

## Chapter 12

# Neural Noise in Electrocommunication: From Burden to Benefits

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**Abstract** Weakly electric fish generate an electric field, called electric organ discharge (EOD), that they use for active electrosensation. This system is used for both object localisation and electrocommunication. Both, objects that are close to the fish and the EODs of other nearby electric fish, modulate the amplitude of a fish's EOD. Localisation signals are low in amplitude and frequency whereas electrocommunication signals are large amplitude signals with higher frequencies. Electoreceptor neurons are tuned to the frequency of the fish's own EOD. This tuning, however, is rather broad to allow for the reception of EODs of other fish with different frequencies. This is the basis for electrocommunication. Spike trains of electoreceptor afferents are surprisingly noisy even in the absence of any external signal. From theoretical studies it is known that in populations of spiking neurons such internal noise can improve the information carried about a common input signal in comparison to the noiseless case. In particular, the processing of high-frequency signals benefits from internal noise and the convergence of large populations of neurons. The target neurons of the electoreceptor afferents, the pyramidal cells in the electrosensory lateral line lobe, are organised in three distinct maps of the electoreceptive body surface that are characterised by different receptive field sizes, i.e. the number of afferents that converge on them, and frequency tuning. The properties of these three maps can be understood based on the differential impact of the noise in the electoreceptor afferent spike trains on the processing of the distinct types of signals arising in localisation and

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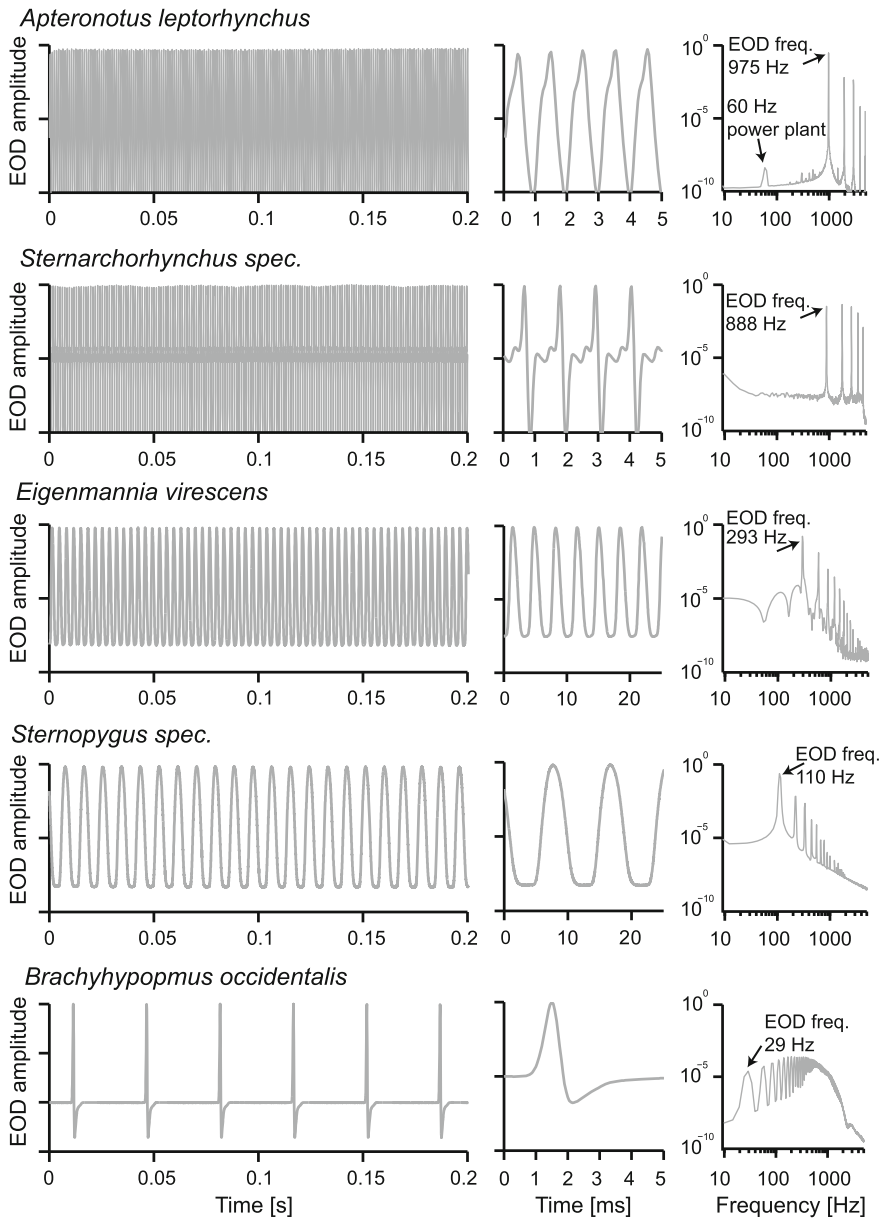
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communication contexts. Further, the noise in the electroreceptors allows for the discrimination of synchronous spikes from all spikes fired by the afferent population. The level of synchrony seems particularly important for encoding high-frequency communication signals. The electrosensory system is thus a showcase for demonstrating how neural systems actually use noise to enhance processing of signals.

## 12.1 Introduction

Considering that the idea of an electric sense seems quite exotic to most of us, it may come as a surprise to hear that the earliest vertebrates presumably had the capability to sense external electric fields (Zupanc and Bullock 2005). Electro-sensation was then lost, but re-evolved in several lineages, among them elasmobranchs and teleost fish, and is found today even in the bill of the platypus (Pettigrew 1999). Several groups of fishes, including the South American gymnotiformes, the African mormyriiformes, siluriform catfish and elasmobranchs, possess a passive, ampullary, electrosense that allows them to detect the weak and low-frequency electric fields generated by the muscle activity of aquatic organisms. Gymnotiform and mormyriiform fishes have a second electrosensory system, the tuberous system that responds to the discharges of their own electric organ (EOD) and to the EODs generated by conspecifics and other species. Their combined electrogeneration and electrosensation system is a dual-use system: on the one hand, it allows the fish to detect objects and navigate their habitat based on perturbations of the electric field caused by objects whose electrical properties differ from those of the surrounding aquatic medium. Because the animal itself provides the energy used to sense its environment, electrolocation can be considered an active sense comparable to echolocation in bats and marine mammals (bats: Schnitzler et al. 2003, Chaps. 9, 10 on marine mammals). On the other hand, the EOD and modulations of its discharge frequency serve a communication function in various contexts ranging from aggressive encounters between males to courtship. It has even been proposed that EOD signals are used to coordinate pack-hunting behaviour in the mormyrid *Mormyrops anguilloides* (Arnegard and Carlson 2005).

Weakly electric fish come in two types, wave-type and pulse-type (Fig. 12.1). Wave-type weakly electric fish generate a quasi-sinusoidal EOD by discharging their electric organ periodically with the pauses between EOD pulses being of similar duration as the pulses themselves. Pulse-type fish, on the other hand, generate brief pulses separated by longer pauses that, in many species, are of variable duration (Møller 1995). This chapter will focus on gymnotiform wave-type weakly electric fish, whose processing of electrosensory information has been investigated in more detail than that of any other group of electric fish (but see Sawtell and Bell 2008; Kawasaki 2005). Of particular appeal has been the



**Fig. 12.1** EOD characteristics of five species of Gymnotiform electric fish. *Brachyhypopomus occidentalis* (bottom) is a pulse-type electric fish, the four other fish are wave-type. *Left column* A 200 ms sequence of EOD recordings. Amplitudes are normalised to the largest positive amplitude value. *Middle column* A close up of the EODs illustrating individual discharges of the electric organ. *Right column* Power spectra of the EOD traces shown in the *left column*

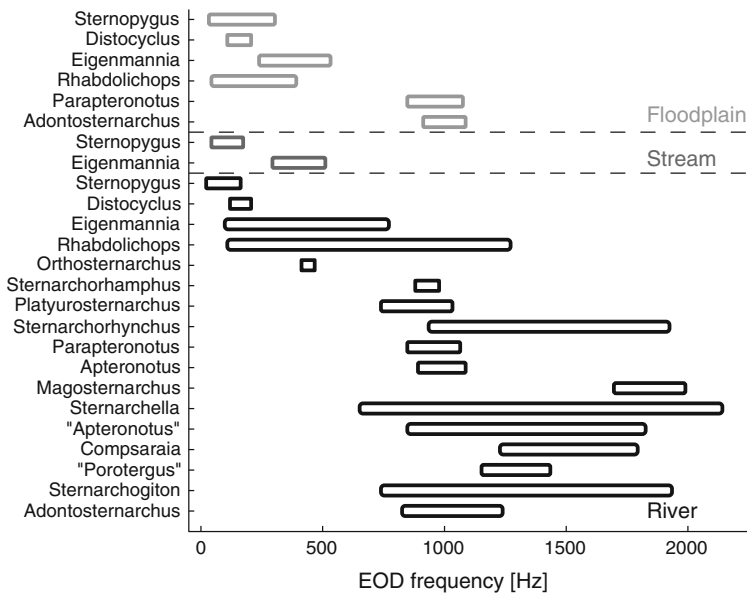
excellent experimental accessibility of the electrosensory system in animals that display normal electric behaviours. As any other sensory system, the electrosense functions in the face of noise that originates from both external and internal sources. Remarkably, compared to other communication channels, such as hearing and vision, electrocommunication in these fish may be relatively little affected by external sources of noise. And with respect to internal sources of noise, the electrosensory system may be a showcase for demonstrating how neural systems actually use noise to enhance information processing.

## 12.2 Electrocommunication

The EOD signals of wave-type weakly electric fish can be largely described by their fundamental frequency and amplitude. As outlined in the following sections, both of these as well as their modulations appear to be used by the fish for communication purposes.

### 12.2.1 EOD Frequency Identifies Species and Individuals

The most basic communication signal of a wave-type weakly electric fish is its EOD frequency, which is individual specific and astoundingly constant; at a time scale of seconds to hours, the standard deviation of the EOD cycle periods is in the sub-microsecond range and the coefficient of variation of the EOD cycle period is as low as  $10^{-4}$ , making the EOD generating mechanism the most regular biological oscillator known (Moortgat et al. 1998). While the baseline EOD frequency of a given fish is quite stable, different individuals of the same species use different frequencies within a certain range that is characteristic for that species (Fig. 12.2). For example, one of the most intensely studied species, *Apteronotus leptorhynchus*, the brown ghost knifefish, occupies a frequency range from approximately 700–1,100 Hz, while the EOD frequency of *Sternopygus macrurus* can take values between 40 and 200 Hz. If fish evaluate EOD frequency for communication purposes, then overlapping frequency ranges of different, co-occurring species could constitute a source of error. Such overlapping frequency ranges have been reported for sympatric species of gymnotiforms (Kramer et al. 1981); there is, however, a lack of data demonstrating syntopy of such species during the breeding season (occurring within the same microhabitat, which makes physical interaction likely, whereas sympatry only implies occurrence in the same general area). Given that the EOD waveforms of many species are quite different due to differences in harmonic content (Crampton and Albert 2006; Turner et al. 2007), and that waveform sensitivity has been demonstrated in *Eigenmannia* (Kramer and Otto 1991), it is conceivable that these fish use waveform information rather than EOD frequency to distinguish their own from other species. Surprisingly, experiments



**Fig. 12.2** Ranges of EOD frequencies of different species in different habitats. *Bars* indicate the distribution of EOD frequencies observed in various genera of gymnotiform fish and how they are distributed across different habitats. The *quotation marks* indicate that the respective group of species is not a well defined genus and should be considered a species group. Redrawn from Crampton and Albert (2006)

on *A. leptorhynchus* suggest the exact opposite: fish showed behavioural responses to playback stimuli as long as the carrier frequency was in the right range, whereas the quite distinct EOD waveforms of various species that were tested had no effect on the responses (Fugère and Krahe 2010). Interestingly, discrimination between individuals based on waveform has been demonstrated in one species of pulse-type gymnotiform fish (McGregor and Westby 1992).

EOD frequency is not only species specific in its range, it can also carry information about age and/or size, sex and dominance. Gymnotiform fish begin to produce a measurable EOD within the first 10 days after hatching (Kirschbaum 1983; Kirschbaum and Westby 1975; Meyer et al. 1987). EOD frequency is initially low and, in *Eigenmannia*, reaches adult values within 20 days (Kirschbaum and Westby 1975), whereas in *Apteronotus*, it takes up to 1 year for EOD frequency to increase from initial values around 300 Hz to between 600 and 800 Hz (Kirschbaum 1983; Meyer et al. 1987). A correlation between body size and EOD frequency has also been observed in adult male *A. leptorhynchus* studied in the laboratory (Dunlap 2002; Triefenbach and Zakon 2003) and in a related apteronotid species, *Sternarchorhynchus* sp., observed in its natural habitat (Fugère et al. 2011). Behavioural experiments on the latter species demonstrated that EOD frequency carries information on dominance status and is used by these fish to decide contests about access

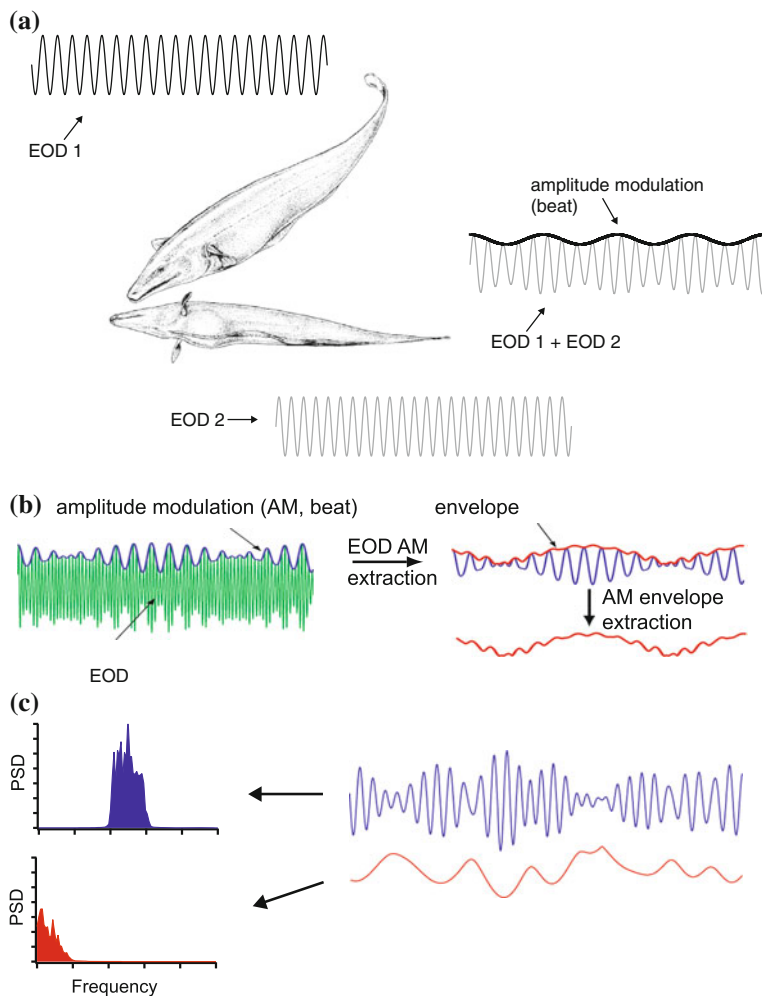
to hiding places (Fugère et al. 2011). EOD frequency has also been found to be sexually dimorphic in many wave-type species (Crampton and Albert 2006). In the family Sternopygidae, which includes *Eigenmannia*, mature males occupy the lower end of a given species' range, whereas mature females occupy the upper end (Hopkins 1972; Hagedorn and Heiligenberg 1985). In many species of the family Apterontidae, which comprises the electric fishes with the highest EOD frequencies, males occupy the high range, whereas at least in *A. albifrons*, this sexual dimorphism appears to be reversed (Dunlap et al. 1998; Crampton and Albert 2006). Not surprisingly, EOD frequency is under control of steroid hormones (e.g. Meyer et al. 1987; Zakon et al. 1991; Dunlap 2002; Cuddy et al. 2011, see below).

Besides developmental and hormonal effects, EOD frequency is strongly correlated with water temperature (Dunlap et al. 2000). Although the temperature of freshwater bodies in the lowland tropical rainforest varies a lot less through the year than that of streams and lakes in the temperate zone, it can fluctuate by several degrees in the course of a day and through the year (Kramer 1978; Flecker et al. 1991). At present, there is no evidence that temporal or spatial variations in temperature affect communication interactions between wave-type electric fish.

How is the frequency of one wave-type fish perceived by another? Because wave-type EODs are almost sinusoidal, the superposition of two EODs will lead to a beat (Fig. 12.3a), that is, a combined signal that oscillates in amplitude and phase at a frequency equal to the difference in EOD frequencies between the two fish. When two animals of the same sex interact, the beat frequency will be relatively low, when two fish of opposite sex interact, the beat frequency can reach values of up to 400 Hz depending on the species. The strength of the beat modulation experienced by a given animal is a function of its distance from the conspecific, because EOD amplitude drops steeply with distance from the source (Knudsen 1975; Chen et al. 2005). In natural groups of fish, multiple EOD signals can interact, leading to multiple simultaneous beats as well as to interactions between the beat frequencies themselves ("beat of beats"; Partridge and Heiligenberg 1980; Tan et al. 2005; Stamper et al. 2010). Depending on the frequency composition of the group, such beats of beats can cause periodic low-frequency envelopes of the original beat signal (Fig. 12.3b). Interestingly, recordings from groups of *Apteronotus* in streams in Ecuador suggest that the fish adjust their EOD frequencies to avoid low-frequency envelopes (Stamper et al. 2010).

### 12.2.2 EOD Amplitude is Related to Body Size

It is conceivable that electric fish not only evaluate the frequency of each other's EOD, but also its amplitude. Based on the strong positive correlation between EOD amplitude and body size (Knudsen 1975), they might assess a neighbour's body size by measuring the strength of its electric field. This relationship is complicated by the decrease in electric field strength with distance as pointed out in the preceding section and by the fact that in pulse-type gymnotiforms and in



**Fig. 12.3** Beats and envelopes. **a** If two fish are in proximity of each other the two individual waveforms will interact. Each fish receives an interference of the two EODs. Both fish perceive their own EOD amplitude modulated by the field of the other one. The resulting amplitude and phase modulation is referred to as the beat. Here, we will only consider the amplitude component (AM, *black line*) of the beat. Its frequency is given by the frequency difference of the individual EODs. The modulation depth of it depends on the relative amplitudes of the individual EODs. For example, since the amplitude of the EODs decline with distance from the fish, at the position of the lower fish the EOD amplitude of the distant upper fish is smaller compared to the lower fish's EOD amplitude. If the fish come closer the modulation depth or contrast of the beat increases. Drawings of *A. leptorhynchus* taken from Hagedorn and Heiligenberg (1985). **b** If the EODs of multiple fish interfere, higher-order AMs occur. These are called envelopes (*red line* in the *top row*). **c** Spectral power that is contained in the beat and envelope. One can observe that the higher-order AMs (i.e. the envelope) have lower frequency power (*bottom traces and power spectra*) than the beat. Modified from Middleton et al. (2006)

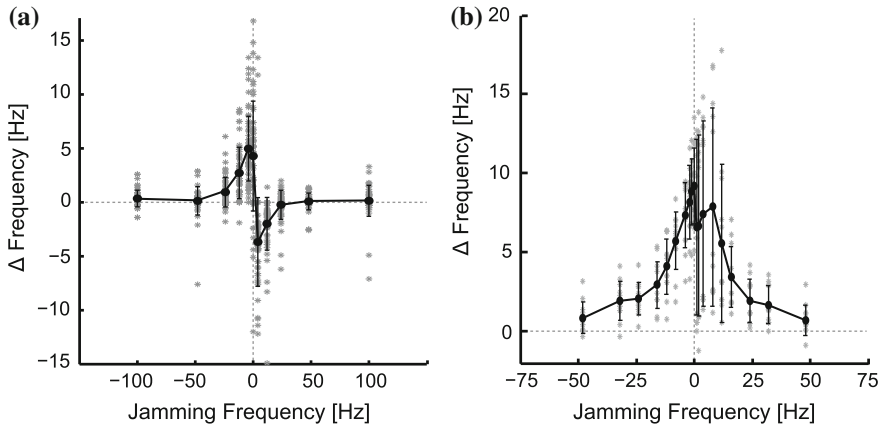
sternopygid wavefish EOD amplitude follows a circadian rhythm (reviewed in Stoddard et al. 2006; Markham et al. 2009). The reduction in amplitude during the daylight hours when the fish are usually hiding, may serve the dual purpose of being less conspicuous to electrosensory predators and of saving energy (Markham et al. 2009; Salazar and Stoddard 2008; Reardon et al. 2011). At night, signal amplitude is boosted, which is expected to increase the range of electrolocation and the signal-to-noise ratio of the electric images on the skin created by the object-induced perturbation of the fish's electric field (Assad et al. 1998). Stronger electric fields will also make fish more conspicuous to conspecifics and to electroreceptive predators. The hypothesis that amplitude plays a role in social signalling in these fish is supported by the observation that male pulse-type fish, *Brachyhypopomus gauderio*, show larger amplitude increases at night than females and that exposure to conspecifics has a boosting effect on EOD amplitude in both *B. gauderio* and *Sternopygus macrurus* (Stoddard et al. 2006; Markham et al. 2009; Salazar and Stoddard 2008).

### ***12.2.3 Electrocommunication by EOD Frequency Modulations***

#### **12.2.3.1 Jamming Avoidance Response**

Wave-type weakly electric fish use several kinds of frequency modulations of their EOD in interactions with conspecifics. The most intensely studied frequency modulation is the jamming avoidance response (JAR) which was first described in *Eigenmannia virescens* (Watanabe and Takeda 1963; Bullock 1969; Bullock et al. 1972a, b). When a fish encounters a conspecific whose EOD frequency is close to its own, the resulting low-frequency beat interferes with the animal's ability to detect nearby objects (Heiligenberg 1973, 1991; Bastian 1987a, b). The fish show extraordinary sensitivity in determining whether their own EOD is of higher or lower frequency than that of their neighbour and, as a consequence, lower or raise their frequency away from that of their neighbour's (Fig. 12.4, also Kawasaki 1997). By increasing the frequency difference, the fish free up the frequency range most critical for electrolocation, hence the term jamming avoidance. The JAR can be viewed as a noise avoidance behaviour, because the low-frequency beat modulation, which affects the entire body surface of the fish and interferes with the animal's prey detection mechanisms, can be seen as strong background noise whose frequency range overlaps with the frequency of object-induced perturbations of the fish's electric field (Nelson and MacIver 1999). In addition to avoiding low-frequency noise, the higher-frequency beats resulting from the JAR have been found to enhance directional selectivity for object movements of neurons in the midbrain (Ramcharitar et al. 2006). The enhancement of directional selectivity is



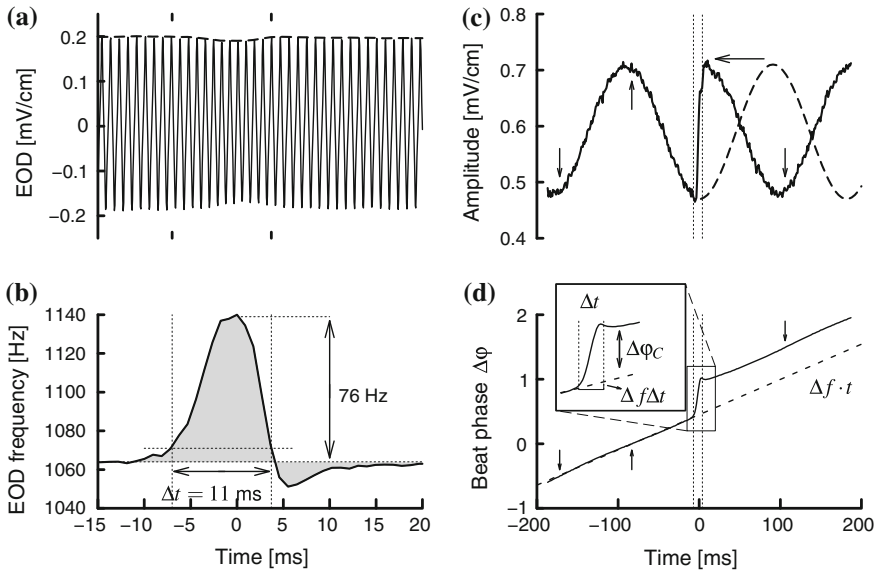


**Fig. 12.4** The jamming avoidance response (JAR). **a** The JAR of *E. virescens*. In response to a jamming beat of various frequencies the fish shifts its EOD frequency to higher or lower values. The strength of the JAR is given relative to the “resting” condition ( $n = 56$ ). Grey asterisks are individual measurements, black dots are averages across all recordings. Error bars are standard deviations. **b** Same as (a) but for *Apterionotus leptorhynchus* ( $n = 6$ ). *A. leptorhynchus* shows only a positive JAR and appears to be unable to lower its EOD frequency actively (Heiligenberg et al. 1996). There is experimental evidence that *A. leptorhynchus* actively uses jamming as an aggressive signal (Tallarovic and Zakon 2005)

caused by frequency-dependent synaptic depression that is most pronounced in the gamma frequency range corresponding to the beat frequencies found in natural groups of *Eigenmannia*.

### 12.2.3.2 Chirps

More rapid frequency modulations have been described in a number of wave-type species, some of them with a duration of hundreds of milliseconds and others, called chirps, that are as short as 10 ms (e.g. Hagedorn and Heiligenberg 1985; Zakon et al. 2002; Zupanc et al. 2006; Turner et al. 2007). Chirps are produced mostly by male fish during aggressive and courtship encounters and have been studied most thoroughly in *A. leptorhynchus* (e.g. Zakon et al. 2002; Hupé and Lewis 2008; Triefenbach and Zakon 2008). In an interaction between two fish, chirps always occur on the background of a beat. The rapid frequency increase and return to baseline causes a phase advance of the beat-related amplitude modulation (AM), experienced by the fish (Fig. 12.5). The most commonly observed chirps are the so-called “small”, or type-2, chirps, which show frequency increases between 60 and 200 Hz and are produced mostly in response to EOD frequencies similar to the fish’s own frequency (Engler and Zupanc 2001). Large chirps, whose frequency excursions can reach several hundred Hertz, are observed more rarely and are produced mostly in response to large EOD frequency differences, that is,



**Fig. 12.5** Chirps and their impact on beats. **a** The EOD of a chirping fish. Small vertical bars indicate beginning and end of a small chirp. During the chirp the EOD frequency is increased and the EOD amplitude is slightly reduced. **b** EOD frequency of the chirping fish shown in **a** as a function of time. The chirp is characterised by its frequency excursion (here about 76 Hz) and duration  $\Delta t$ . **c** Amplitude of the resulting beat as a function of time (*solid line*). *Dashed line* indicates the undisturbed beat. The chirp, occurring at time 0 induces a phase advance of the beat. **d** beat phase  $\Delta\phi$  as a function of time. The chirp occurs at time 0 and induces the phase shift ( $\Delta\phi$ ). Figure modified from Benda et al. (2005)

on a background of high-frequency beats. They are thought to play a role in courtship and spawning (Hagedorn and Heiligenberg 1985; Bastian et al. 2001), but have also been proposed to serve as submissive signals of low-frequency males towards dominant males with a high EOD frequency (Cuddy et al. 2011). Similar to communication signals in other species and modalities (e.g. Goodson and Bass 2001; Albers et al. 2002; Gutzler et al. 2011; Allee et al. 2008; Pasch et al. 2011), chirping has been shown to be regulated by steroid hormones (Dunlap et al. 1998, 2002, 2011; Dunlap 2002), serotonin (Telgkamp et al. 2007; Smith and Combs 2008), and also by arginine-vasotocin (Bastian et al. 2001).

### 12.3 External Sources of Noise

The electrosensory system is exposed to noise from several sources, but their impact on electrocommunication may be small compared to noise effects on other communication channels. Noise of abiotic origin includes the electric fields caused

by lightning. As discussed by Hopkins (1973), wave-type weakly electric fish are expected to be relatively immune to lightning-related electrical noise due to the quasi-sinusoidal nature of their EOD that contrast with the randomly occurring brief lightning pulses. A more serious, anthropogenic problem for some wave-type species may be electropollution from power plants and power lines, which emit electric fields at 60 Hz and its higher harmonics that can be picked up by simple electrodes over large distances (R. Krahe, personal observation). It is conceivable that “line noise”, due to its harmonic structure, interferes with the EOD signals of a number of wave-type species (van der Sluijs et al. 2011). It is still unknown if species avoid producing EOD frequencies at 60 Hz and its harmonics in the vicinity of settlements and power lines or if some of these species even disappear from heavily polluted areas because of electrical interference.

The weak and local AMs caused by objects in the vicinity of an electric fish (much less than 1 % modulation in amplitude for a typical prey item close to the skin; (Nelson and MacIver 1999; Chen et al. 2005) can also be obscured by large-scale AMs due to the fish’s own body movements. Chief among those may be tail bending, which changes the geometry of the electric field (Heiligenberg 1975). The signal driving the electroreceptors in the skin, the transdermal potential difference, will increase in amplitude on the side of the body to which the tail is bent, and decrease on the opposite side (Bastian 1995; Chen et al. 2005). The change in transdermal potential amplitude caused by tail bending is in the range of several percent of the baseline value (Heiligenberg 1975; Chen et al. 2005). The undulations of the anal fin that propel the fish forward and backward may also lead to modulations of the animal’s own electric field, but the effect has not been quantified so far.

When two or more fish interact, the frequency of the beat modulations is determined by the difference in EOD frequency between the animals (Fig. 12.3). The contrast, i.e., the strength of AM during the beat, depends on the distance between fish, because the strength of the electric field of a fish falls off steeply with distance (Knudsen 1975; Rasnow and Bower 1996; Chen et al. 2005). Therefore, contrast will be modulated as fish move relative to each other. These second-order AMs are also called envelopes. Similar, but periodic, envelopes of beat signals are created when three or more fish interact (Middleton et al. 2006; Stamper et al. 2010); this is because the beats between a fish and its neighbours will themselves interfere and create a “beat of beats”. Although these envelopes may contain important information for a fish, such as the distance from conspecifics and the EOD frequency relationships in groups, it is conceivable that envelopes can interfere with the fish’s ability to electrolocate objects, and may thus constitute noise in the context of foraging. This is supported indirectly by the finding that EOD recordings of groups of *Apteronotus* in their natural habitat did not contain envelope power at very low frequencies (Stamper et al. 2010).

In the following sections, we will first discuss various ways in which the electrosensory system deals with noise that may be considered as a burden for detecting and processing important sensory signals. The last section will take a

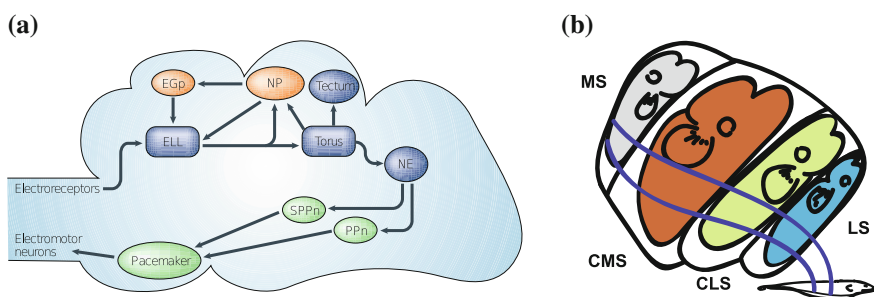
different, and complementary, approach by looking at the benefits of noise for neural processing in general and electrosensory processing of communication signals in particular.

## 12.4 Neural Tuning

In order to understand how different sources of noise can affect the encoding of electrosensory information we will now discuss how the nervous system processes electric signals in gymnotiform weakly electric fish (Fig. 12.6). After a short introduction of the electrosensory periphery we first consider the frequency tuning of the electrosensory system, before we describe the role of neuronal noise in sensory processing.

The circuitry involved in electrosensation and electric behaviour has been studied in great detail and an enormous amount of information is available on the neuroanatomy of the system, its neurotransmitters and neuromodulators, and the transmitter receptors and ion channels (for reviews, see Berman and Maler 1999; Bell and Maler 2005; Maler 2009b). This extensive knowledge forms an excellent foundation for in-depth studies of neural processing, which have been facilitated by the experimental accessibility of the electrosensory system under *in vivo* conditions and the persistence of electric behaviours, such as the JAR and chirping, in immobilised preparations.

The first point to note about the electrosensory system is that its circuitry takes up a large proportion of the brain volume (Maler et al. 1991), which can be seen as an indirect argument for its dominant role among the senses of electric fish. Sensing electric fields starts with the electroreceptor organs which are distributed



**Fig. 12.6** The electrosensory system. **a** Overview of the brain of the weakly electric fish illustrating the main components of the electrosensory circuitry. *ELL* electrosensory lateral line lobe, *NP* nucleus praeeminentialis dorsalis, *EGp* eminentia granularis pars posterior, *NE* nucleus electrosensorius, *PPn* prepacemaker nucleus, *SPPn* sublemniscal prepacemaker nucleus. Figure taken from Rose (2004). **b** The *ELL* is separated in four segments/maps. *MS* medial segment, *CMS* centromedial segment, *CLS* centrolateral segment and *LS* lateral segment. Figure taken from Krahe et al. (2008)

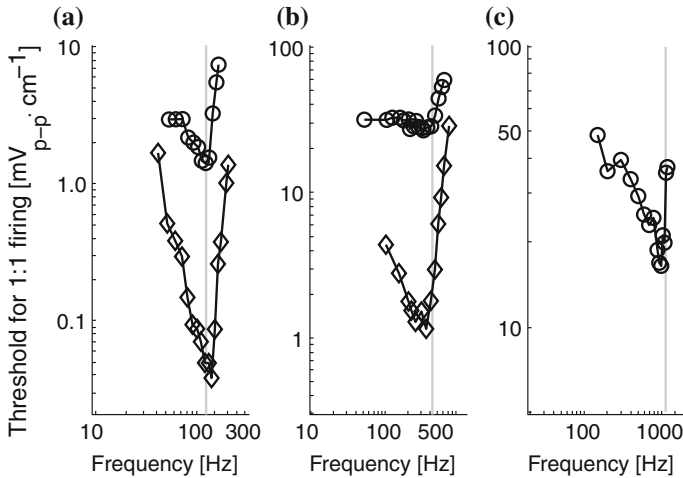
all over the skin, and of which two basic types exist: the first one, ampullary electroreceptors are sensitive to low-frequency electric fields generated by muscle activity of other organisms and, at least in *Eigenmannia*, to EOD interruptions, which in this genus contain low-frequency power and are produced in communication interactions (Metzner and Heiligenberg 1991). The second type of electroreceptors consist of the so-called tuberous electroreceptors, which sense the fish's own EOD and its perturbations. Each receptor organ is composed of a number of electroreceptors, which are innervated by the electroreceptor afferents that carry electrosensory information to the hindbrain via the octavolateralis nerve (Zakon 1986a). The skin of an adult *A. albifrons* contains approximately 15,000 tuberous receptor organs compared with approximately 700 ampullary organs and roughly 300 neuromasts for the mechanosensory lateral line (Carr et al. 1982). Within the population of tuberous primary afferents, two sub-populations are observed, so-called P-units and T-units (Scheich et al. 1973). T-units respond in a precisely phase locked, one-to-one fashion to the fish's own EOD pulses, while the P-units fire probabilistically, and their response probability for a given EOD pulse depends on its amplitude.

### ***12.4.1 Matched Tuning of Electroreceptors to EOD Frequency***

The active electrosensory system is used for the two purposes introduced above: electrolocation and electrocommunication. In both cases the AM of the carrier, the EOD, contains information that needs to be extracted. The AM sets the probability with which a P-unit emits a spike during an EOD cycle. Thus, the P-unit afferents encode the time course of the AMs in their firing rate. As in other AM coding systems, such as the auditory system (see Chaps. 3, 4, 6, 8 and 10), the electroreceptors as well as their afferents are specifically tuned to the fish's own EOD frequency (Hopkins 1976; Viancour 1979a, b; Knudsen 1974; Fig. 12.7). The tuning of receptors and receptor afferents is interpreted to constitute a matched filter (Hopkins 1976), which will be discussed below.

#### **12.4.1.1 Emergence of Tuning**

Evidence from newly regenerating electroreceptors, which initially show a rather broad, coarse tuning and eventually are adjusted to the fish's EOD frequency, indicates that the tuning is only in part genetically defined (Zakon 1986b). Fine tuning appears to be achieved via hormonal influence. Steroid hormones affect the EOD frequency as well as the receptor tuning (Meyer et al. 1987; Keller et al. 1986). In *Apteronotus* treatment with 5- $\alpha$ -dihydrotestosterone (DHT) increases and 17- $\beta$ -estradiol decreases the EOD frequency. Interestingly the tuning of the



**Fig. 12.7** Tuning of electroreceptors. Example tuning curves of tuberous T-units (diamonds) and P-units (circles) of three different species of weakly electric fish. **a** *Sternopygus macrurus*, **b** *E. virescens* and **c** *Aptereronotus albifrons* (only P-units). The tuning curves show the field intensity (in peak-to-peak amplitude per cm) required for a 1:1 firing (one action potential per EOD cycle) of the cell at various frequencies of an artificial electric field. This is the upper limit of the operating range, and, for P-units, therefore not representative of the behaviourally relevant range of field intensities. The tuning curves are matched to the fish's own EOD frequency (indicated by the grey lines). Redrawn from Hopkins (1976)

electroreceptors shifts accordingly. A further line of evidence in this direction comes from the correlation of the EOD frequency with the maturation of the animals. In *Aptereronotus* the EOD frequency of newly hatched fish starts at 300–400 Hz and increases with maturation (Meyer et al. 1987).

#### 12.4.1.2 Tuning Mechanism

The question arises by which mechanisms the tuning of the cells is established. At the best frequency the electroreceptors show a resonance behaviour (e.g. Viancour 1979b; Keller et al. 1986; Meyer et al. 1987; Zakon 1986b) which is also known from auditory hair cells. In these,  $\text{Ca}^{2+}$ -activated  $\text{K}^+$  ion channels are responsible for oscillatory behaviour (e.g. bullfrog hair cells, Lewis and Hudspeth 1983). The close relationship between hair cells and electroreceptors suggests that the same mechanism may apply here (Keller et al. 1986). Changing the density of these channels via hormonal influence can affect the resonance behaviour and thus the tuning. A modelling study by Koch (1984) demonstrated that a population of such  $\text{Ca}^{2+}$ -activated  $\text{K}^+$  channels can render the membrane *quasi-active* inducing resonance behaviour. The density of such channels defines the resonance frequency.

As any other biological mechanism, the tuning is also influenced by temperature. For both the EOD and the receptor tuning similar effects with  $Q_{10}$  values in

the range if 1.4–1.6 have been observed (e.g. Enger and Szabo 1968; Hopkins 1976; Dunlap et al. 2000). Because temperature affects EOD frequency and receptor tuning in similar ways, changes in water temperature are not expected to interfere with the coding of localisation and communication information.

### 12.4.1.3 Matched Filtering in a Multi-Purpose System

The close match between the receptor's best frequency (frequency with lowest threshold, Fig. 12.7) and the frequency of the fish's own EOD suggests that the filter characteristics constitute a matched filter turning electrosensation into a private channel of information acquisition. This notion, however, needs to be discussed in some more detail.

If only the carrier frequency is of interest, a sharply tuned matched filter would reject all frequencies that are not relevant, e.g. those due to biotic or abiotic noise sources. The tuning of electroreceptors and of auditory hair cells has been interpreted as a mechanism for reducing noise and increasing response specificity (e.g. Hopkins 1976; Ricci et al. 2005, see also Chaps. 8 and 10). Similar mechanisms are found in various other systems. For example, neurons in the auditory system of certain species of bats exhibit a very sharp tuning to the *reference frequency*, i.e. the frequency of their call's echo (e.g. Suga 1965; Pollak and Bodenhamer 1981). But how does the level of specificity found in the frequency tuning of the electroreceptors relate to their role in electrosensation? Many other sensory systems consist of an array of receptors that, as a population, but not individually, cover the relevant stimulus space. In weakly electric fish the electrosensory receptors serve two purposes each with its own requirements, but there is only a single population of similarly tuned P-units that has to cover the behaviourally relevant frequency range. For electrolocation (auto-communication) a sharp tuning should be advantageous because all information is contained in the AMs of the fish's own EOD, and contamination from other frequencies should be avoided.

Communication with conspecifics, however, would not be possible with an extremely sharp receptor tuning for two reasons. First: when two, or more, individuals are in proximity, their EODs interfere, resulting in a beat (Fig. 12.3). This beat carries information about the nature of the interaction (same-sex or opposite-sex encounter; interacting with a dominant or subordinate animal). Accordingly, the production of the different chirp types depends on the context of the encounter, i.e. the beat frequency (Engler and Zupanc 2001). To sense a beat, the receiving fish must be sensitive not only to its own EOD but also to the frequency of the other fish. Because encounters in *Apteronotus* can easily produce beats up to 400 Hz, the tuning must be wide enough to permit sensing such signals, especially when considering that large EOD frequency differences, i.e. high beat frequencies, are likely to occur in mating contexts. Second: The communication signals themselves (chirps) are characterised by frequency excursions of up to several hundred Hertz (Fig. 12.5). The various chirp types are produced in different contexts (agonistic, submissive, mating) and a sharp receptor tuning would not

permit to discriminate chirps which have frequency excursions shifting the beat to frequency ranges outside the range that can be sensed. The tuning of the electroreceptors is thus constrained by these two purposes. An optimal tuning can only be a compromise between noise rejection and sensitivity bandwidth. Whether the tuning width matches the frequency range that naturally occurs for a given species remains unknown.

#### **12.4.1.4 Electrocommunication Interferes with Electrolocation**

The multi-purpose usage of the broadly tuned electroreceptors for both electrolocation and -communication signals makes the electrosensory system vulnerable to interferences among the two types of signals. Low-amplitude electrocommunication signals can be obscured by distortions of the electric field by nearby objects and non-conducting boundaries, such as the water surface. Vice versa, strong jamming signals from conspecifics, that overwhelm electrolocation signals, affect electrolocation on the behavioural as well as the physiological level (Matsubara and Heiligenberg 1978; Bastian 1987a, b). By means of the JAR (see above, Bullock 1969) the fish actively move the jamming beats out of the AM frequency range of electrolocation signals to higher frequencies. The frequency shifts due to the JAR, however, are relatively small compared to the width of the tuning curves (compare Figs. 12.4 and 12.7). Further separation between electrolocation and -communication is left to the neural system. For example, the generation of a “negative image” removes predictable low-frequency distortions (see below).

#### **12.4.1.5 Receptor Tuning as a Species-Specific Filter**

The tuning seen in the electroreceptors restricts the band of frequencies that affect the P-unit responses. With this, the perception of other wave-type species that share the same habitat, but use different frequency bands (Fig. 12.2), is greatly reduced. In that way, a species-specific, rather than an individual-specific, frequency channel is established. The broader tuning resembles to some extent the tuning of ascending neurons in bush-crickets which show species-specific tuning (e.g. Stumpner 2002, see also Chap. 3) interpreted to act as a frequency filter for the songs of conspecifics.

Still, the match between the individual EOD frequency and the individual receptor’s best frequency makes the fish most sensitive to their own carrier frequency. This fits experimental results on mormyrids showing that electrolocation is more robust against disturbances than electrocommunication (Schief et al. 1971). The EODs of pulse-type electric fish, however, pose a problem for syntopic wave-type fish. These pulses have spectral power in a very broad range (Fig. 12.1, last row, right column) and thus will contaminate the field even of very sharply



tuned receptors. The discharge rates of pulse-type fish are quite low and thus contamination from EOD pulses is limited to occasional and short time windows.

The tuning of the electroreceptors thus appears to be a compromise between the constraints imposed by electrolocation and electrocommunication. Optimal noise rejection is sacrificed for an increased bandwidth of the communication channel. This trade-off shares some similarity with olfactory communication in moths. There, male moths respond to a wider variation of pheromones than are usually produced by female moths. The wider acceptance window, or tuning, is of advantage if failure to respond is more expensive than a false alarm (see [Chap. 13](#)).

### ***12.4.2 Temporal Tuning of Primary Afferents for AMs***

Besides the frequency tuning discussed above, P-units have temporal response characteristics which act as frequency filters on the AM signal. Measurements of the P-unit sensitivity to AMs of increasing frequency suggest that they have high-pass characteristics that attenuate low frequencies (Bastian [1981](#); Nelson et al. [1997](#); Chacron et al. [2005](#); Benda et al. [2005](#)). For electrolocation and prey detection this seems to be counterproductive because the AMs induced by moving objects and prey have mainly low-frequency power (Bastian [1981](#)). Still, the fish are well able to detect and successfully capture prey (Nelson and MacIver [1999](#)). Nelson and MacIver ([1999](#)) suggest that the high-pass characteristics of the P-unit afferents may assist prey capture by serving as a predictive filter pointing to the location at which the prey will be next. By applying information theoretic measures Chacron et al. ([2005](#)) could show that despite the high-pass characteristics, low frequencies are similarly well represented in the responses as higher frequencies. This is attributed to reduced low-frequency noise due to correlations between consecutive interspike intervals (Chacron et al. [2001, 2004, 2005](#)). In the context of electrocommunication, i.e., the encoding of chirps in the P-unit responses, the high-pass behaviour arising from spike-frequency adaptation was concluded to be advantageous by separating the responses to the transient chirps from low-frequency background modulations (Benda et al. [2005](#)).

### ***12.4.3 Spatio-Temporal Tuning in the ELL***

Upon entering the hindbrain, each primary afferent fibre trifurcates, so that three somatotopic maps of the body surface are formed in the electrosensory lateral line lobe (ELL) of the hindbrain (Carr et al. [1982](#); Heiligenberg and Dye [1982](#)). Based on their arrangement in the ELL, these maps are called lateral segment (LS), centrolateral segment (CLS) and centromedial segment (CMS). A fourth map, the medial segment (MS) is dedicated to processing ampullary information (Fig. [12.6b](#)). T-units synapse onto spherical cells, which send axons to the torus

semicircularis of the midbrain, where EOD phase information is compared between different parts of the body surface for computations involved in the generation of the JAR (Heiligenberg 1991). P-units, on the other hand, synapse onto pyramidal cells in the ELL as well as on local interneurons.

The pyramidal cells of the ELL come in two types, E-cells and I-cells, analogous to the ON and OFF cells of the lateral geniculate nucleus (Krahe and Gabbiani 2004). E-cells respond with excitation to increases in EOD amplitude, whereas I-cells respond with excitation to decreases in amplitude. Similar to thalamic relay neurons, pyramidal cells have antagonistically organised spatial receptive fields with excitatory centre and inhibitory surround (E-cells) or inhibitory centre and excitatory surround (I-cells) (Maler et al. 1981; Shumway 1989; Bastian et al. 2002). E- and I-cells can each be further subdivided into superficial, intermediate and deep cells according to the location of their somata in the pyramidal cell layer of the ELL and the length of their apical dendrites (Bastian and Courtright 1991). These six pyramidal cell types have been found to be arranged in columns containing one cell of each type (Maler 2009a).

A common feature in nervous systems is the increasing stimulus specificity from the periphery to higher processing stages in the brain which extract behaviourally relevant information from the continuous flow of sensory information. This is precisely what is seen in the electrosensory system of the weakly electric fish. While the electroreceptor afferents reliably code for AMs of the carrier (e.g. Chacron et al. 2005; Gabbiani 1996) the pyramidal cells in the ELL respond much more specifically (Gabbiani 1996). The ELL pyramidal cells in the different maps show different temporal coding properties ranging from high-pass in the lateral segment (LS) to low-pass characteristics in the CMS, tuning them to different temporal aspects of the sensory input (Krahe et al. 2008). High-pass tuning itself is induced by the increased expression of SK (small-conductance potassium) channels in the LS that suppresses the responses to low frequencies (Ellis et al. 2007). Measurements of these *in vivo* tuning properties match those found under *in vitro* conditions (Mehaffey et al. 2008).

The spiking activities of electroreceptor afferents are independent from each other (Chacron et al. 2005; Benda et al. 2006). Pyramidal cells integrate convergent information from the number of afferents within their receptive fields. Across the ELL maps the receptive field size changes from small (CMS) to large in the LS (Maler 2009a) making them better suited for electrolocation or electrocommunication, respectively (see below).

Dendritic mechanisms can lead to bursts of action potentials in pyramidal neurons (Doiron et al. 2001). The role of these bursts is different in the different maps. In the CMS bursts increase the representation of prey-like signals. In the LS, on the other hand, fast, transient AMs as induced by chirps lead to bursting (Marsat et al. 2009). Bursting makes the coding of communication signals more robust against noise (Ávila-Åkerberg et al. 2010).

### ***12.4.4 Feedback Removes Predictable Information***

A striking similarity between ELL pyramidal cells and thalamic relay neurons is the extensive feedback both types of neurons receive on their apical dendrites (Krahe and Gabbiani 2004). Two feedback pathways arise from the isthmus nucleus praeeminentialis dorsalis (NP, Fig. 12.6a), which receives electrosensory input from a subset of pyramidal cells. The so-called direct pathway projects from NP directly back to the ELL. It has been discussed to be involved in a sensory searchlight mechanism originally proposed by Francis Crick for corticothalamic circuitry (Crick 1984; Bratton and Bastian 1990). Another set of output neurons of NP projects to the eminentia granularis posterior (EGp) of the cerebellum, from where parallel fibres innervate the molecular layer of the ELL which contains the apical dendrites of the pyramidal cells. This indirect feedback pathway is thought to be involved in gain control and the cancellation of redundant sensory input (Berman and Maler 1999).

Sensory systems in general are set up as change detectors. Anything that is novel could be important, whereas sensory input that is predictable does not carry much information and should be disregarded. Predictable inputs to the electrosensory system arise, for example, from movements of the fish's tail, which change the geometry of the electric field, and from periodic AMs due to interaction with nearby conspecifics. These signals can also be viewed as highly structured narrow-band noise sources. Superficial and intermediate ELL pyramidal cells display a pronounced plasticity in their responses to such predictable electrosensory signals; their responses decline gradually thanks to an active mechanism that learns to counterbalance the feed-forward input from primary afferents by generating a "negative image" of the predictable input (Bastian 1995). Such negative image mechanisms that cancel redundant sensory input have been proposed by Curtis Bell to be a primary function of cerebellum-like structures in general (reviewed in Bell 2002). Interestingly, the ELL, which is located directly ventral of the eminentia granularis posterior of the cerebellum, is itself a cerebellum-like structure. A massive set of parallel fibres originating from cerebellar granule cells courses through the molecular layer of the ELL, where they interact with the large apical dendrites of ELL pyramidal cells (Berman and Maler 1999). Proprioceptive and electrosensory feedback provided by the parallel fibres has been shown to mediate the cancellation of predictable input due to tail bending and beats. Also, this mechanism potentially improves the signal of an object in front of background water plants, roots or rocks as well (Babineau et al. 2007).

An interesting problem for such a mechanism is that the plastic neurons that learn to disregard predictable input cannot themselves provide information on the redundant signals to higher brain centres. Thus, another, non-plastic, pathway is needed whose activity can be used by cerebellar feedback to cancel the sensory responses of the plastic neurons. This non-plastic pathway, which continues to respond to predictable signals, was found to consist of deep pyramidal cells in the

ELL, which project to the nucleus praeminentialis dorsalis, from where information is relayed to the cerebellum (Bastian et al. 2004).

The suppression of predictable sensory responses due to tail bending, or the continued presence of a conspecific, is expected to increase the signal-to-noise ratio of responses to novel signals, such as prey or chirps (change detection). This has indeed been shown through in vivo electrophysiological experiments in *A. leptorhynchus* (Marsat et al. 2009), where cerebellar feedback to plastic pyramidal cells supports the firing of bursts in response to chirps riding on a background beat.

### 12.4.5 *Beyond the ELL*

The next stage of electrosensory processing is the torus semicircularis where information from the time-coding (T-unit) system and the amplitude-coding pathway converges (Heiligenberg and Rose 1985) and input from the tuberous and ampullary maps is integrated (Metzner and Heiligenberg 1991). In addition, many toral neurons show direction-selective responses to objects moving along the fish (Ramcharitar et al. 2005). From the torus, one pathway leads to the optic tectum, which processes information on the motion of objects (Bastian 1982), and another to the nucleus electrosensorius. The latter contains neurons exquisitely sensitive to the sign of the frequency difference between a fish's EOD and that of its neighbour, a computation that has been shown to be instrumental for the JAR (Heiligenberg 1991). The nucleus electrosensorius provides input to two prepacemaker nuclei, the mesencephalic sublemniscal prepacemaker and the diencephalic prepacemaker (Heiligenberg et al. 1996), which, in turn, controls the medullary pacemaker nucleus that determines EOD frequency (Fig. 12.6a).

The following discussion of the role of noise in electrosensory processing will focus on the amplitude-coding pathway, specifically P-units and ELL pyramidal cells.

## 12.5 Noisy Neurons

Apart from the extrinsic sources of noise discussed above, electrosensory processing is also affected by intrinsic neuronal noise. This section first describes the noise observed in individual electroreceptor afferents and later reviews the effects of noise in populations of spiking neurons. In many cases, intrinsic noise is seen as a problem that is destructive and needs to be eliminated by averaging over many neurons. In populations of spiking neurons, however, the presence of noise and reliable information transmission are not necessarily contradictory.

### 12.5.1 Neuronal Noise Introduced by Primary Afferents

The frequency tuning of the electroreceptors leads to a high degree of temporal coupling to the fish's EOD (Fig. 12.8a, b). This imposes a temporal structure on the responses. Under baseline conditions, i.e. when no external signal is applied, P-units exhibit highly irregular response patterns, shown for *A. leptorhynchus* (e.g. Nelson et al. 1997) as well as *E. virescens* (Fig. 12.8). This is expressed in the broad multimodal distribution of the interspike intervals (ISI) shown in Fig. 12.8c, (see also Nelson et al. 1997). The response regularity can be described by the coefficient of variation ( $CV_{ISI}$ ) relating the standard deviation of the observed ISIs to their mean. Perfect regularity would lead to a  $CV_{ISI}$  close to zero, while random Poisson-like firing of action potentials results in CVs around one.

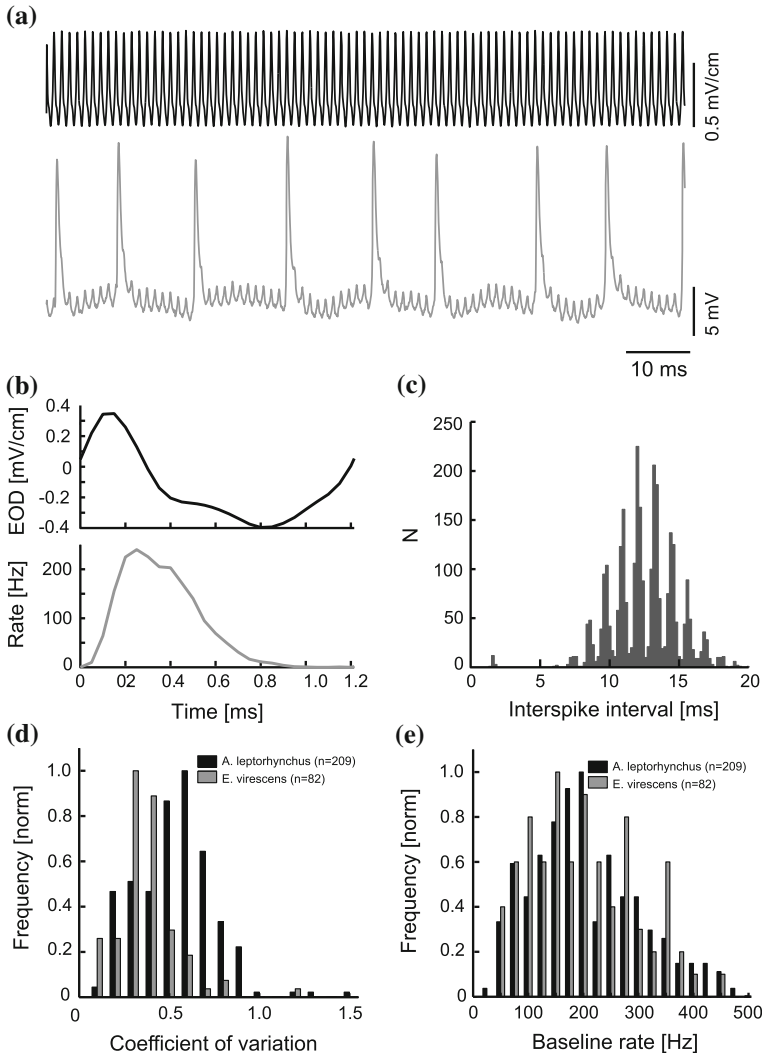
The CVs observed in *Apteronotus* and *Eigenmannia* P-units are rather large for primary afferents ( $0.54 \pm 0.23$  and  $0.37 \pm 0.17$  for *Apteronotus* and *Eigenmannia* P-units, respectively, Fig. 12.8d). Despite the apparently high degree of response variability the internal noise in the P-units was shown to be too small to distinctly affect the coding of AM signals (Kreiman et al. 2000). Interspike-interval correlations, as found in P-units, were further shown to reduce low-frequency response variability and increase information transfer (Chacron et al. 2001, 2004).

In addition to the high degree of response irregularity the population of electroreceptor afferents exhibits a considerable level of heterogeneity that can be viewed as a static noise source. Both, the  $CV_{ISI}$  (Fig. 12.8d) as well as the baseline rates (Wessel et al. 1996; Gussin et al. 2007) are widely distributed (Fig. 12.8e). It is, however, not clear (i) what the reason for these differences is, nor (ii) what the consequences for the coding of electrosensory information are. Heterogeneity found on higher processing levels, however, was concluded to be beneficial for coding of electrosensory information (Marsat and Maler 2010; Ávila-Åkerberg et al. 2010).

Why are the P-units so noisy, even in the unperturbed baseline condition? To answer this question we first introduce some general coding properties of populations of noisy neurons in the following section.

### 12.5.2 Noise in Populations of Spiking Neurons

In contrast to graded neurons that more or less operate linearly on an input signal, the generation of action potentials is a highly non-linear process that endows spiking neurons with interesting computational possibilities. For example, the all-or-none property of action potentials is the basis for decision processes. Either an input signal was able to trigger an action potential or not. Making decisions or classifications is not at all possible with linear systems. Similarly, noise in spiking neurons can have effects that are impossible in linear systems. In the following paragraphs, we introduce some very general and fundamental concepts on the role



**Fig. 12.8** P-unit baseline characteristics. **a** Recording of P-unit baseline activity (*bottom trace*, grey) and the EOD (*top trace*, black). Action potentials couple to the EOD. **b** Close up to the coupling. The *top trace* shows a single EOD cycle. *Bottom trace* PSTH averaged across all recorded EOD cycles. **c** Interspike-interval (ISI) histogram. Coupling to EOD leads to the dented structure of the ISI histogram. The response regularity is summarised with the  $CV_{ISI}$  of the ISIs. **d** Population heterogeneity is represented by the broad distributions of baseline rates of *Apteronotus leptorhynchus* and *E. virescens*. **e** Distribution of CVs observed in *Apteronotus leptorhynchus* and *E. virescens*

of noise in spiking neurons. These concepts are in no way specific to the electrosensory system, they apply to all neural systems. We need these concepts to be able to understand why the electroreceptor afferents are so noisy.

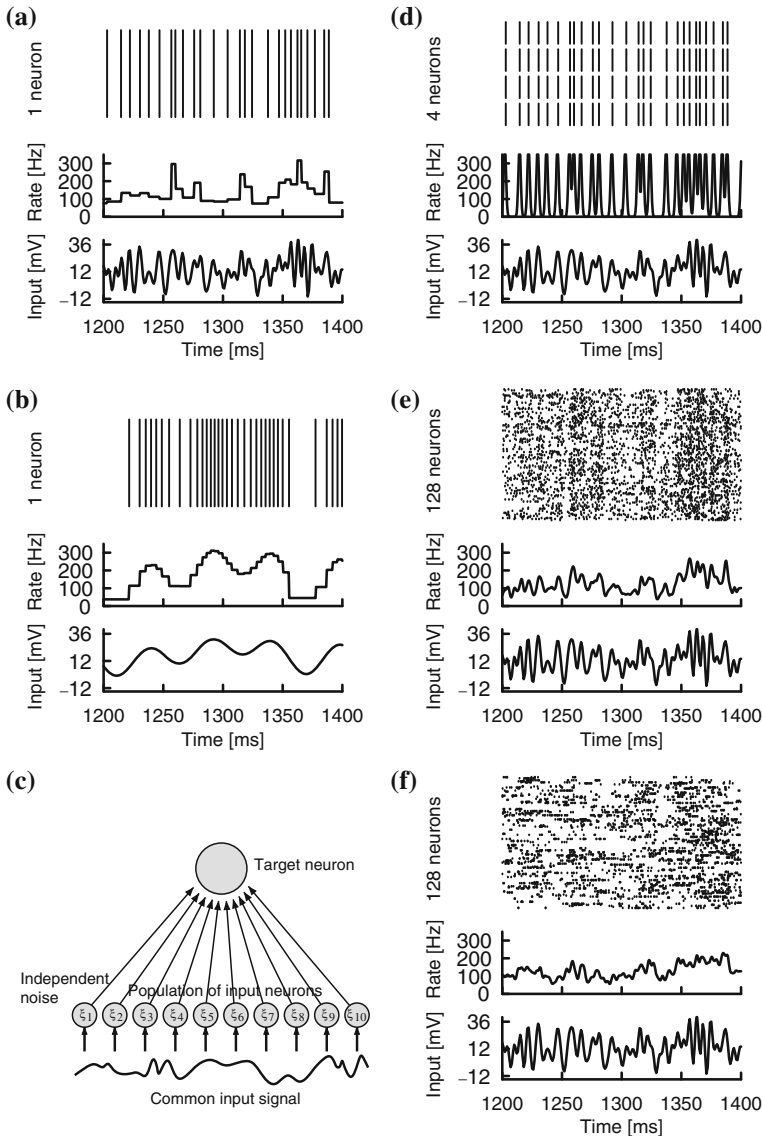
Best known for a possible beneficial role of noise in neural systems is the phenomenon of sub-threshold stochastic resonance (e.g. Bulsara and Zador 1996, Jaramillo and Wiesenfeld 1998). A weak sub-threshold input signal does not trigger any action potentials in a noiseless neuron. The addition of some intrinsic noise once in a while pushes the membrane potential over the firing threshold. This random generation of action potentials is more likely whenever the signal amplitude was high (and thus the membrane potential was closer to threshold) and less likely whenever the signal amplitude was low. In this way the number of action potentials per time contains some information about the amplitude of the sub-threshold input signal. However, if the noise level is too strong the noise itself dominates the generation of action potentials and less information about the signal is conveyed. Thus, there is an optimal non-zero noise level for a given signal amplitude, for which most information about the signal is encoded in the resulting spike train. There is a resonance in information transmission with respect to the noise level. Therefore, the term “stochastic resonance”.

This example of sub-threshold stochastic resonance already illustrates three important aspects: (i) A non-linearity, here the firing threshold, is needed for the noise to have a beneficial effect. (ii) Because of the non-linearity the noiseless case does not perform optimally. In the example, the information transmitted about the sub-threshold input signal is even zero. (iii) Not the absolute noise level determines the performance of the system but rather its relation to the signal amplitude, i.e. the signal-to-noise ratio (SNR).

Let us now turn to the case of suprathreshold signals that drive even a noiseless neuron sufficiently so that the neuron responds with some mean firing rate that is modulated according to the input signal (Fig. 12.9b). In this case a single neuron “samples” the input signal with its instantaneous rate (inverse interspike interval) and similar to the Nyquist theorem can maximally transmit signal frequencies up to about half its firing rate (Knight 1972; Pressley and Troyer 2011). Given two successive action potentials with interspike interval  $T$  there is no way to figure out whether these two spikes have been generated by a sinusoidal signal of period  $T$  or by one with half the period (twice the frequency, Fig. 12.9a). Only if there are at least two spikes per signal period, i.e. the firing rate is at least twice the maximum frequency of the input signal, one can imagine that the signal waveform can be inferred from the action potentials of a single neuron (Fig. 12.9b). Because the maximum firing rate of neurons is limited this sets a limit to the maximum frequency of an input signal that can be encoded by a single neuron.

The situation changes for a population of noisy neurons. Consider many identical but independent neurons (no lateral connections), a so-called homogeneous population, all receiving the same input. A downstream target neuron reads out the action potentials from all neurons in the population (Fig. 12.9c). Such a convergent feed-forward network is a common and basic network motif in neural systems.

If the neurons in the population were all noiseless, they would all fire at the same times (given they are forgetful, i.e. current leaks through the membrane). The responses are highly redundant and the population carries just the same information



**Fig. 12.9** Noise improves signal representation in populations of spiking neurons. Shown are spike rasters (*top panels*), firing rates (*middle panels*) and input signals (*bottom panels*) obtained from simulations of standard leaky integrate-and-fire neurons with firing threshold at 10 mV, reset voltage at 0 mV, membrane time constant of 10 ms, input resistance of 1 (therefore the current stimulus is in mV and the noise intensity in  $\text{mV}^2/\text{Hz}$ ) and additive white noise. **a** The instantaneous rate of a single noiseless neuron cannot resolve fluctuations of the input signal faster than the interspike intervals. **b** Input signals that are much slower than the interspike intervals are well represented by the instantaneous rate of noiseless neurons. **c** In a feed-forward convergent network the input neurons are independent and all receive the same input signal. **d** A population of noiseless neurons is identical to a single neuron. The population rate does not capture the signal waveform. **e** With the right amount of noise, the population rate follows also fast fluctuations of the signal well. **f** Too much noise deteriorates the population response

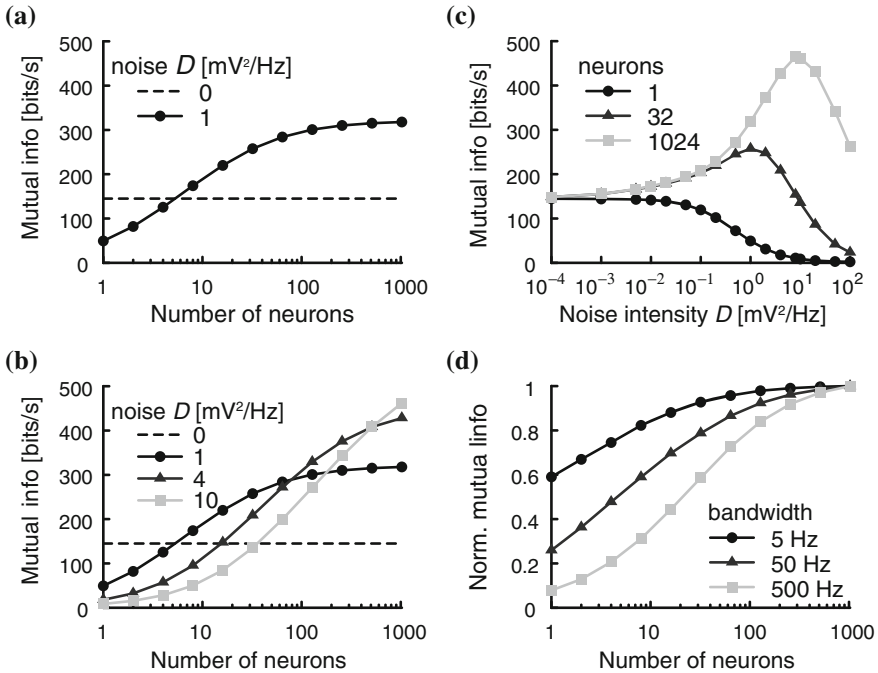


as a single neuron. So, nothing would be gained by having more than a single neuron representing the input signal (Fig. 12.9d). With a sufficient amount of intrinsic noise, however, each of the neurons in the population will fire at more or less different times. This way, the population samples the common input signal at any point in time (Fig. 12.9e). When the signal is weak only a small fraction of the population will fire, and when the signal is strong a much larger fraction will fire an action potential. Thus, the population rate  $r(t)$ , defined as the fraction of neurons in a population that fires a spike within a small period of time, will nicely represent the input signal (Knight 1972; Manwani et al. 2002). This is the firing rate that is usually measured as the PSTH from multiple trials recorded in a single neuron. The independent intrinsic noise sources decorrelate the responses of the neurons and thus reduce redundancy. Each neuron contributes slightly different information about the input signal.

In particular, even signal frequencies that are much higher than the firing rate can be transmitted by such a population of neurons (Fig. 12.9e). How exactly is described by power law functions that depend on the specific dynamics of the spike generator (Fourcaud-Trocmé et al. 2003). Contrary to common sense, the membrane time constant does not set any limit to the information carried about a suprathreshold signal (Pressley and Troyer 2011).

Although the intrinsic noise reduces the information about the input signal that is carried by a single neuron, summing up or averaging the responses of the whole population of noisy neurons can result in a much better representation of the signal than a single noiseless neuron can provide (Fig. 12.10a, Stocks and Mannella 2001). The common more pessimistic view on this characteristic is that, because of the noisy responses, upstream neurons have to average over many neurons to get rid of the noise. This view neglects the fact that by means of this averaging over a population of noisy spiking neurons potentially much more information about the input signal can be gained than in the noiseless case. Note also that in the context of computing Bayesian inference the variability of neural responses can be directly used for encoding the uncertainty of the estimated mean (Knill and Pouget 2004). How much noise in a population can enhance the mutual information depends on the properties of the signal and is in particular strong for high-frequency signals. In addition, the higher the noise level, the more the neurons are decorrelated, and the more information can be transmitted, provided the number of neurons in the population is large enough. The more noise is in the system, the more neurons are needed for achieving the same fidelity of the population code (Fig. 12.10b).

Noise in such homogeneous populations of neurons with a common input signal is thus potentially beneficial for signal representation. Furthermore, for a given number of neurons and a given class of input signals there is an optimal noise level that maximises the mutual information between signal and population response (Fig. 12.10c), because too much noise will eventually deteriorate the code (Fig. 12.9f, suprathreshold stochastic resonance, Stocks and Mannella 2001). Experimentally, however, this optimality of the noise level has not been shown yet.



**Fig. 12.10** Mutual information between input signal and population response. **a** The mutual information of a population of noisy neurons (*solid line*) increases with the number of neurons and can get much higher than the mutual information of noiseless neurons (*dashed line*). **b** The stronger the noise, the more neurons are needed to achieve the same mutual information. However, with even more neurons the mutual information can be increased even further. **c** For a given population size the mutual information is maximised by a particular non-zero noise level. **d** The higher the bandwidth of the signal (high-pass filtered Gaussian white noise with cutoff-frequency as indicated) the more neurons are needed before the mutual information saturates. Shown are simulations of the same leaky integrate-and-fire neuron as in Fig. 12.9. Mutual information was estimated from the coherence between input signal and spiking activity. The mean firing rate was 75 Hz

Usually the intrinsic noise of a neuron is thought to arise from ion channel noise, i.e. the stochastic opening and closing of voltage- or ligand-gated ion channels (White et al. 2000); and thus is a fixed quantity. Note that in higher brain centres the noise level could also be controlled by the amount of balanced excitatory and inhibitory synaptic input (Chance et al. 2002). What a peripheral sensory system in general cannot control is the amplitude of the sensory signal in relation to the fixed noise level. However, the size of the neural population can be adapted as well as the convergence ratios of the target neurons (on long, probably evolutionary time scales). For a given signal amplitude and frequency content the mutual information between the population response and the signal first increases with the number of neurons in the population, but eventually saturates (Fig. 12.10a). The minimum number of neurons needed for maximum mutual

information depends on the noise level, the signal amplitude and the frequency content of the signal. The higher the signal amplitude (higher SNR) or the lower its frequency the fewer neurons are needed for a maximum information transmission at a given noise level (Fig. 12.10d).

To summarise, let us highlight four aspects of coding common input signals in populations of noisy neurons; (i) Intrinsic noise exerts its beneficial role only in spiking neurons, not in graded-potential neurons. (ii) Populations of independent neurons are required—in single neurons noise in general deteriorates the coding quality (however, under certain assumptions even in single neurons noise can be beneficial, as for sub-threshold stochastic resonance discussed above). (iii) The relevant quantity that determines the fidelity of the representation of a common signal in a population of spiking neurons is not the absolute noise level, but the signal-to-noise ratio. For a two-fold increase in signal amplitude one needs twice as much intrinsic noise in order to achieve the same coding performance (Stocks and Mannella 2001). (iv) The frequency content of the signal is also an important factor. For lower maximum frequencies of the signal fewer neurons are sufficient.

In addition to the intrinsic noise discussed above, another kind of noise results from the heterogeneity of neurons in a given population. Neurons are not identical in their response properties; they have different thresholds, sensitivities, baseline firing rates, membrane time constants, adaptation strength, etc. Even without any intrinsic current noise this heterogeneity has a similar effect in that it decorrelates the responses of the neurons and thus results in an enhanced representation of the signal. A heterogeneous population has in addition the possibility to cover much wider ranges of input intensities by having different sensitivities.

In light of these fundamental properties of neural populations, the high intrinsic variability of P-units and their strong heterogeneity is not so surprising any more. By averaging over many noisy P-units the pyramidal cells in the ELL can obtain much more information about a signal than from a population of homogeneous and noiseless P-units. Let us now return to the active electrosensory system and discuss the characteristics of the natural signals the system has to process and how the information carried by the P-units is integrated and processed at the next level of the electrosensory pathway, the ELL.

### ***12.5.3 Decoding Population Codes in Three Different Maps of the ELL***

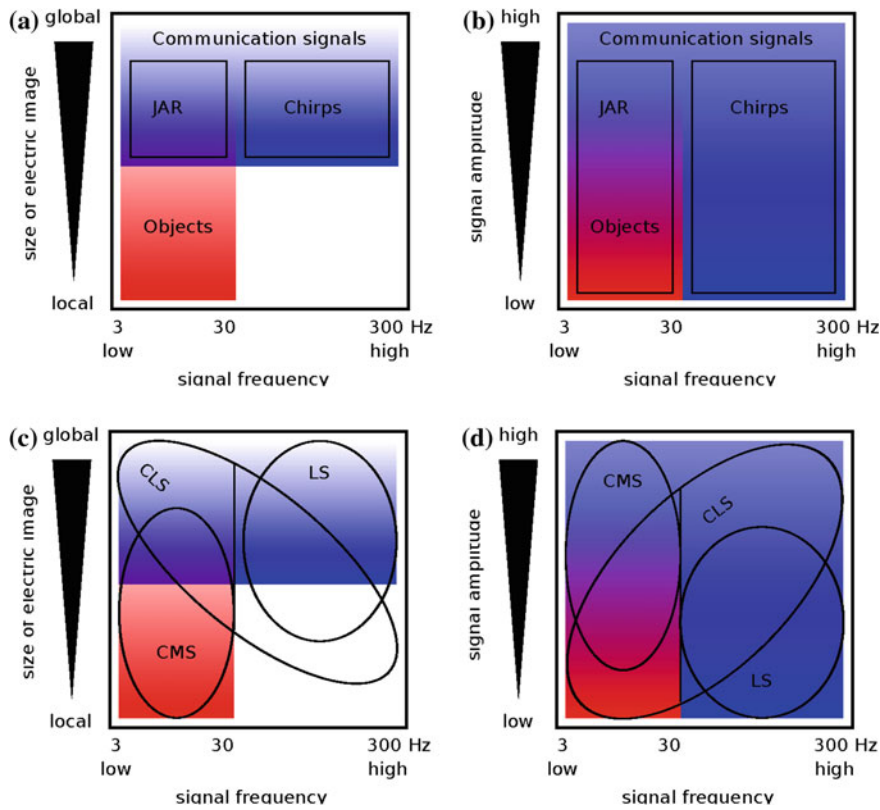
As described above the electrosensory system has to deal with several different classes of electric signals that differ in amplitude, frequency content and spatial extent and thus require different processing strategies in the electrosensory pathway. In fact, the receptor afferents of the active electrosensory system project onto three different types of pyramidal cells that are arranged in three separate maps, the CMS, CLS and LS (Fig. 12.6b) that differ in receptive field size and temporal tuning properties.

For the task of object localisation the fish have to extract the three coordinates for the relative position of the object as well as its size from the information available in the three ELL maps. Lewis and Maler (2001) and Maler (2009b) recognised that this is a multi-parameter estimation problem and investigated it in simulations using Fisher-information on the spike count. They conclude that the parameters can be successively obtained from the three maps (Lewis and Maler 2001) and that this parameter estimation is heavily influenced by possible synaptic scaling that normalises for receptive field sizes (Maler 2009b). The spike-count responses of the pyramidal cells are modelled with Gaussian functions describing their receptive fields plus additive noise. The noise strength was fixed across cells and the same for all the maps. However, this simple assumption models only the additional intrinsic noise of the pyramidal cells themselves and neglects the noise from the P-unit input. The latter, however, depends on the interacting effects of population size, signal amplitude and signal frequency and thus determines the fidelity and thus the noisiness of the representation of a signal by the population of P-unit afferents as explained in the previous section.

Therefore, we here qualitatively evaluate the role of the three ELL maps by summarising the different types of electric signals in terms of the properties that are important in the context of population codes introduced above (Fig. 12.11a, b). The relevant quantities are signal amplitude (in relation to the intrinsic noise level), signal frequencies and spatial extent. The latter defines the number of electroreceptor afferents receiving the same input signal. We then compare these requirements with the known properties of the target neurons, in particular, their frequency tuning and receptive field size, i.e. the number of receptor afferents converging onto a single pyramidal cell (Fig. 12.11c, d).

Let us first discuss the signals arising from distortions of the EOD by nearby objects that are used by the fish for electrolocation (Lissmann and Machin 1958, red regions in Fig. 12.11). If the objects are “far” away (at most a few centimetres, Nelson and MacIver 1999; MacIver et al. 2001), the electric images they cast on the body of the fish are faint in amplitude and blurred. They cover several centimetres on the body surface and thus provide weak input to many (hundreds) of P-units. If the fish approaches an object the electric image gets stronger and more focused. This is called a “local” stimulus that excites only a few (tens) of receptors. How the shape and amplitude of electric images look in detail has been studied both experimentally and theoretically (Heiligenberg 1975; Bastian 1981; Bacher 1983; Rasnow 1986; Chen et al. 2005; Babineau et al. 2006). The temporal properties of these signals are mainly determined by the speed (typical 9 cm/s) of the fish swimming past an object (MacIver et al. 2001). Temporal frequencies are low and range from a few Hertz for distant objects to about 25 Hz for nearby prey (Nelson and MacIver 1999).

Thus, for electrolocation we expect the target neurons of the electroreceptor afferents, the pyramidal cells in the ELL, to be sensitive to low signal frequencies. This excludes pyramidal cells of the LS because of their high-frequency tuning (Krahe et al. 2008) and leaves the CMS and CLS as the only segments that are sensitive to low-frequency signals (Shumway 1989; Krahe et al. 2008). Because of



**Fig. 12.11** Properties of electrosensory signals and ELL maps. Objects generate small (“local”) to intermediate sized, low-frequency and medium to small amplitude signals (amplitude modulations of the EOD). In contrast, communication signals are global and of larger amplitudes. In the context of JARs, communication signals are low-frequency, in chirping contexts communications signals usually contain higher frequencies. **a** The different classes of signals shown in a plane of electric image size versus signal frequency. *Stronger colours* indicate larger amplitudes of the signals. **b** Same as in (**a**) but as a function of signal amplitude and frequency. *Stronger colours* indicate more global, spatially diffuse signals. **c** and **d** The ellipses indicate regions in the stimulus planes for which the three ELL maps are best suited. The CMS with its small receptive fields and low-frequency tuning is best for localised, low-frequency signals that are not too small in amplitude. These are objects and JAR stimuli. The LS with its large receptive fields and high-frequency tuning is great for high-frequency communication signals, in particular with small amplitudes. The CLS with intermediate receptive fields switches from low-frequency tuning under local stimulation to high-frequency tuning for global signals (indicated by the vertical line, Chacron et al. 2003; Krahe et al. 2008). Therefore, both distant objects and strong communication signals might be processed in this segment

the very weak signals evoked by distant objects, the pyramidal cells might need to integrate over hundreds or even thousands of electroreceptor afferents to gain the necessary sensitivity (Maler 2009b). Therefore, it seems surprising, why the LS pyramidal cells integrating over more than one thousand afferents are not suited for

electrolocation, because of their high-frequency tuning. However, since the electrolocation signals are low-frequency, the information about these signals might already saturate at smaller numbers of input neurons (Fig. 12.10d). The medium-sized receptive fields of the CLS might therefore be an adequate solution for detecting distant objects. Under sufficiently local stimulation, CLS pyramidal cells are also tuned to the required low-frequency signals (Chacron et al. 2003; Krahe et al. 2008). Once an object gets closer, even less neurons are needed to compensate for the intrinsic noise of the P-units, because of the stronger signals (for example, in Fig. 12.10b a population of 100 neurons transmits about 260 bits/s at a noise intensity of  $10 \text{ mV}^2/\text{Hz}$ . The same mutual information is achieved with just 30 neurons at a smaller noise level of  $1 \text{ mV}^2/\text{Hz}$ , i.e. higher signal-to-noise ratio). Here the CMS with its small receptive fields might take over in order to match the spatial resolution of the electrosensory system to the more detailed electric image (Rasnow 1986; Lewis and Maler 2001; Maler 2009b).

The second stimulus class are the various kinds of communication signals that result from the superposition of the EODs of several fish, in particular beats, envelopes and chirps (blue regions in Fig. 12.11). These “global” stimuli affect large numbers of electroreceptors in a similar way (Kelly et al. 2008). The amplitude of these signals is given by the amplitude of the other fish’s EOD at the location of the perceiving fish. Therefore, communication signals can be much larger in amplitude in comparison to electrolocation signals for nearby fish. But communication signals can also be arbitrarily small, since the far field of electric fish is that of a dipole, whose amplitude drops inversely with the squared distance. So communication signals potentially cover a huge range of amplitudes. Assuming a detection threshold of  $0.5 \text{ } \mu\text{V}/\text{cm}$  (Knudsen 1974) other fish can be detected up to a distance of about 1.5 m (Knudsen 1975)—two orders of magnitude more than for electrolocation.

The communication signals can be further classified according to their temporal properties. On the one hand, low-frequency beats up to about 20 Hz that elicits a jamming avoidance response (JAR) and on the other hand beats of higher frequency that elicit chirps and related behaviours (Hupé and Lewis 2008). Because of the low frequency (Fig. 12.10d) and larger amplitude (lower noise intensity in Fig. 12.10c) of JAR signals integration over a few receptor afferents should be sufficient to get close to the maximum information that can be retrieved from the noisy P-unit population. Indeed, a lesion study has shown that the CMS is necessary and sufficient for JAR behaviour (Metzner and Juranek 1997). JAR behaviour can be evoked by small amplitude beats ( $<0.1 \%$  contrast) as well (Rose and Heiligenberg 1985; Kawasaki 1997). How well these small-amplitude signals are encoded in the CMS or whether the CLS with its larger receptive fields is needed for tiny jamming signals in order to compensate for the lower signal-to-noise ratio, remains to be investigated.

The higher frequencies of fast beats and chirps profit the most from the noise of the P-units if the target cell average over many neurons (light grey curves in Fig. 12.10b–d). This would fit the pyramidal cells in the CLS or even the LS with their larger receptive fields. The above mentioned lesion study showed that it is the

LS that is necessary and sufficient for chirping behaviour (Metzner and Juranek 1997). The fish are also very sensitive to low-amplitude beat signals (Knudsen 1974), which would be generated by the presence of distant fish. In this regime, the LS would play out its strength given the high number of P-unit afferents converging onto each pyramidal cell (more than one thousand, Maler 2009a). However, the fish might also want to localise the conspecific. For this, the smaller receptive fields of the CLS might be more appropriate to better evaluate the various geometries of the electric images resulting from the interaction of two nearby fish (Kelly et al. 2008).

In summary, given the large variety of electric signals the noise introduced by the electroreceptor afferents themselves seems to be appropriately used by the pyramidal cells in the different segments of the ELL. In particular, the noise is necessary to enhance encoding of high-frequency communication signals and to potentially increase the information about small amplitude signals. How exactly the number of neurons projecting onto the pyramidal cells is optimised given the fixed noise level of the P-units remains, however, to be investigated. Vice versa, one can ask whether the noise level of the P-units and their heterogeneity is optimised for the observed convergence ratios and required spatial resolutions.

Here, we have discussed only the direct input to the ELL neurons. However, as described above, the pyramidal cells also receive feedback from two distinct feedback pathways. In particular, spatially extended predictive input is subtracted from the responses of superficial pyramidal cells by means of a “negative image” mechanism, thus improving the representation of novel signals. The feedback also decorrelates the responses in the LS (Chacron and Bastian 2008) and thus potentially allows for further increases in sensitivity in higher processing stages like the Torus semicircularis by averaging over the LS cells.

Also, in addition to static snapshots of the electric images the fish could make use of motion signals (Babineau et al. 2007). For instance, during prey capture the fish scan the prey object and in a closed-loop fashion adapt their movement to the gained information about object location until capturing the prey within about one second (MacIver et al. 2001). This rapid behavioural sequence also sets tight limits for potential temporal integration mechanisms to improve prey detection. In the ELL, neurons are not particularly sensitive to motion signals, but they might pick up the signal upstrokes or downstrokes generated by moving objects (Gabbiani 1996). At the next stage of electrosensory processing, in the Torus semicircularis, some neurons indeed show direction-selective responses (Ramcharitar et al. 2005, 2006; Chacron et al. 2009).

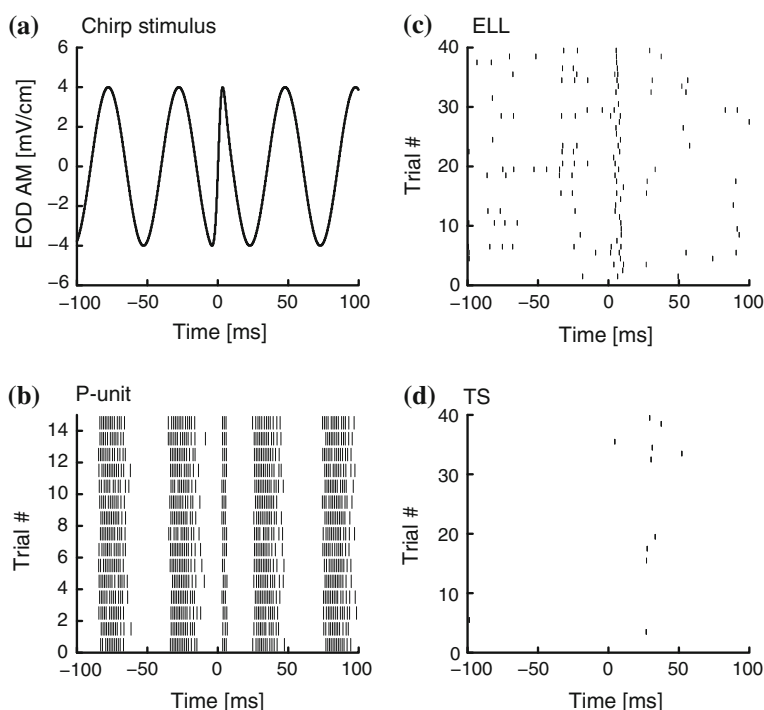
#### ***12.5.4 Synchrony Code and Chirps***

So far, we discussed how electric signals might be represented by means of populations of noisy neurons. However, sensory systems also need to process information. Relevant features of the sensory input need to be detected (Gabbiani 1996) and



irrelevant signals should be discarded (Bastian 1995). In the following, we show how a neural system can make use of noisy neurons in order to extract certain features from a sensory signal. For this, we first look closer at communication signals, in particular how chirps (Fig. 12.5) are processed by the first stages of the electrosensory system.

The firing rate of P-unit afferents follows the periodic amplitude modulation of a low-frequency beat. A small chirp briefly advances the beat and thus introduces a higher frequency amplitude modulation (Fig. 12.5c). This faster signal evokes a stronger firing rate response (Fig. 12.12b) that briefly synchronises the P-unit population (Benda et al. 2005, 2006). On higher beat frequencies the situation reverses. Then the fast beat signals synchronise the receptor afferents and the small chirp briefly desynchronises the population response (Hupé et al. 2008). Similarly, large chirps that are usually emitted on high beat frequencies desynchronise the P-unit afferents as well (Benda et al. 2006).



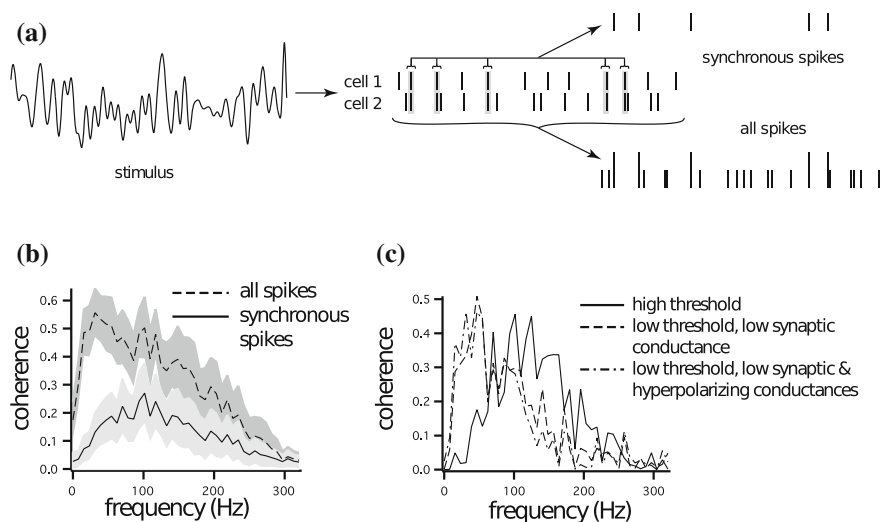
**Fig. 12.12** Encoding of chirps in the electrosensory system. **a** The amplitude modulation of a 20 Hz beat with a 14 ms wide chirp with a 100 Hz frequency excursion centred at time  $t = 0$  ms is the input signal. **b** A P-unit receptor afferent responds well to both the beat and the chirp. The response to the chirps is, however, usually stronger and more precisely timed than the one to the beat. **c** Pyramidal cells in the LS of the ELL weakly respond to the beat but reliably generate a burst in response to a chirp. **d** In Torus semicircularis some cells selectively respond to chirps and not to the beat any more. Data kindly provided by Henriette Walz (*panel b*) and Maurice Chacron (*panel c, d*)



What the chirps do is to change the level of synchrony in the P-unit population. This synchrony code is an additional coding dimension that is only possible in a population of spiking neurons. To differentiate between synchronous and asynchronous spikes that are fired in response to a common input is only possible because of the high noise level in the P-unit population. Without noise the activity of a neural population receiving a common input signal would be highly redundant and most spikes would be synchronous anyways.

Reading out synchronous spikes requires a non-linear operation like coincidence detection that can be achieved, for example, by linear synaptic summation and a high firing threshold. Such mechanisms potentially process the incoming information such that some aspects are tossed away. What if a pyramidal cell would only read out synchronous spikes from the population of P-unit afferents?

Middleton et al. (2009) followed this idea. They first quantified what kind of information the synchronous spikes carry about the input signal in comparison to all spikes. For this they extracted “synchronous spike trains” and “all spike” spike trains from recorded afferent responses to broad-band noise signals (Fig. 12.13a). The coherence between the input signal and one of these two spike trains is a lower bound estimate of the mutual information as a function of signal frequency. Interestingly, while all spikes code best for low signal frequencies, the synchronous spikes do not code for low frequencies but rather selectively encode higher frequency components of the input signal (Fig. 12.13b).



**Fig. 12.13** Synchronous spikes code for high-frequency signals. **a** From the spike trains of P-unit afferents one can construct a spike train that is just the sum of all spikes and another one that extracts only spikes that simultaneously occurred in both spike trains. **b** The coherence as a spectral measure of information transmitted about the input signal is low-pass for all spikes and high-pass for synchronous spikes. **c** A model of the pyramidal cell taking its receptive field and high firing threshold into account also responds in a high-pass manner to the input signal. Figures from Middleton et al. (2009)

Naively one could suggest that there should be some pyramidal cells with low firing thresholds that decode all spikes and thus are low-pass coherent with the input signal. Other pyramidal cells with high firing thresholds should decode the synchronous spikes only and thus show a high-pass coherence with the input signal. However, if both these cells integrate over the same number of input neurons, this would mean that the mean firing rate of the synchronous-spike decoder is much lower than the one of the all-spike decoder. Simulations of the pyramidal cell responses to the recorded P-unit afferent spike trains showed that both large receptive fields and high firing thresholds are required for the synchronous-spike decoder and small receptive fields and lower firing thresholds for the all spike decoder. Only then, they have about the same firing rates and the characteristic high-pass or low-pass coherence with the input signal, respectively (Fig. 12.13c, Middleton et al. 2009). Indeed, there is experimental evidence from *in vitro* work that CMS pyramidal cells with their small receptive fields have indeed a lower threshold compared to the LS pyramidal cells with their large receptive fields (Mehaffey et al. 2008). This fits well with the tuning properties of the pyramidal cells measured *in vivo*: CMS cells are low-pass whereas LS cells are high-pass (Krahe et al. 2008), indicating that LS pyramidal cells read out synchronous spikes from the population of P-unit afferents.

For the chirps this would mean that the brief synchronisation of the P-unit population is well encoded by the pyramidal cells of the LS while the asynchronous response to low-frequency beats is suppressed. Recordings from the ELL only partly support this hypothesis: in the LS only the superficial pyramidal cells receiving the negative image through feedback loops (see above) encode a small chirp with a signal-to-noise ratio that is enhanced in comparison to the responses of the P-unit afferents (Fig. 12.12b, Marsat et al. 2009; Marsat and Maler 2010). At the next level of the electrosensory pathway, the Torus semicircularis, a sub-population of cells responds selectively to chirps (Fig. 12.12c, Vonderschen and Chacron 2011). Thus, the signal-to-noise ratio of the chirp responses over the beat is successively improved in higher sensory areas and thus facilitates detection of chirps (see Signal Detection Theory, Chap. 2). In this sense, the beat is the noise in which the chirps are embedded.

## 12.6 Conclusion

The exotic electrosense of weakly electric fish shares several features with auditory and visual systems. The sensory signals are amplitude modulations of periodic carriers, similar to acoustic signals. A two-dimensional array of electroreceptors provides spatial information about nearby objects and conspecifics that cast electric images on the fish, similar to visual images that are processed by the retina. The active electrosensory system processes two different classes of AM signals simultaneously: communication and electrolocation signals.

Except for the evolutionarily young anthropogenic 60 Hz electropollution there is virtually no external noise in the frequency bands used by the active electro-sensory system at least of wave-type weakly electric fish. However, the highly structured and narrow-band electrocommunication signals interfere with the electrolocation signals, and thus constitute a noise source for electrolocation. Vice versa, electrolocation signals could be a relevant noise source for low amplitude communication signals.

Instead of being narrowly tuned to the fish's EOD frequency that carries the electrolocation signals, P-units are rather broadly tuned and thus open up a relatively wide frequency range that is used by conspecifics with their individual EOD frequencies and communication signals like, for example, chirps. Because of the low level or even lack of external electric noise the wide tuning of the P-units seems not to impair electrolocation.

Most strikingly, the electroreceptor afferents themselves introduce an unexpected amount of noise into the system—both as intrinsic noise and through their heterogeneity. Fundamental properties of populations of spiking neurons receiving a common input signal, however, show that such noise potentially improves the information about the signal. In particular, frequency components that are higher than the typical firing rate of the individual neurons benefit from this effect.

In this context, weakly electric fish prove to be an excellent model system to study such noisy population codes. First, the different classes of electric signals are well specified by just three parameters amplitude, frequency and spatial extent. Second, the target neurons of the electroreceptor afferents, the pyramidal cells in the ELL, are nicely separated in three distinct maps that differ in receptive field size and temporal tuning properties. In the lateral segment, pyramidal cells integrate over more than one thousand afferents and thus receive a high-quality input about high-frequency communication signals. Although of small amplitudes, the low-frequency electrolocation signals do not benefit from very large input populations. For these input signals the pyramidal cells in the centrolateral and centromedial segments with their smaller receptive fields are better suited.

Because of the noisy responses of the primary afferents, pyramidal cells could read out the level of synchrony and by this non-linear mechanism process incoming information. This is in particular relevant for encoding chirps, short duration modulations of EOD frequency used as communication signals. Depending on context, these chirps either synchronise or desynchronise the P-unit population. In vivo and in vitro data suggest that pyramidal cells in the lateral segment of the ELL indeed extract synchronous spikes from the P-unit afferents.

In this chapter, we have laid out some concepts and supporting experimental data on the role of noise in networks of spiking sensory neurons. These concepts are not limited to the electrosensory system of weakly electric fish, but we feel that this system has much to offer in terms of understanding how neural circuits use noise. The electrosensory system appears to be exposed to relatively little extrinsic noise. Instead, it appears to generate remarkably large levels of intrinsic noise. One wonders if we should start looking for a negative correlation between levels of extrinsic and intrinsic noise across sensory systems.

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