The source of frequency noise in ampullary electroreceptor afferents

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Signals in the primary afferents of ampullary receptor organs of catfish, such as *Ictalurus nebulosus*, are encoded by the spike rate. The afferents respond to stimulation with a change in firing frequency. Sensitivities of 1 Hz/nA have been recorded at bandwidths of $0.1<f< 30$ Hz. Without stimulation the afferents are spontaneously active and subject to frequency noise, i.e. they fire irregularly. Primary afferents do not seem to have a stimulus detection threshold. Under experimental conditions the frequency noise can be suppressed. Noiseless neurons fire at a lower rate and are less sensitive than noisy neurons. Frequency noise is not affected by convergence of presynaptic elements, whereas the stimulus-evoked response is. Signal transmission between receptor cells and afferents is mediated by a glutamergic synapse. Both spontaneous activity and stimulus-evoked modulations of the spontaneous activity are thought to represent a neurotransmitter release and consequently depolarization of the electroreceptor cell (Bennett and Clusin 1979). Strangely enough, it is possible to influence spontaneous activity and stimulus-evoked responses independently when neurotransmitter release is manipulated experimentally (table 1, fig. 1).

Protocol	Change in spontaneous activity	Change in stimulus–evoked response
Temperature change	Yes, proportional	No, different
Denervation	Yes	No
Regeneration	Yes	No
Administration of Cd^{2+}	50% Reduction	100% Reduction
Convergence	No	Yes

Table 1. Synopsis of experimentally induced changes in afferent firing.

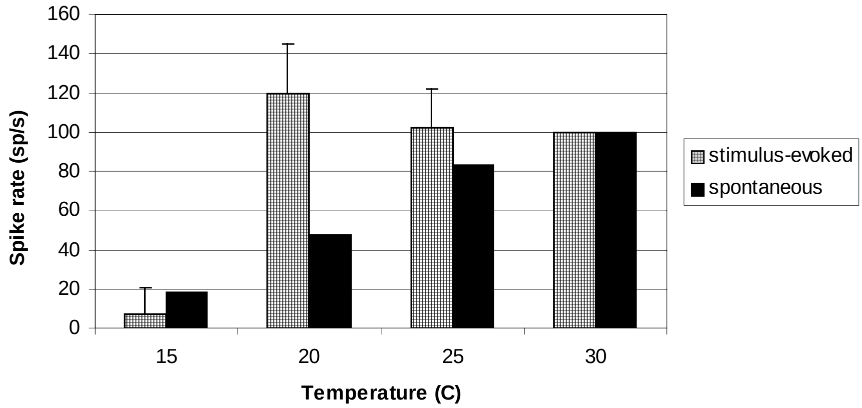

Fig. 1 Spontaneous activity (black bars) and stimulus-evoked activity (cross-hatched) of primary afferents of ampullary electroreceptor organs in *Clarias* at various temperatures. The spike rate is expressed relative to the activity at 30 ºC. The stimulus-evoked response is an average of responses to sinusoidal stimulation a 1, 3, 10, and 30 Hz.

Although the ampullary electroreceptor organ has bandpass filter properties, there also seems to be DC-coupling to some degree. This is particularly evident after the administration of solutions with different ion compositions and histological fixatives. Further, a strong inhibitory DC current makes the organ insensitive and reduces the irregularity of the firing. The insensitivity to external stimulation always corresponds to a low-noise spontaneous activity, at about 60% of the normal level of spontaneous activity.

An explanation for the discrepancies mentioned above can be given by an alternative model described by Roth (1979). This model proposes a path of high electrical conductivity between the electroreceptor cell and the primary afferent. Extracellular recordings of single unit action potentials in the lumina of ampullary organs support this model. The high conductivity path allows direct stimulation of afferent fibers, i.e. without the usual mediation of neurotransmitter, despite the presence of a chemical synapse.

However, both Roth's model and that of Bennett and Clusin can only explain experimental data partially. Therefore, a synthesis of both models, which we shall call the Transmitter Gated Electrical Synapse model (TGES), appears to be a better predictor of afferent firing in electroreceptor organs. The TGES model states that the primary afferent fiber shows regular spontaneous activity in absence of neurotransmitter release, most likely based on HH-equations. The regular firing can be modulated by electrical stimuli that are 10 to 100 times stronger than stimuli that modulate noisily firing afferents. An active synapse increases the spontaneous firing rate and adds frequency noise. Also, active synapses make the generator area of the afferent fiber directly accessible to current and raise the sensitivity to electrical stimuli (Peters and Denizot 2004).

According to the TGES model, frequency noise in firing rate of primary afferents of electroreceptor organs is predominantly caused by release of neurotransmitter and must be characterized as shot noise. In general, the noisier the firing, the more sensitive the electroreceptor organ. The signal-to-noise ratio is enhanced by the convergence of receptor cells onto the same primary afferent. Detection criteria are apparently implemented by higher order neurons.

Summing up:

1. The noise encountered in firing patterns of primary afferents is most likely shot noise due to the release of neurotransmitter.
2. The Transmitter Gated Electrical Synapse model is a better predictor of firing patterns than a plain neurotransmitter model
3. AC-related firing rate codes for electrical stimuli. DC-related firing codes for the ion composition of the aquatic environment and temperature, and also for strong electrical stimuli.

References

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