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# Cellular and circuit properties supporting different sensory coding strategies in electric fish and other systems

Gary Marsat<sup>1,2</sup>, André Longtin<sup>1,2,3</sup> and Leonard Maler<sup>1,2</sup>

Neural codes often seem tailored to the type of information they must carry. Here we contrast the encoding strategies for two different communication signals in electric fish and describe the underlying cellular and network properties that implement them. We compare an aggressive signal that needs to be quickly detected, to a courtship signal whose quality needs to be evaluated. The aggressive signal is encoded by synchronized bursts and a predictive feedback input is crucial in separating background noise from the communication signal. The courtship signal is accurately encoded through a heterogeneous population response allowing the discrimination of signal differences. Most importantly we show that the same strategies are used in other systems arguing that they evolved similar solutions because they faced similar tasks.

## Addresses

<sup>1</sup> Department of Cellular and Molecular Medicine, University of Ottawa, Canada

<sup>2</sup> Center for Neural Dynamics, University of Ottawa, Canada

<sup>3</sup> Department of Physics, University of Ottawa, Canada

Corresponding author: Marsat, Gary ([gmarsat@gmail.com](mailto:gmarsat@gmail.com))

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## Introduction

An important question in neuroscience is to understand how a neural code is matched to the characteristics of the natural signals. Some sensory signals are quickly detected by the nervous system, such as a noxious stimulus or an alarm call, causing rapid avoidance or an escape reflex. The nervous system must extract these signals from the background noise and, past a certain signal-to-noise ratio, trigger a behavioral response. Other signals carry information on a range of time scales and their local temporal details are important. These signals must be encoded by the nervous system in a way that enables downstream neurons to extract relevant information on multiple time scales. In this review we describe principles underlying the coding of these two types of stimuli in the context of communication signals in electric fish. We show how the

circuitry and the cellular properties are matched to the respective signal properties to produce an efficient behaviorally relevant encoding. We further argue for their applicability to sensory processing in a wide range of organisms and modalities.

We first focus on an aggressive signal (Figure 1a) and describe how the cellular and network properties are linked to a spike burst code that allows sensitive detection of the signal. We discuss how feedback influences the burst-generating mechanism to permit efficient stimulus extraction in the presence of competing signals. We then look at the accurate encoding of courtship signals (Figure 1b) by a population of electrosensory neurons, allowing fine discrimination of stimuli attributes. The heterogeneity of the cells' responses, due to a diversity in their cellular and synaptic properties, plays a crucial role by increasing the amount of information carried by the population.

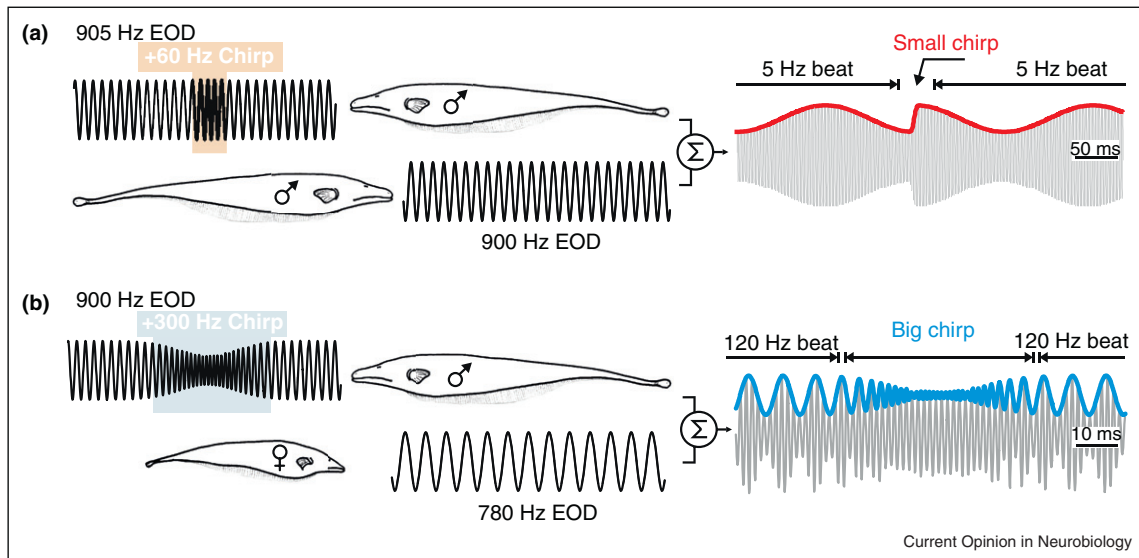
## Electrocommunication and electroreception

Electric fish produce a weak electric field around their body to navigate, find prey and communicate with one another [1]. Gymnotiform wave-type electric fish have an electrical organ that continuously discharges at a constant rate. The summation of the electric fields from two interacting fish cause amplitude modulations called beats. Interacting fish are thus constantly exposed to these background beat modulations. The most common type of communication signals, chirps, consist of transient increases in the frequency of the electrical organ discharge (EOD; Figure 1) that disrupt the regular, sinusoidal beat modulation. They are typically used in two contexts: courtship and aggressive encounters. During agonistic interactions, lower frequency beats tend to occur, and males typically produce several chirps per seconds in between bouts of attacks [2]. These 'small chirps' are short and consist of a small increase in the EOD frequency. A male courting a female however, will produce 'big chirps' [3] which will interrupt high-frequency beats typical of male–female interactions. The nervous system must therefore extract chirps from background beats.

These signals are sensed by thousands of cutaneous electroreceptors. The most numerous electroreceptor (P-unit) is sensitive to EOD amplitude modulations [4] and encodes both the beats and chirps. P-units encode chirps into changes in the synchrony with which the population fires. Small chirps usually increase synchrony,

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Figure 1



Communication signals in electric fish. Electric fish produce several types of communication signals in a variety of contexts. We focus our review on two simple and common cases as depicted in this figure. **(a)** Two dominant males with similar EOD frequencies engage in an agonistic interaction and emit small chirps. The summation of the two EOD frequencies will cause a sinusoidal amplitude modulation (beat) of frequency equal to the difference in EOD frequency. This beat is constantly present during interactions. Small aggressive chirps are transient (10–20 ms) increases in the frequency of the EOD (by 50–180 Hz). The chirp, being much shorter than the beat's period, causes a sudden shift in the phase of the beat (right panel). Sensory neurons encode the amplitude change associated with this signal (red trace in right panel). **(b)** Male–female interaction will typically be associated with higher frequency beats since females tend to have much lower EOD frequencies than males. During courtship, males produce big chirps consisting of longer (>20 ms) and larger EOD frequency increases (300–900 Hz) during which the amplitude of the EOD decreases. The amplitude modulation associated with this signal is thus very different than for the case described in (a). Note that on the left panels, the characteristics of the signal (e.g. frequency or duration) have been exaggerated to illustrate clearly the differences between (a) and (b).

whereas big chirps decrease it [5], but this relationship depends on context [6]. This synchrony–desynchrony code must be decoded by the next stage in electrosensory processing: the electrosensory lateral line lobe (ELL). Different but interconnected neural circuits are specialized for processing small chirp-evoked receptor afferent synchrony versus big chirp-triggered desynchrony (Figure 2a,c).

### Bursting and detection of small chirps

The ELL is divided in three topographic maps. Its output cells are organized in several layers and come in two intermingled types: the E-cells respond to increases in EOD amplitude and I-cells to decreases. Depending on the map, layer and cell type, the cellular, network and response properties of the cells vary greatly [7,8] although they are embedded in a common local microcircuit. When presented with small chirps, superficial E-cells of the lateral map respond most strongly by emitting spike bursts (Figure 2b) [9].

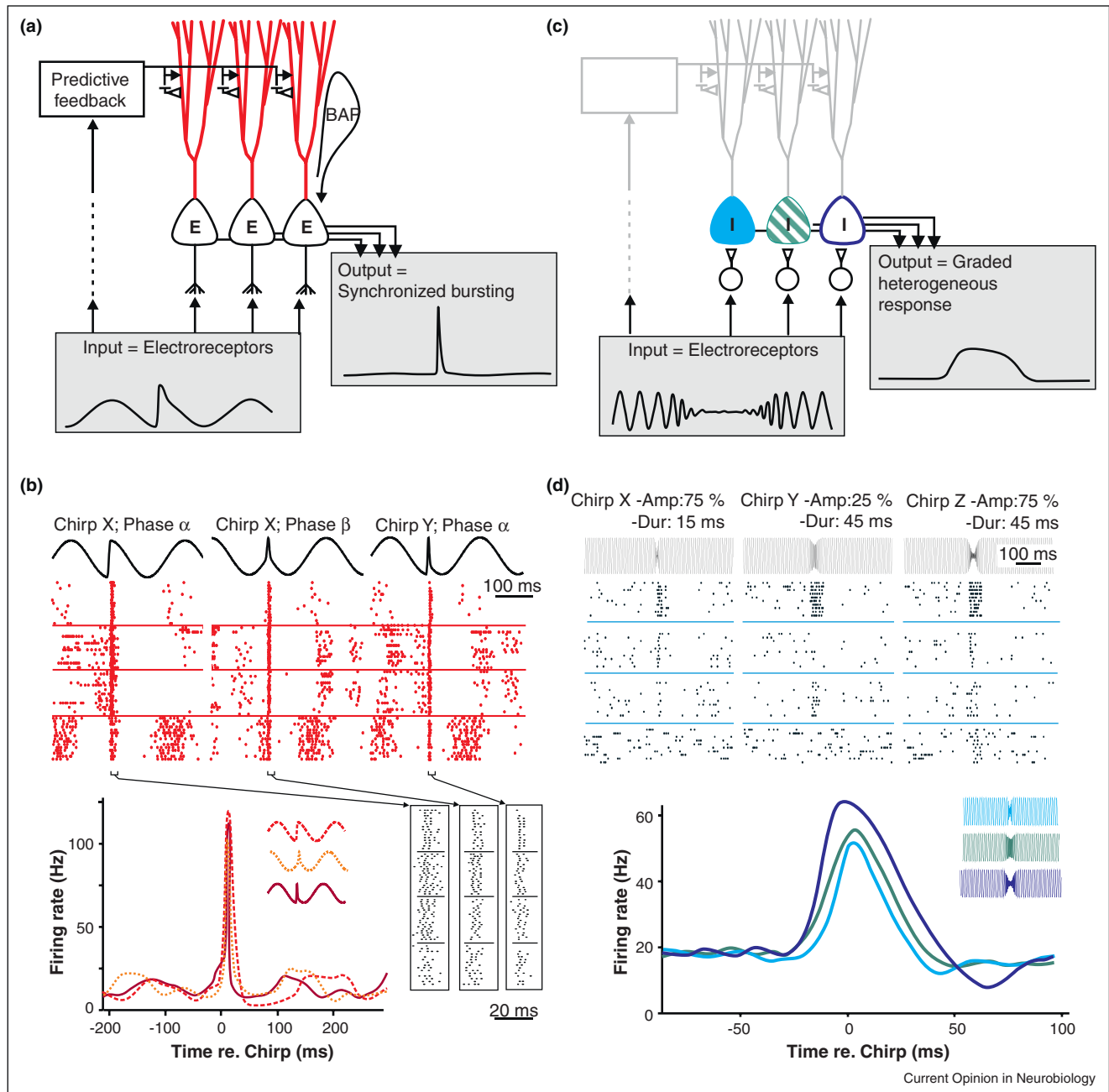
### Synchronized bursting and reliable signal detection

Bursts are commonly observed in a wide range of sensory systems where they signal the occurrence of behaviorally relevant stimulus features [10]. In many systems, the features that trigger bursts are transient and salient or

unexpected features: unexpected chirps interrupting a repetitive background (i.e. a beat) in electric fish [9]; salient peaks in ultrasound amplitude in crickets [11]; motion reversal or a 'missed' periodic stimulus in the retina [12,13]; or a sharp luminosity contrast in the lateral geniculate nucleus (LGN) [14]. In all these systems, the stimulus simultaneously affects many neurons leading to synchronous bursting across the population. Circuits downstream of the ELL could clearly identify the occurrence of a chirp with a simple threshold mechanism since synchronous bursts in LS E-cells (Figure 2b) are rarely produced by other natural stimuli [9].

Although it is now clear that synchronous bursting reliably signals the occurrence of specific stimulus features, recent studies have tried to assess whether burst structure carried additional information about the detailed structure of these stimulus features. Burst can carry information in their interspike-intervals (ISIs) or spike count (see e.g. [15]). However, the accuracy with which information is encoded is very sensitive to noise [16,17]. In the LGN burst ISIs carried less information than the ISIs of non-burst spikes [18]; the authors concluded that the small burst ISIs are not a reliable source of information. Moreover, even when burst structure carries information, this does not necessarily mean that the information is used by

Figure 2



Circuitry and response of ELL pyramidal cells to communication signals. **(a,c)** Schematics highlighting elements of the circuitry and neural properties that are important for the processing of communication signals. The gray boxes showing the shape of the input and output for chirp stimuli are meant to illustrate roughly the input–output operation performed by the circuit. **(b,d)** Responses of pyramidal cells to three exemplars of small and big chirps. **(a)** E-cells respond to small chirps. They receive direct inputs from electroreceptors as well as feedback inputs from deep E-cells (not shown). Apical dendrites are highlighted because they play a key role in the response: first, the feedback they receive attenuates the response to the beat input to the basal dendrites; second, the bursting response to the chirp is mediated by backpropagating spikes in these dendrites; and third, feedback is thought to modulate bursting and thus the response to small chirps. **(b)** Small chirps elicit a stereotyped burst response whereas the beat is only weakly encoded. Top: raster plots of the responses of four cells to three small chirp stimuli (the burst response is blown up below). Bottom: mean ( $n = 13$  neurons) instantaneous firing rate in response to these three chirps. Note that similar responses are elicited when the cell is presented with different small chirps at the same phase of the beat, or by the same small chirp at different beat phases. **(c)** I-cells respond best to big chirps. They receive disynaptic inputs from electroreceptors. They also receive feedback input but its importance for their response to big chirps has not been examined. Heterogeneity in the population of I-cells (depicted here with somas of different colors) allows a more accurate encoding of big chirp characteristics. **(d)** Big chirps elicit graded responses that vary from cell to cell. As a consequence the population response can be used to discriminate between two different big chirps. Top: raster plots of the responses of four cells to three big chirp stimuli. Bottom: mean ( $n = 13$  neurons) instantaneous firing rate in response to these three chirps.

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downstream circuits. In crickets the information encoded in the bursts' ISIs does not influence behavioral output [19]. In electric fish, Marsat and Maler [20<sup>••</sup>] showed that the detailed structure of the amplitude modulation associated with a small chirp is dependent on the background beat (Figure 2b). Since the chirp-elicited burst response encodes the amplitude modulation of the chirp + beat it cannot discriminate between chirps *per se* [20<sup>••</sup>,21<sup>•</sup>].

In summary, synchronous bursts in many systems allow the reliable detection of a salient signal, but the internal burst structure may contain little useful information.

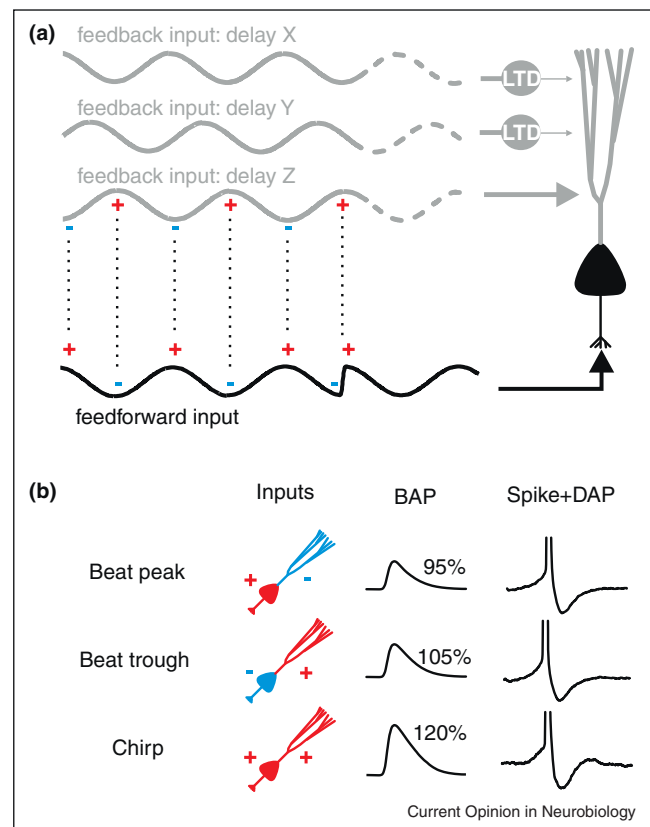
#### Cellular and circuit properties enhancing stimulus detection

Reliable signal detection requires that the signal be stronger than background noise. Increasing the signal-to-noise ratio means reducing noise and/or amplifying the signal. In the present case, the signal of interest is the small chirp and the background 'noise' is the spatially and temporally redundant low-frequency sinusoidal beat. Bursts are central to both the active cancellation of the background beat response and to enhancing the chirp-evoked response of ELL neurons. Electroreceptors responding to beat-plus-chirp excite the basal dendrites of pyramidal cells. Parallel fibers originating from cerebellar granule cells provide an input to the apical dendrites of these pyramidal cells that is in antiphase with this feedforward signal, thus significantly reducing the response to the low-frequency beat [22].

A recent paper [23<sup>•</sup>] combined modeling and *in vivo* experiments to show how burst dynamics in conjunction with synaptic plasticity shape the feedback input. Depression of feedback synapses occurs only when presynaptic and postsynaptic bursts coincide in a small time window [24]. Bursting allows the selection of parallel fiber input with the appropriate delay to be in antiphase with the stimulus (Figure 3a; [23<sup>•</sup>]), with different stimulus frequencies requiring different delays. The model predicted the existence of feedback frequency channels, and this strong prediction was then experimentally confirmed. Burst size is correlated with the time window for LTD [24] with smaller bursts — associated with higher frequencies — resulting in shorter windows. These relations allow feedback to effectively cancel both low (large bursts) and higher (small bursts) frequency global signals; beyond 20 Hz bursts are no longer elicited and cancellation no longer occurs. These results demonstrate that burst dynamics allow synaptic depression to operate selectively on the repeating bursts, thereby reducing redundancy. A similar principle is observed in crickets where the efficiency of an inhibitory input is dependent on presynaptic and postsynaptic coincident bursting. As a result sound localization cues carried by the nervous system are enhanced selectively for stimulus features that elicit bursts [25,26].

Besides canceling the background beat, feedback also enhances the chirp-evoked burst response. Bursting depends on spike backpropagation into pyramidal cell apical dendrites [27] receiving feedback cancellation input (Figure 2a). The backpropagating spike causes a depolarizing after-potential enhancing the probability of producing spikes in quick succession (i.e. bursting). Chirps shift the phase of the beat so that, after the chirp, feedback is in phase with the stimulus rather than

Figure 3



Feedback and response to small chirps. **(a)** Feedback is routed through many pathways of different lengths and thus arrives in the ELL with various delays. Depression (burst-dependent LTD) weakens the feedback inputs that arrive in phase with the feedforward signal thus leaving only antiphase feedback inputs. Note that both the feedback and the feedforward inputs contain excitatory and inhibitory components. During low frequency, spatially and temporally redundant stimuli, the inputs from basal dendrites (feedforward) and apical dendrites (feedback) are of opposite polarity, thus leading to an attenuated response. Small chirps cause a sudden shift in beat phase, thus a shift in feedforward polarity, before the feedback can change (feedback loop time is on average 20 ms). **(b)** Depending on the stimulus, excitation will arrive either at the apical dendrites (coincident with stimulus beat troughs), or at the basal dendrites (with beat peaks), or at both (coincident with a chirp). When both the feedback and the feedforward are excitatory, the backpropagating spikes (BAP) are enhanced [28]. As a consequence, the depolarizing after-potential (DAP) that follows each chirp-evoked somatic spike is larger [9] and this increases the probability of bursting. Note that the size of the BAP was exaggerated to show differences but numbers are accurate.

out of phase (Figure 3a). Therefore the apical and basal dendrites and soma will be depolarized (Figure 3b). This transient depolarization of both apical dendrites and soma enhances the backpropagating spike and thus boosts the depolarizing after-potential [9,28]. Thus, the predictive feedback that cancels redundant low-frequency beats also prepares the ELL for detection of unexpected chirps.

Signal detection through bursts seems linked to breaking a redundant predictable pattern in other systems as well. In the retina, ganglion cells adapt their response to periodically presented flashing stimuli but emit a strong burst if the timing of the flash is disrupted by as little as 5 ms [13,29]. A similar result was found when a smoothly moving object reversed its motion direction [12]. A modeling study suggests that transient calcium release in the network tunes an oscillation to the period of the visual stimulus [30]. This oscillation can be seen as a predictor against which the stimulus is compared, with a mismatch causing bursting. In the LGN, burst generation relies on T-type channels which are deinactivated by hyperpolarization [31]. The thalamic reticular nucleus receives cortical feedback input and inhibits the LGN. Halassa *et al.* [32] have shown that stimulation of the thalamic reticular nucleus enhances bursting by LGN relay neurons for a few hundred milliseconds. This may contribute to the modulation of stimulus-evoked LGN bursting by cortical feedback [33]. Whether cortical feedback regulation of bursting might implement a predictive modulation of retinal input in LGN has not, however, been explored.

In summary, feature detection by bursts can be modulated by feedforward and feedback inputs. Studies in electric fish showed that the network inputs and the cellular dynamics together operate selectively on the neural burst code.

### Neural heterogeneity and discrimination of big chirps

Courtship signals can carry information about male quality. When courting females, males often produce big chirps which are categorically different from aggression-associated small chirps (Figure 1; [34]). Big chirps evoke graded and diverse increases in the firing rate of ELL I-cells (Figure 2d; [20]). The E-cells responding to small chirps provide little information about the big chirps. The diverse big chirp-evoked responses from individual I-cells combine into a noise-free, invariant, population response. The heterogeneity of the I-cell population response improved encoding so that the response of eight or nine cells was sufficient for discrimination between two different big chirps. The heterogeneity discussed here is due to I-cells having, for example, slightly different frequency tuning, baseline firing rates or thresholds. These differences allow each neuron to

convey slightly different information and thus reduce response redundancy across the population.

Neural heterogeneity has been identified in several systems [20,35–37,38,39] as improving the accuracy of population codes, but the source of the heterogeneity is generally not known. In the olfactory system, however, mitral cell intrinsic biophysical heterogeneity decorrelates the response across the population and leads to more efficient odor encoding [39]. In the cricket auditory system, the population of receptors sensitive to courtship songs produce heterogeneous responses and this low redundancy across the population allows each neuron to contribute significantly to the total information transmitted [38]. Most notably the authors contrasted this coding strategy with that of another receptor type that burst and present greater across-population redundancy. As in electric fish this stereotyped burst response supports the detection of threatening predator calls.

An interesting link can be made between the role of response heterogeneity on population coding and the influence of biophysical diversity on motor patterning proposed by Marder and colleagues (for a recent review see [40]). They showed that diverse combinations of biophysical and network characteristics can lead to an invariant and optimal activity pattern across a neural network. In our ‘sensory’ case, the heterogeneity allows a noise-free, invariant population response. Contrary to the motor network [40], diversity is here necessary to achieve invariance. Nevertheless, in both sensory and motor systems, an invariant population response arises because of the appropriate distribution of heterogeneous cell properties.

### Conclusion

We have contrasted the processing of two different communication signals and described some of the network and cellular properties involved (see Figure 2 for a graphical summary). In one case, a bursting response allows the reliable detection of the stimulus. The interplay between the bursting dynamics and predictive feedback input allows for both filtering out background signals and extracting unexpected signals. In the other case heterogeneity allows a courtship signal to be efficiently encoded through graded variation in firing rate, thereby allowing discrimination of signals with different qualities. The generality of these principles is highlighted by comparisons with other systems. The very different auditory system of cricket presents particularly striking parallels: coding principles underlying the detection of predator threats versus the description of courtship song show parallel differences [38,41]. Our review highlights how neural coding strategies are shaped by behaviorally important constraints. The neural microcircuitry combines with not only the feedforward and feedback architecture, but also with subtle intrinsic cellular dynamics to reach solutions concurrently supporting different signal processing tasks.

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