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Review

Computational mechanisms of mechanosensory processing in the cricket

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Summary

Crickets and many other orthopteran insects face the challenge of gathering sensory information from the environment from a set of multi-modal sensory organs and transforming these stimuli into patterns of neural activity that can encode behaviorally relevant stimuli. The cercal mechanosensory system transduces low frequency air movements near the animal's body and is involved in many behaviors including escape from predators, orientation with respect to gravity, flight steering, aggression and mating behaviors. Three populations of neurons are sensitive to both the direction and dynamics of air currents: an array of mechanoreceptor-coupled sensory neurons, identified local interneurons and identified projection interneurons. The sensory neurons form a functional map of air current direction within the central nervous system that represents the direction of air currents as three-dimensional spatio-temporal activity patterns. These dynamic activity patterns provide excitatory input to interneurons whose sensitivity and spiking output depend on the location of the neuronal arbors within the sensory map and the biophysical and electronic properties of the cell structure. Sets of bilaterally symmetric interneurons can encode the direction of an air current stimulus by their ensemble activity patterns, functioning much like a Cartesian coordinate system. These interneurons are capable of responding to specific dynamic stimuli with precise temporal patterns of action potentials that may encode these stimuli using temporal encoding schemes. Thus, a relatively simple mechanosensory system employs a variety of complex computational mechanisms to provide the animal with relevant information about its environment.

Key words: cricket, mechanoreception, neural coding, neural maps.

Introduction

Animals within their sensory environments face the challenge of transducing and interpreting relevant sensory information in order to enact the appropriate behavioral responses to the stimuli. Neuroscientists who wish to understand how sensory systems accomplish these tasks are faced with three major challenges: (1) to understand the relationships between spatio-temporal activity patterns in sensory neural ensembles and the information they convey, (2) to understand how the spatio-temporal patterns are decoded by cells at the next processing stage, and (3) to understand how computations (e.g. pattern recognition) are carried out on that decoded information. These challenges are difficult or impossible to separate from one another in many cases, since the functions of representation, decoding and computation are often concatenated. For example, in the human visual system, the transformation in the spatial representation of visual space between the retina and the primary visual cortex is thought to enable a computation carried out by postsynaptic cells: the complex log transformation of visual images (Schwartz, 1994). Over the last several decades, researchers in several institutions around the world have been studying these problems with considerable success in a much simpler mapped sensory system: the cercal sensory system of the cricket. The cercal system is implemented around a representation of stimulus direction and dynamics, and demonstrates the essential features of neural maps found in more complex systems, including mammalian visual and auditory systems. This review will discuss progress toward understanding the structure and operation of the cercal system within the context of the neural computations it mediates, and summarize insights into the mechanisms through which information-processing algorithms are implemented within this system. These insights may well be generalized to more complex systems.

Overview of the cercal sensory system

Every orthopteran insect has a cercal sensory system, which mediates the detection, localization and identification of air currents. The receptor organs for this modality are two antenna-like appendages called cerci at the rear of the abdomen, covered with mechanosensory hairs. Air currents in the animal's immediate environment move these hairs and, thereby, activate the receptor neurons at the base of the hairs. Fig. 1 shows the basic structure of the cercal sensory system in *Acheta domestica*: the cerci, mechanosensory afferent neurons and the projection interneurons.

The cercal system was shown in early studies to be of critical importance for the oriented escape response (Boyan et al., 1986; Camhi, 1980) and jumping (Hoyle, 1958). However, it is a considerable oversimplification to classify this system as an 'escape system', just as it would be an oversimplification to categorize our own visual system with that label. Rather, the cercal system can be thought of as functioning as a low-frequency, near-field extension of the animal's auditory system. The emerging picture of the cercal system and its associated behaviors is fairly complex. Air particle displacement directed at the cerci can elicit at least 14 distinct responses, including evasion, flight, offensive reactions, scanning, freezing, and various reactions during male stridulation, and the response can depend on the behavioral state of the animal as well as the context of the environment (Baba and Shimozawa, 1997). In

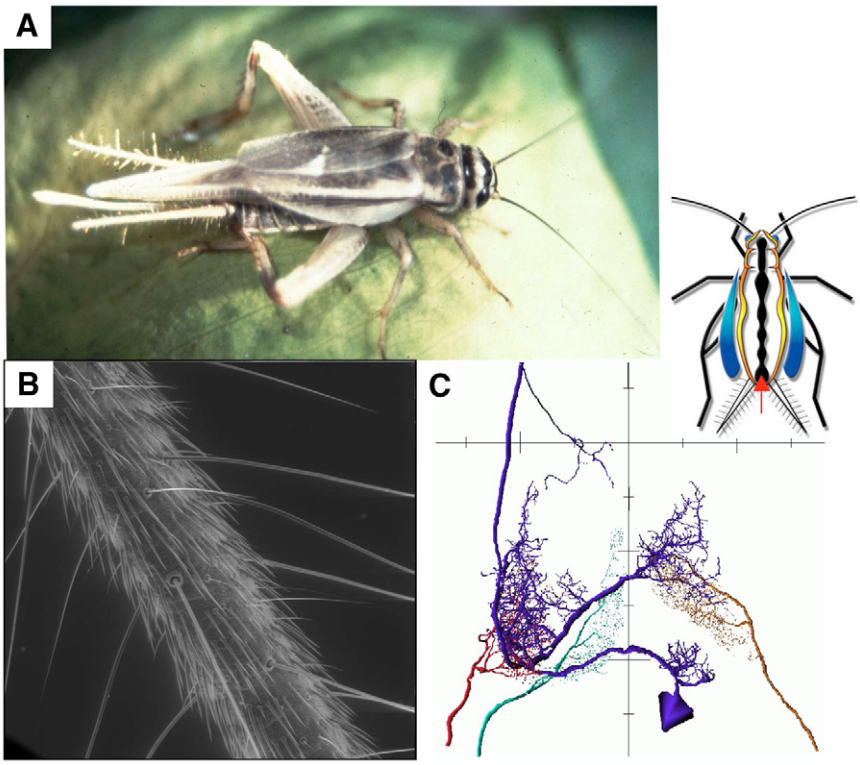

Fig. 1. The cricket cercal system. (A) *Acheta domestica*. The cerci are the two antenna-like structures, covered with fine hairs, extending from the rear of the abdomen. This is a female: the ovipositor can be distinguished between the two cerci. (B) Scanning electron microscope close-up of a segment of the cercus. The cercus is approximately 1 cm in length. (C) Computer reconstructions of a primary sensory interneuron (blue) and three primary sensory afferents (red, light blue and brown) in their correct anatomical relationships. These cells were stained in different animals and the reconstructions were scaled and aligned to a common coordinate system. Scale: 40 μm between tick marks on the scale bars. The inset shows a cartoon of a cut-away view of the cricket nervous system. The terminal abdominal ganglion, where the sensory neurons and interneurons are located, is indicated with a red arrow.

addition to sensitivity to air particle displacement stimuli mediated by the filiform receptors we study, the cercal system is also responsible for mediating behavior related to orientation relative to gravity as well as a variety of touch and chemotactic sensations *via* other types of sensor on the cerci (Sakaguchi and Murphey, 1983; Murphey, 1985; Heusslein and Gnatzy, 1987). Our discussion will be limited to the filiform receptors sensitive to air particle displacement.

Filiform mechanoreceptor array

In the common house cricket *Acheta domestica*, which is the species we study, each cercus is approximately 1 cm long in a normal adult cricket, and is covered with approximately 750 filiform mechanosensory hairs. These hairs range in length from less than 50 μm to almost 1.5 mm (Landolfa and Miller, 1995). Each hair is supported at its base by a viscoelastic socket that enables the hair to pivot within its socket, rather than bending along its shaft (Thurm, 1964; Thurm, 1965a; Thurm, 1965b; Thurm, 1983; Thurm and Kuppers, 1980). Each hair's directional movement axis is determined by the orientation of a hinge-like structure in the socket. The 750 hairs on each cercus are arrayed with their movement axes in diverse orientations within the horizontal plane, insuring that air currents of sufficient velocity will deflect all of the filiform hairs to some extent: each hair will be deflected from its rest position by an amount that is proportional to the cosine of the angle between the air current direction and the hair's movement axis.

Unlike the mammalian cochlea, where efferent neural feedback can fine-tune the responsiveness of the auditory transducers, mechanical filtering of air current stimulus amplitude and frequency in the cercal system is determined solely by the biomechanical configuration of the hairs (Kanou and Shimozawa, 1984; Kumagai et al., 1998; Osborne, 1997; Shimozawa and Kanou, 1984a; Shimozawa and Kanou, 1984b; Shimozawa et al., 1998; Cummins et al., 2007; Cummins and Gedeon, 2007; Gedeon et al., 2007; Heys et al., 2008). Specifically, the primary determinants of each hair's frequency filtering properties are its length, mass and the viscoelastic properties of its socket: these properties determine the hair's moment of inertia, spring stiffness, and extension into the boundary layer of moving air surrounding the cercus.

The movements of the ensemble of hairs will therefore depend on the direction and dynamics of the air current. Thus, the internal representation of any particular air current (e.g. the air current caused by the wing beats of an approaching predatory wasp) will be a complicated spatio-temporal pattern of activity across the entire array of synaptic arborizations of these filiform afferents within the cricket's nervous system.

Since the beginning of studies of the cercal sensory system, researchers have noted the extremely low inter-animal variability in the placement and characteristics of the filiform hairs (Landolfa and Jacobs, 1995; Landolfa and Miller, 1995; Walthall and Murphey, 1986). The importance of the cerci for the animal's survival, the coupling between cercal structure and function, and the extremely low inter-animal variability of cercal receptor hair array structure are all consistent with the conjecture that these structural attributes have been subject to substantial selective pressure, and may be nearly optimal from an engineering standpoint, if only we could determine the appropriate, behaviorally relevant metrics for optimality.

Sensory receptor neurons

Each mechanosensory hair is innervated by a single spike-generating mechanosensory receptor neuron. These receptors display directional and dynamical sensitivities that appear to be derived largely from the mechanical properties of the hairs themselves (Humphrey et al., 1993; Kämper and Kleindienst, 1990; Landolfa and Jacobs, 1995; Landolfa and Miller, 1995; Roddey and Jacobs, 1996; Shimozawa and Kanou, 1984a; Shimozawa and Kanou, 1984b). The amplitude of the response of each sensory receptor cell to any air current stimulus depends upon the direction of that stimulus, and these

directional tuning curves of the receptor afferents are well described by cosine functions (Landolfa and Jacobs, 1995; Landolfa and Miller, 1995). The response amplitudes also depend upon the frequency composition of the stimulus waveforms, and generally follow the trend that would be predicted from the mechanical filtering properties of the hairs: receptors innervating long mechanoreceptor hairs (>900 μm) are most sensitive to low frequency air currents (<150 Hz), and receptors innervating medium length hairs (500–900 μm) are most sensitive to frequency ranges between 150 and 400 Hz (Roddey and Jacobs, 1996; Shimozawa and Kanou, 1984a; Shimozawa and Kanou, 1984b). Receptors innervating the shortest hairs (50–500 μm) respond to frequencies up to 1000 Hz.

Internal representation of air current direction and dynamics

The axons of the receptor afferents project in an orderly array into the terminal abdominal ganglion to form a continuous representation (i.e. neural map) of the direction of air currents in the horizontal plane (Bacon and Murphey, 1984; Jacobs and Theunissen, 1996; Jacobs and Theunissen, 2000; Paydar et al., 1999). That is, the afferent synaptic terminals form an ordered array across which there is a continuous, systematic variation in the value of their peak sensitivities to air current direction. The synaptic terminals from afferents having similar peak directional sensitivities arborize in adjacent areas, and the spatial segregation between afferent arbors increases as the difference in their directional tuning increases.

The systematic mapping of stimulus direction across a subset of the afferents has been demonstrated in several recent studies in which anatomical and physiological measurements were taken from a representative sample of afferents near the base of the cerci proximal to the terminal abdominal ganglion (Jacobs and Theunissen, 1996; Paydar et al., 1999; Troyer et al., 1994). Anatomical reconstruction of the afferent arborizations was used to construct a three-dimensional model of this proximal portion of the afferent map in the form of a probabilistic atlas. This basic structure is shown in Fig. 2. By combining the predicted responses of each class of afferent with this information about the spatial location of their terminal arborizations within the neural map, predictions have been made of the spatial patterns of synaptic activation that would result from sustained, unidirectional air currents (Jacobs and Theunissen, 2000; Paydar et al., 1999; Troyer et al., 1994). Recently, Ogawa and colleagues actually visualized ensemble activity patterns of filiform afferents using calcium imaging (Ogawa et al., 2006), and found these patterns to be consistent with the predictions.

Preliminary predictions have also been made of the dynamic spatio-temporal activation patterns across the ensemble of proximal filiform afferents for sinusoidal air current stimuli (Jacobs and Pittendrigh, 2002; Cummins et al., 2003). However, these predictions of the dynamic response patterns may significantly underestimate the complexity of the actual dynamic response patterns, since they did not take differential conduction delay along the cercus into account. As we have recently demonstrated, spikes arriving at the terminal abdominal ganglion from distal cercal mechanoreceptors have a significantly greater latency than spikes arriving from more proximal receptors, due to the added conduction time along the length of the cercus (Kennel et al., 2005). This ‘dispersion’ of the spiking input from afferents, which would otherwise have identical directional and dynamic response characteristics, could be of considerable functional significance. In other words, the cercus is acting as a ‘delay line’. We are currently investigating the differential anatomical projections of these distal receptors, and examining the functional significance of these delay-line characteristics. Preliminary evidence suggests that the primary sensory interneurons could, in fact, extract and use this delay information.

Primary sensory interneurons

The 1500 sensory afferents synapse with a group of approximately 30 local interneurons, and approximately 20 identified projecting interneurons that send their axons to motor centers in the thorax and integrative centers in the brain. It is important to note that these 20 or so projecting interneurons represent the entire ensemble for all information captured by the 1500 sensory receptors and transmitted to higher processing stages. This represents a huge compression.

Like the afferents, these interneurons are also sensitive to the direction and dynamics of air current stimuli (Jacobs et al., 1986; Kanou and Shimozawa, 1984; Miller et al., 1991; Theunissen and Miller, 1991; Theunissen et al., 1996). Researchers have measured stimulus-evoked neural responses in several projecting and local interneurons, using several different classes of air current stimuli and electrophysiological techniques. Recently, optical recording techniques using Ca^{2+}-sensitive dyes have also been used to examine the mechanisms underlying synaptic integration in cercal interneurons (Ogawa et al., 2006; Ogawa et al., 2008). The stimuli that have been used range from simple unidirectional air currents to complex multi-directional, multi-frequency waveforms. Two important general conclusions from all of these studies are as follows.

(1) Primary sensory interneurons extract and encode information about stimulus direction based solely on the shape and position of their dendrites within the afferent map. In other words, stimulus direction is represented by a ‘place code’ in the afferent map. This excludes the necessity for synaptic specificity mechanisms, through which the postsynaptic interneuron would connect to a specific subset of presynaptic inputs based on an ‘identity code’ (mediated, for example, by recognition of a specific cell-surface marker).

(2) The frequency sensitivity of each interneuron is a function of two independent factors: (a) its inherent frequency filtering properties, and possibly (b) the position of its dendrites within the afferent map. That is, stimulus frequency is largely a function of intrinsic and synaptic properties of the interneuron, but may also emerge as a place code if the delay-line characteristics mentioned above turn out to be of significance.

In the remainder of this review, we will focus on our recent analyses of neural coding at this interface between the sensory afferents and the primary sensory interneurons, using some analytical approaches from information theory and statistics.

Neural coding in the cricket cercal system

Tuning curve analyses

Neural coding is defined as the mapping between stimuli in the environment and their representation in patterns of electrical activity in the nervous system. The earliest efforts toward discovering the nature of these mappings stretch back over 80 years to the work of Adrian and colleagues on stretch receptors in the leg muscles of frogs (Adrian and Zotterman, 1926). They employed what is now known as the tuning curve technique: a stimulus is presented to the nervous system in which a single parameter can be systematically varied over the course of several trials. For each presentation of the stimulus with a specific value of the parameter of interest, an output of the nervous system is measured, generally a count of the number of action potentials in a small window of time during or after the stimulus presentation. Another tuning curve metric is to measure the time to the first response that can be discriminated or, inversely,

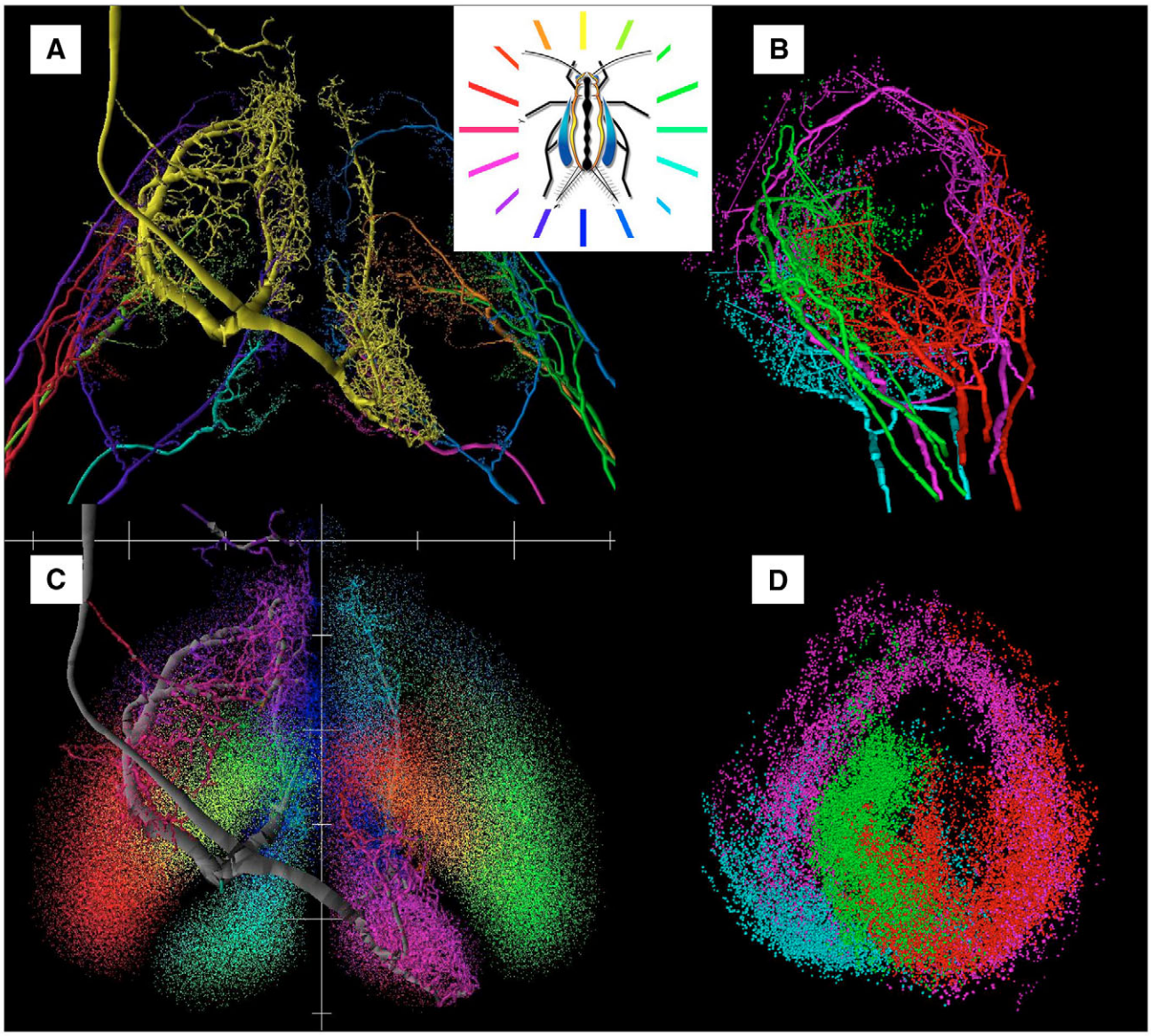

Fig. 2. Anatomical prediction of synaptic connectivity between filiform sensory afferents and interneurons. (A) A reconstruction of interneuron right (R)10-2 is shown in yellow. Afferent arbors from 12 different filiform hair receptors are shown in other colors. The color of each afferent corresponds to its direction of peak activation. These 12 classes span the range of all different classes of receptor directional sensitivities. Inset cartoon shows the color code indicating the preferred stimulus direction with respect to the cricket body coordinates. (B) Composite view (saggital) of 11 different sensory afferents from the left cercus illustrating the continuous representation of direction selectivity within the nervous system. Cells with similar directional tuning arborize near each other and those tuned to other directions are spatially segregated showing their color. (C) Image of the afferent map of air current direction, from both cerci, with an image of the compartmental model of interneuron 10-2 imbedded in the map. Each directional class of afferent arbors is transformed into a 'statistical cloud' corresponding to the density of synaptic terminals for that stimulus direction. This provides a direct demonstration of the neural map of direction. The overlap between the sensory interneuron with the afferent map of air current direction predicts synaptic connectivity from the afferents onto that interneuron. Here we just mask the interneuron dendrites with the color corresponding to the statistical cloud of afferent synapses in that region. (D) Image of the distribution of synaptic varicosities of the population of sensory afferents from the left cercus tuned to different air current directions from the left cercus. Same view as in B. The varicosities form a continuous three-dimensional structure in the neuropil. Note that the peak directional tuning of the varicosities changes continuously with location around the structure. Starting at the top of the structure (pink) and moving clockwise [red, yellow (out of view), green and blue].

the mapping is reported as the minimum value of a stimulus parameter that elicits any activity in the nervous system. Solving the neural coding problem is then just reduced to determining the input–output relationship defined by the function relating the values of the stimulus parameter to the measured output of the cell. An example of such a relationship is shown in Fig. 3: the directional tuning curve of interneuron right 10-2a from *Acheta domestica*.

Although this method is simple to use and yields a good first-order assessment of neural function, it relies on two rather strict sets of assumptions. First, it is assumed that a single, generally static parameter of the stimulus is important for the nervous system. This can be a problem when the nervous system actually depends on a dynamic stimulus, or a stimulus that cannot be easily parameterized. Second, the choice of how the response is measured necessarily

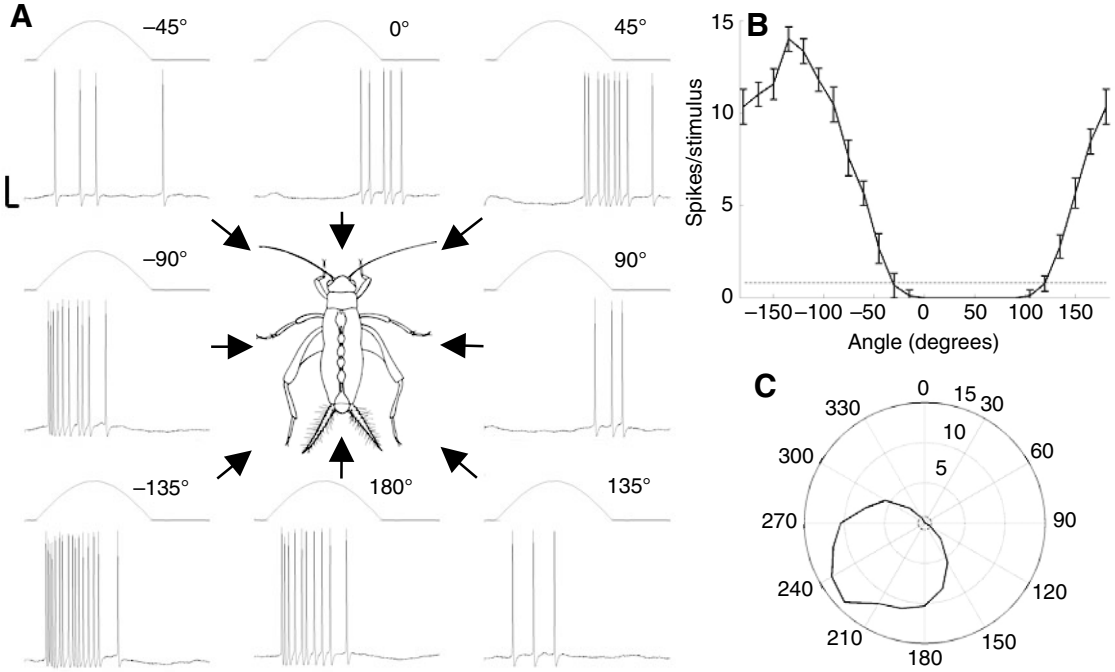

Fig. 3. Directional tuning curve for interneuron 10-2a. (A) Single puffs of air from eight different directions relative to the cricket (top traces) elicit various patterns of spiking activity (bottom traces) in an interneuron of class R10-2a. Scale bar: *x* 10 ms, *y* 875 mm s^{-1} (stimulus)/10 mV (intracellular membrane potential). (B) To generate the tuning curve the same cell as in A was presented with 10 stimuli from each of 24 different directions in the horizontal plane (15° separation between samples). The number of spikes elicited in the 60 ms window following stimulus onset was counted for each trial, and mean and s.d. across trials is shown as a function of stimulus direction. The spontaneous firing rate of the cell was also determined, and the gray broken line shows the expected number of spontaneous spikes in a 60 ms window. Note that stimuli from angles –15° to 105° inhibit the firing activity of this cell below the spontaneous rate, which can also be seen as a slight hyperpolarization in the membrane potentials of A. (C) The mean values from B, plotted in polar instead of Cartesian coordinates.

requires a strong assumption about the nature of the code itself, usually that the information about the stimulus is completely contained in the firing rate.

The method has been extensively used to demonstrate the directionality of the cercal system, beginning with the use of directional oscillatory sound stimuli (Tokareva and Rozhkova, 1973; Edwards and Palka, 1974; Palka et al., 1977; Palka and Olberg, 1977), and later being refined to stimuli consisting of single puffs of air (Westin et al., 1977; Tobias and Murphey, 1979; Westin, 1979; Aldworth et al., 2008; Miller and Jacobs, 1984; Jacobs and Miller, 1985; Jacobs et al., 1986; Miller et al., 1991; Theunissen and Miller, 1991; Bodnar et al., 1991; Baba et al., 1991; Baba et al., 1995; Kolton and Camhi, 1995) (Z.A., A. G. Dimitrov, G. Cummins, T. Gedeon and J.P.M., manuscript submitted). In one set of experiments, it was shown that two bilateral pairs of interneurons (10-2a and 10-3a) formed a functional unit capable of detecting air particle displacement at moderate velocities from all 360° of space in the horizontal plane (Miller et al., 1991; Theunissen and Miller, 1991). Similarly, by statistically sampling the cercal afferent population, Landolfa and colleagues were able to determine the directional sensitivity of the entire afferent array (Landolfa and Jacobs, 1995). These population-level tuning curves have in turn led to theoretical work on how neural coding is implemented in populations of neurons, both in interneurons (Salinas and Abbott, 1994; Butts and Goldman, 2006) and afferents (Ergun et al., 2007).

These studies spanned the system from the receptor level to the local and projecting interneurons of the terminal abdominal ganglia, though most of the studies with air particle displacement stimuli (rather than oscillatory sound stimuli) focused on interneurons 10-2a and 10-3a. For the sake of completeness, average tuning curves elicited by air particle displacement stimuli for 222 cells (127 of whose morphology was confirmed by staining) from classes 8-1a, 9-1a, 9-1b, 10-1a, 7-2a, 8-2a, 9-2a, 9-3a, 10-2a and 10-3a are shown in Fig. 4. Interneuron 11-1a was never recorded from in over 500 recordings, but it has been reported to be sensitive to multiple stimulus directions and especially stimuli with angular velocity [i.e. vortices termed 11-1c (see Kämper, 1984) and NGI-5 (see Baba et al., 1991)]. Fig. 4C shows the peak directions for all of the giant interneurons with uni-modal tuning.

As detailed in (Miller et al., 1991), the four interneurons composed of left and right 10-2a and left and right 10-3a form a functional unit sensitive to low velocity air displacement from all 360° of directional space in the horizontal plane (Fig. 4Biii). Based on observed stimulus–response measurements, information theoretic calculations demonstrated that the ensemble responses of these four interneurons to uni-directional air puffs contain enough information that an 'upstream' decoder could determine the direction of the source with an accuracy of about 10°, even if that decoder were limited to a simple ratio of spike counts as the operative neural coding scheme (Miller et al., 1991; Theunissen and Miller, 1991). It has been speculated that interneurons 9-2a and 9-3a may form a second such functional unit sensitive to higher velocities of air movement (Miller et al., 1991). Giant interneuron GI 7-2a and probably GI 8-2a receive input from the clavate hairs and so are sensitive to acceleration due to gravity (Sakaguchi and Murphey, 1983). But here and in other studies (Kämper, 1984; Kohstall-Schnell and Gras, 1994) GI 7-2a was also found to respond to air particle displacement at sufficiently large stimulus levels. Along

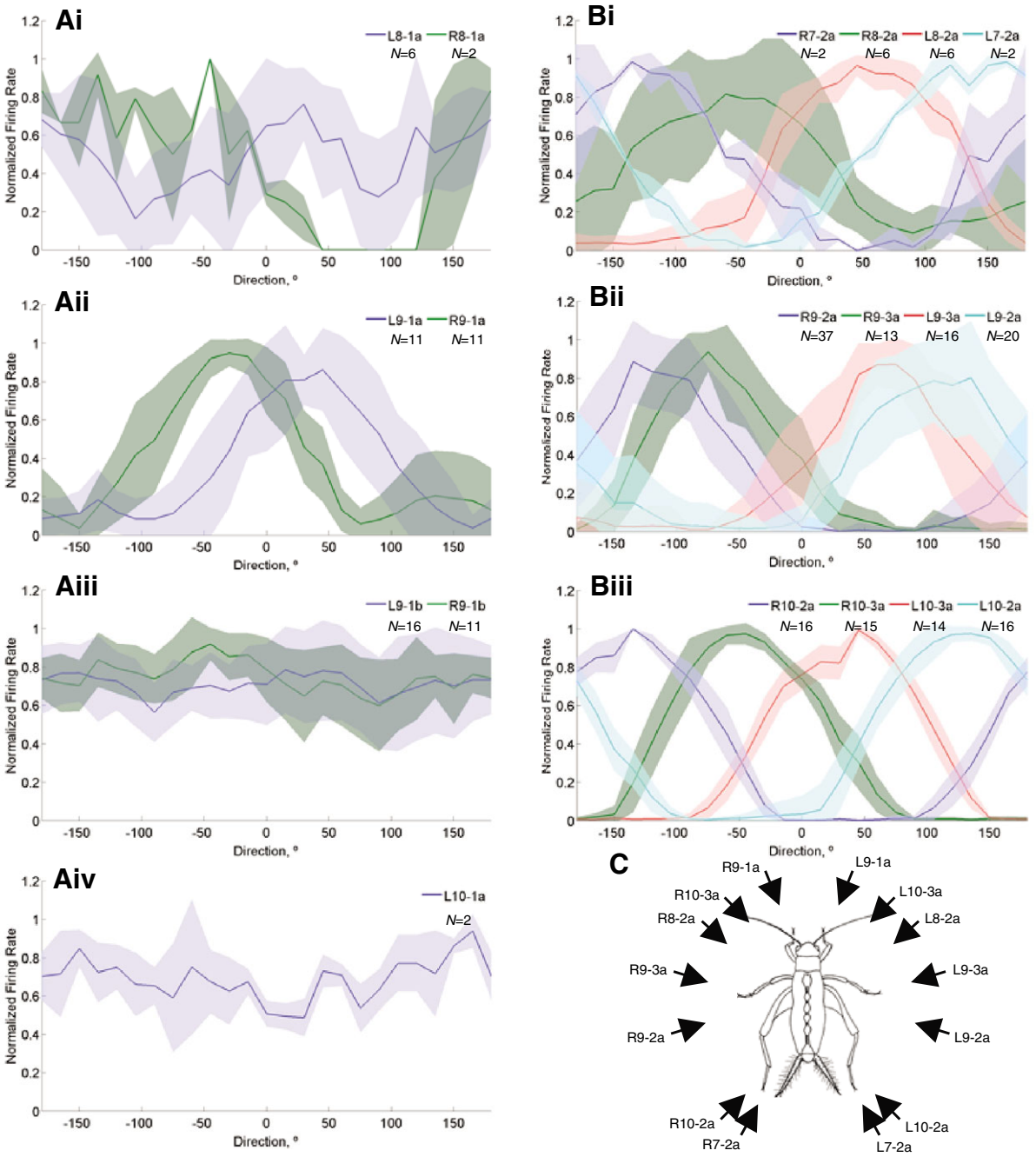

Fig. 4. Directional tuning curves for ventral giant interneurons (vGIs) and dorsal giant interneurons (dGIs). (A) Mean Cartesian tuning curves for interneurons with axons in the ventral group, with amplitude normalized to maximal firing rate. The shaded background represents ±1 s.d. across the populations of specified neurons. Ai: 8-1a (medial giant interneuron, MGI); Aii: 9-1a (lateral giant interneuron, LGI); Aiii: 9-1b; Aiv: 10-1a. (B) Mean Cartesian tuning curves for dGIs, grouped into potential functional units (data format as in A). Bi: 7-2a and 8-2a; Bi: 9-2a and 9-3a; Bi: 10-2a and 10-3a. (C) Representation of peak directional selectivity of all GIs with unimodal directional tuning in relation to the cricket. R, right; L, left.

with 8-2a, 7-2a has directional tuning such that the two pairs of cells could form yet another functional unit, sensitive to very high intensity air particle displacement (Fig. 4Bi).

White noise, kernels, stimulus reconstruction and information rates

A second approach to the coding problem is the 'white noise' approach of Wiener, popularized for use in neuroscience by Marmarelis, Naka and colleagues (Wiener, 1958; Marmarelis and Naka, 1972). The goal in this methodology is to predict the output of a potentially non-linear system to a stochastic input signal, usually Gaussian white noise (GWN). The white noise approach was first used to study the cercal system in experiments on the afferent layer and local non-spiking interneurons of the cockroach (Kondoh et al., 1991a; Kondoh et al., 1991b). For the afferent layer the first- and second-order kernels together provided a very good fit to experimental data, while in the local interneuron the first- and second-order filters only combined to describe about half of the neural response (the contribution of the second-order filter was negligible).

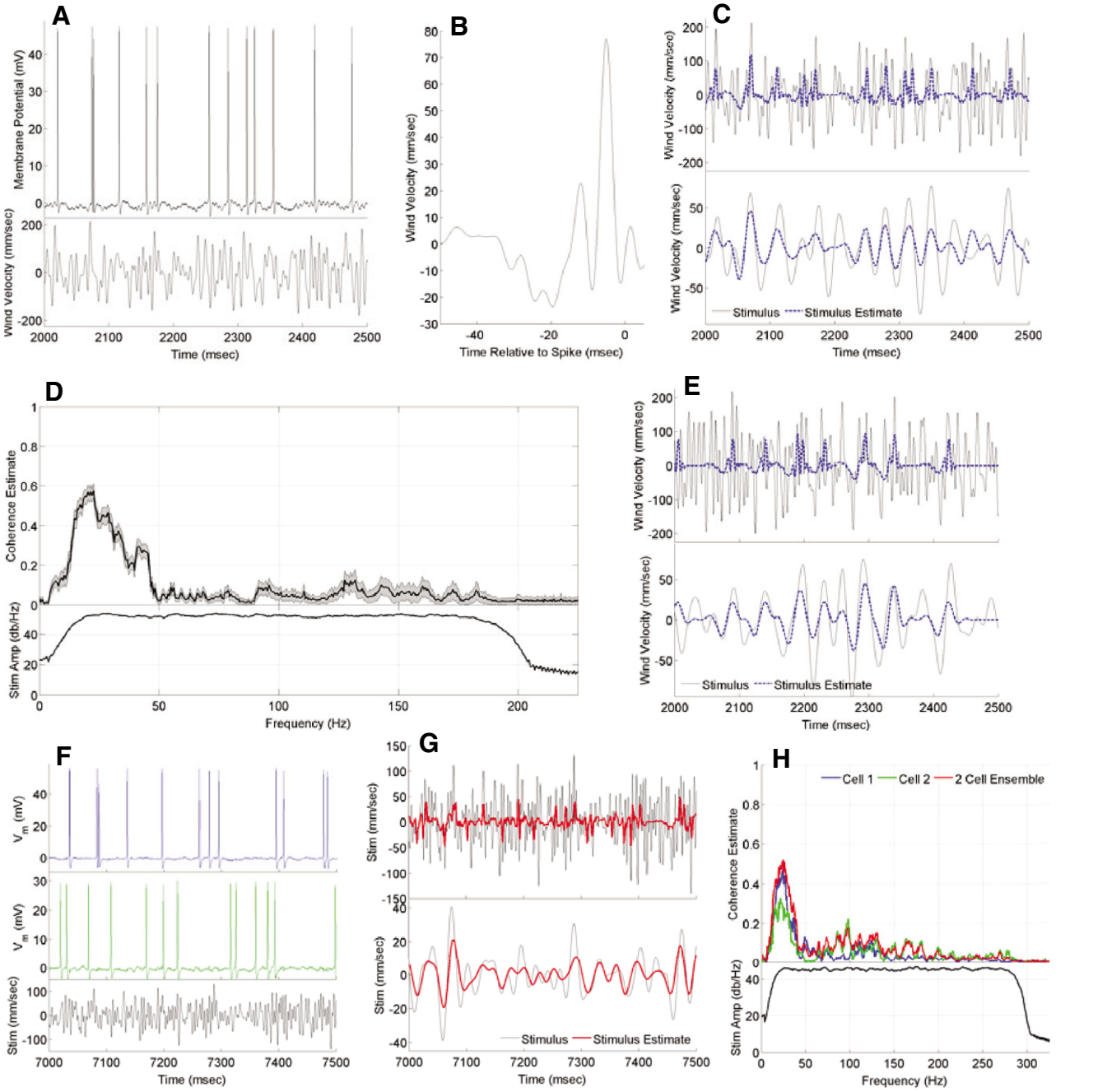

Fig. 5. Stimulus reconstruction and coherence measurements. (A) A 500 ms recording of 10–200 Hz band-passed Gaussian White Noise (GWN; r.m.s.=73 mm s^{-1}) stimulation (lower panel) and elicited response (upper panel) in a right 10-2a interneuron (same cell as in Fig. 3). (B) Linear kernel obtained from a full 100 s of simultaneously recorded stimulus and response data. (C) Stimulus from A (black) and best linear estimate obtained from stimulus reconstruction using kernel in B (broken blue line). The upper panel shows the full stimulus and stimulus estimate; the lower panel shows both after low-pass filtering below 50 Hz. (D) Upper panel: stimulus–response coherence mean (black line) ±1 s.d. (gray background), calculated over 10 repeats of stimulus. Lower panel: power spectra of stimulus (upper and lower panels calculated from data in A). (E) Stimulus reconstruction using kernel from B on a test data set where the stimulus was drawn from the same statistical distribution as the stimulus in A (upper and lower panels same convention as in C). (F) Simultaneous recording for 500 ms of R10-2a (blue, not the same cell as A) and L10-3a (green) in response to a 10–300 Hz band-passed GWN stimulus (lower trace, r.m.s.=43 mm s^{-1}). (G) Estimated reconstruction of stimulus in F using combined kernel from R10-2a and L10-3a (upper and lower panels same convention as in C and E). (H) Upper panel: coherence curves from data in F obtained using only cell R10-2a (blue), only cell L10-3a (green), and both cells together as a functional unit (red). Lower panel: power spectrum of stimulus from F.

Bialek and colleagues approached the neural coding problem from the organism's viewpoint. Rather than trying to model the encoding problem (i.e. how stimuli get transduced to neural output), their method addresses decoding: estimation of the stimulus that elicited a specific spike train (Bialek et al., 1991; Rieke et al., 1997). The mathematics is essentially the same, though in this case the neural response becomes the input variable, while the 'output variable' that is being estimated is the stimulus. This approach has been called

'reverse reconstruction' to denote its inversion of the more traditional white noise analyses. This type of analysis enables elements of information theory to be applied to the problem of characterizing a neuron's input–output characteristics, and allows quantitative calculations of the amount of information that could be decoded from a neuron's spike trains, in terms of bits (Shannon, 1968; Cover and Thomas, 1991), given a set of assumptions about that cell's encoding scheme. This approach has been used to investigate coding in the first two layers of the cricket cercal system, yielding valuable insights. One study of frequency sensitivity to broadband (10–400 Hz) stimuli concluded that all four cells in one functional ensemble (left and right 10-2a and 10-3a) have identical frequency tuning, concentrated in the 10–50 Hz range (Theunissen et al., 1996). An associated study applied the same information theoretic approach to analyze dynamical encoding characteristics of filiform mechanoreceptors.

Fig. 5 shows several aspects of this type of analysis of data from interneurons 10-2a and 10-3a. The cell under study was stimulated with a dynamically changing air current, directed along the axis corresponding to that cell's peak sensitivity. The velocity of the air current varied according to a band-limited (10–200 Hz) GWN function. The spike train elicited by this stimulus was recorded (Fig. 5A). The first-order Volterra kernel (also referred to commonly as the first-order 'stimulus reconstruction' kernel) was then extracted (Fig. 5B). This kernel corresponds to the best estimate of the average stimulus waveform leading up to a single spike, if the coding is linear. Within the context of neural coding, the notion of linearity does not refer to the spike-generation process itself: it is well known that the Hodgkin–Huxley equations are non-linear, i.e. that doubling the current input to a cell will yield a voltage response that is not necessarily double. Rather, linearity of coding implies that all of the information in patterns of two or more spikes can be decoded by analyzing 'one spike at a time', i.e. that the information in spikes is additive. In other words, the 'meaning' of a short-interval doublet of spikes would correspond to the 'meaning' of two single spikes offset by the observed doublet interval. It is certainly possible to have a non-linear process like spike generation serving as the basis for the production of a linear coding scheme (e.g. rate coding), since it is a change in the spike rate, not the spike shape, that encodes the information.

The kernel waveform is interesting in and of itself: it yields an estimate of the aspect of the stimulus that leads to a spike. These kernels can also be used to quantify the 'performance characteristics' of a cell under the assumption of linearity, by (a) obtaining an estimate of the entire stimulus waveform that was presented to the cell, and then (b) comparing that estimate with the actual waveform that had, in fact, been presented. The approach is conceptually very simple: starting with the observed spike train elicited in the experiment, construct an estimated stimulus waveform by 'stamping down' an image of the reconstruction kernel every time a spike occurred, and add up all of the kernel waveforms. In regions where spikes are isolated by intervals longer than the duration of the kernel, the estimated stimulus waveform will simply be a kernel-shaped bump in the stimulus waveform. Where there are sequences of spikes that come very close together in time, the kernels will overlap, and the summation over the kernels will yield a complex waveform. The next step of the analysis is simply to compare the estimated stimulus waveform with the actual waveform: if the estimate and actual stimulus are superimposable, then the cell was 'perfectly' encoding the stimulus waveform. This is, of course, never the case: the estimate will deviate from the actual stimulus in some respects. The extent to which the estimate deviates from the real stimulus yields a quantitative measure of (a) the limitations of the cell in capturing the information about the stimulus, (b) the 'noise' in the encoding process, and (c) the possible errors in assumptions about the encoding scheme. In the studies of the cricket interneurons, it was found that stimulus waveform could be decoded with relatively high fidelity using a linear decoder, but only within a relatively narrow frequency range (10–70 Hz).

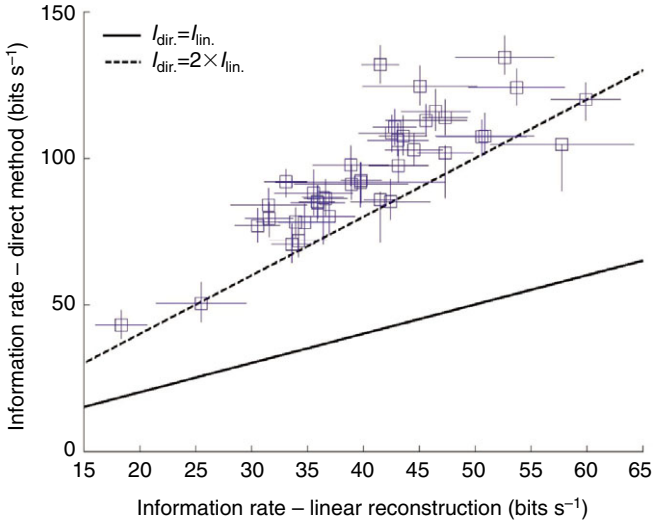

Fig. 6. Failures of the linear reconstruction approach: comparison of information rates from stimulus reconstruction and direct method measurements in the dGIs. Error bars on the linear reconstruction information estimate are s.d. across trials; error bars on direct method estimate represent 95% confidence. *I*, information rate; dir., direct; lin., linear.

In these studies, the measure used for assessing the 'fidelity' of encoding was the magnitude squared coherence function, which has also been called the 'gain function' in the neurophysiological literature. A mathematical derivation is beyond the scope of this review, but an excellent description and discussion of this function is presented in Borst and Theunissen (Borst and Theunissen, 1999). Briefly, the gain function represents the encoding characteristics of the neuron as a function of frequency: the higher the gain at a particular stimulus frequency, the more information is encoded by that cell about that frequency. A gain of 1 would correspond to a perfect match or superimposability between the estimated and actual stimuli, and thus indicate a 'perfect' encoder, zero noise, and a valid set of assumptions. A gain of zero would indicate a substantial problem in one or more of these three aspects of the analysis. Fig. 5D demonstrates the narrow band encoding mediated by this cell: this neuron encodes information about the direction of air current stimuli, but only for those stimuli with frequency components within the 10–50 Hz range.

Non-linear encoding

As mentioned above, the kernel-based analyses of the cercal sensory system were based on the assumption that neural coding is a linear process in those cells. This is equivalent to the assumption that the best estimate of the stimulus waveform leading up to the doublet is what you would predict by adding up two copies of the kernel for a single isolated spike (Fig. 5B), offset by the doublet interval, as described above. Aldworth and colleagues (Aldworth et al., 2005) (Z.A., A. G. Dimitrov, G. Cummins, T. Gedeon and J.P.M., manuscript submitted) have just demonstrated that this is not the case.

Fig. 6 demonstrates that the reverse reconstruction method (based on the use of the kernel approach assuming linearity) grossly underestimates the information content in the neural spike train, as assayed by a model-independent approach called the 'direct method' (Strong et al., 1998; Victor, 2002; Paninski, 2003; Nemenman et al., 2004; Kennel et al., 2005; Shlens et al., 2007). This figure also reports the interesting result that the cricket interneurons are transmitting information about stimulus dynamics at rates of up to 130 bits s^{-1}. Through a novel analytical approach, Aldworth determined a range of spike doublets that are in essence a different neural symbol from two single spikes, and derived the kernel for these doublets. His new approach also corrected a substantial source of error implicit in earlier approaches toward kernel extraction, and enables the neurophysiologist to get an accurate estimate of the temporal resolution of neural encoding. For the cricket sensory interneurons we study, the temporal precision is of the order of 5 ms. In other words, a higher-order circuit would not be able to decode the time of occurrence of an event that elicited a spike in that neuron with a temporal precision better than 5 ms.

Conclusions

Our general concept of the functional 'engineering design' of the cercal system, derived from all of the work that has been done on this system in our lab and other labs over the last few decades, supports the concept of the cercal system being a generalist system (like an auditory or visual system) rather than a specialized feature-detection and escape system using 'command neurons' (like the lateral giant interneurons in the escape system in crayfish or the Mauthner cells in zebra fish). That is, there is no strong evidence for feature detector cells at either the receptor or first-order interneuron stages of processing. Instead, the filiform mechanoreceptor array captures a very well-sampled image of the air current field surrounding the animal, and represents the image of that field as activity across a continuous map of that field in the terminal abdominal ganglion (TAG), in the same sense that the information from our own retinae project a continuous map of visual space into our visual cortex. The first-order sensory interneurons that extract information from this sensory map at this first processing stage are also generalists: the computations these interneurons appear to carry out include (at least) the following operations: (a) noise reduction through signal averaging across many sensory afferents, (b) extremely efficient re-encoding of the direction of air current stimuli, *via* a huge dimensional reduction of the activities of the 1500 sensory afferents down to a four-interneuron ortho-normalized code (Theunissen and Miller, 1991; Salinas and Abbott, 1994), (c) coding of the spectral composition of dynamic air currents *via* the relative activity levels of different interneurons having different frequency sensitivity bands, and (d) (still speculative) the representation of the curl of air currents *via* interneurons sensitive to vortices rather than linear air streams. The information available at this first-order sensory interneuron interface is extraordinarily good from an engineering perspective, in terms of the temporal and angular accuracy and precision. Based on this generalist information represented at the first stage of processing, more complex processing operations (such as feature detection and target identification) are, presumably, computed at higher levels of the nervous system by more specialized cells and circuits.

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