precise phase locking is seen in primary afferent neurons of haltere and wing campaniforms and JO scolopidia (Sane et al. 2007; Fox and Daniel 2008; Pratt et al. 2017). Although higher-order encoding in invertebrate systems has not been characterized in comparable detail to the vertebrate system, a parallelism to vestibular afferents is observed in the *Drosophila* JO, with B1 cells retaining a close phase relationship to the stimulus and envelope-following A2 cells encoding phase-invariant motion energy (Mamiya and Dickinson 2015; Azevedo and Wilson 2017). This early separation into phase-locked and phase-invariant coding in the processing of JO mechanical stimuli mirrors the encoding by irregular and irregular vestibular afferents. While it is an open question whether this arises from a functional parallelism between the two systems, this convergence nonetheless highlights architectural similarities in mechanosensory system organization seen across widely disparate taxa.

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