1 To-note

other models/papers to P-units:

Bastian 1981a Electrolocation I. How the electroreceptors of Apteronotus albifrons code for moving objects and other electrical stimuli

(Benda and Herz, 2003)

2 Introduction

1. sensory input important for all life etc.
2. electric fish
    (a) general: habitat,
    (b) as model animal for ethology
    (c) electric organ + eod
    (d) sensory neurons p- and t(?)-type
3. sensory perception
    (a) receptor → heterogenic population
    (b) further analysis limited by what receptors code for - P-Units encoding
    (c) p-type neurons code AMs
4. goal be able to simulate heterogenic population to analyze full coding properties → many cells at the same time needed → only possible in vitro/ with model simulations
5. Possible to draw representative values for model parameters to generate a population ?

2.1 Apteronotus leptorynchus

- to mention: size range, tank conditions,
- continuous sinusoidal electric organ discharge EOD with near constant amplitude and frequency (Moortgat et al. 1998)
- EOD carrier signal for AMs caused by nearby objects like prey or other electric fish
- prey stimuli are dominated by low frequencies

2.2 general P-unit notes

- consist of 25-40 receptor cells and a nerve fiber that makes synaptic contact to at least 16 active neurotransmitter release sites per receptor cell. (M.V.L. Bennett, C. Sandri, K. Akert, Fine Structure of the tuberous electroreceptor of the high-frequency electric "sh Sternachus albifrons (gymnotiformes), J. Neurocytol. 18 (1989) 265.)
- most abundant tuberous receptor

- spikes in probabilistic manner to upward phase of EOD
- important characterization P-value probability of spiking per EOD cycle estimated as p-unit frequency divided by EOD frequency typical values 0.1-0.6 (Bastian 1981a, Xu et al 1997)
- rapidly adapting (Benda et al. (2005) Xu et al. (1996)) often studied with SAMs or RAMs
- can predict up to 80% of the AM using reverse correlation and coherence but no obvious decoding mechanism
- linear coders of intensity, additive noise models are suitable Gussin et al. 2007
- ISI correlations important to detect both slow and fast varying stimuli (Chacron et al., 2001a) The negative correlation reduce low frequency noise and information is preserved at higher/central neurons (Chacron et al., 2005b)

2.3 neural and population coding

2.4 nerve recordings

- sample descriptions in: Hernriettes phd, Gussin et al. 2007, Benda et al. 2005

3 Mat&Met

1. Data generation
   (a) How data was measured / which data used
   (b) How data was chosen -¿ at least 30s baseline, 7 contrasts with 7 trials
   (c) experimental protocols were allowed by XYZ (before 2012: All experimental protocols were approved and complied with national and regional laws (file no. 55.2-1-54-2531-135-09). between 2013-2016 ZP 1/13 Regierungspräsidium Tübingen and after 2016 ZP 1/16 Regierungspräsidium Tübingen)
   (d) description of data -¿ Baseline properties, FI-Curve with images made from cells
   (e) make a point of using also bursty cells as part of what is new in this work!
2. behavior parameters:
   (a) which behaviors were looked at / calculated and why (bf, vs, sc, cv, fi-curve...)
   (b) how exactly were they calculated in the cell and model
   (c) stimulus protocols
3. Construction of model
   (a) Explain general LIF
   (b) parameters explanation, dif. equations
   (c) Explain addition of adaption current

    (d) note addition of noise + factor for the independence from step size
    (e) addition of refractory period
    (f) check between alpha in fire-rate model adaption and a-delta in LIFAC

4. Fitting of model to data
    (a) which variables where determined beforehand (None, just for start parameters)
    (b) which variables where fit
    (c) What method was used (Nelder-Mead) and why/(how it works?)
    (d) fit routine ? (currently just all at the same time)

3.1 Equations characterization

Baseline

p-Value:

$$p = \frac{neuronfrequency}{EODfrequency} \tag{1}$$

coefficient of variation:

$$CV = \frac{STD(ISI)}{\langle ISI \rangle} \tag{2}$$

serial correlation: (TODO: check!)

$$sc_i = \frac{\langle ISI_{k+j} ISI_k \rangle - \langle ISI_k \rangle^2}{VAR(ISI)} \tag{3}$$

burstiness: (TODO: what definition?)
vector strength:
FI-Curve:

3.2 model construction

- PIF - LIF - LIFAC - LIFAC + refractory period
- explain why adaption current and not a dynamic threshold: chosen AC other possibilities(dyn. thresh. voltage hyperpol.) why AC is better.
- what things could be the physiological base for the different parts of the model

4 Results

- Results fitting
    - Errors of model behavior to cell behavior
    - Comparison model-vs-cell behavior distribution
    - correlations between parameters and behavior
    - correlation between final error and behavior parameters of the cell → hard to fit cell "types"

  -
  - comparison SAM stimuli response

- "working with the models"
  - model parameter distribution
  - model parameter correlations
  - (TODO: drawing random models ????)

5 Discussion

5.1 Fitting quality

- strongly bursty cells not well fitted with a gap between first EOD and the gauss distribution, but this is possible in the model just seems to be a "hard to reach" parameter combination. more start parameters changes in cost function.

- additionally bursties might need more data to be "well defined" because of the more difficult pre-analysis of the cell itself (high variance in rate traces even with a mean of 7-10 trials)

- different fitting routine / weights might also improve consistency of the fitting

- Model CAN fit most types of cells except for double burst spikes in ISI hist (1st and 2nd EOD have high probability) and some with higher level structure in ISI hist are probably not possible with the current model

- f-I curve works but is still not fully consistent slope of f_0 strongly affected by miss detections so not the best way of validating the f_0 response.

- b-correlations:

- Data correlation between base rate and VS unexpected and missing in the model.

- data correlation between base rate and f_0 expected as f_0 f_∞ and f_∞ base rate (appeared in the model)

- Model correlation between base rate and burstiness probably error because of the problems to "fit the gap" between burst and other ISIs. (appeared in model)

- above probably causes base rate - SC correlation and this causes the additional SC - f_∞ correlation over f_∞ base rate

- In total it can deliver good models over a large space of the heterogeneity especially with the addition burstiness, but it is not yet verified with a different stimulus type like RAM or SAM and also need further investigation to it's quality for example because of the mismatched correlations → robustness analysis should be done

5.2 random models

- Gauss fits are in some cases questionable at best
- resulting parameter distributions as such also not really that good
- Parameter correlations have 4–5 correlations whose significance is strongly inconsistent/random even when using 1000 drawn models (while compensating for higher power): thus acceptable result??
- behavior distribution not perfect by any means but quite alright except for the VS. Which definitely needs improvement! Maybe possible with more tweaking of the gauss fits.

6 Paper

6.1 Limits of linear rate coding of dynamic stimuli by electroreceptor afferents

Daniel Gussin, Jan Benda, Leonard Maler, 2007, J neurophysiol (Gussin et al., 2007)

P-units may code for the intensity and slope of the stimulus and if the higher neuronal structures can separate these two parts they can detect the very weak signals they use in their behavior.

6.1.1 Introduction

- definition of neural code needs map between external signal and resulting spike trains AND demonstration that downstream neural circuits can interpret this mapping and therefore direct behavioral output.

  original code often assumed to be linear rate coding needs only temporal summation over some time window to decode

  linear code breaks down for dynamic signals and neurons with time-dependent conductances (adapting currents)!

  then more sophisticated methods like spike-triggered stimulus averages (STA) are used to estimate the linear encoding of signals but no obvious decoding mechanisms are implied.

6.2 Simple models of bursting and non-bursting P-type electroreceptors

Maurice J. Chacron, Andre H Longtin , Leonard Maler, 2001
(Chacron et al., 2001b)

- simple math. model of P-units for just the **baseline behavior**.
- uses dynamic threshold, abs refractory period, for bursty cells added a delayed depolarization current
- wasn't "fitted" to data just compared, chosen and fixed(?) parameters

6.3 Negative Interspike Interval Correlations Increase the neuronal capacity for encoding time-dependent stimuli

Maurice J. Chacron, Andre H Longtin , Leonard Maler, 2001
(Chacron et al., 2001a)

- Based on baseline behavior and AM stimuli
- Two different encoding might be used for low-frequency and high-frequency signals.
- low-frequency: rate-code (mean firing frequency) in a counting time that reduces variability of the spike train (minimum in spike train variability caused by negative ISI correlations)
- high-frequency: spike timing

6.4 Electroreceptor neuron dynamics shape information transfer

Maurice J. Chacron, Leonard Maler, Joseph Bastian, 2005
(Chacron et al., 2005b)

- increased low frequency information is contained in the spike trains because of the negative serial correlation. This increased information is still available in central neurons.
- conventional tuning curves don't capture the contained low-freq information and predict bad tuning for low frequencies, information tuning curves show the good coding of low frequencies.
- ISI correlations have a noise shaping effect that increases the low-freq coding potential

6.5 Characterization and modeling of P-type electrosensory afferent responses to amplitude modulations in wave-type electric fish

M.E. Nelson, Z. Xu, J.R. Payne, 1997
(Nelson et al., 1997) (TODO: go over once more how does their model work)

- quantitative model of baseline and response to AM stimuli
- not a LIF model

6.6 Non renewal statistics of electrosensory afferent spike trains: Implications for detection of weak sensory signals

Rama Ratman and Mark E. Nelson, 2000
(Ratnam and Nelson, 2000)

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6.7 Delayed excitatory and inhibitory feedback shape neural information transmission

Maurice J. Chacron, Andre H Longtin , Leonard Maler, 2005
(Chacron et al., 2005a)

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6.8 Encoding of Communication Signals in Heterogeneous Populations of Electroreceptors

Henriette Walz PhD 2013 (Walz, 2013)

1. data generation - recordings

2. model simulations - construction of model
3. Simulation protocols
4. Data analysis - calculation of behavior parameters
    - (a) calculation of baseline parameters
    - (b) calculation of fi curve parameters
    - (c) stimuli step SAM(?) noise(?)
    - (d) goodness of fit
    - (e) sensitivity analysis (influence of par on model)

7 Possible Sources

7.1 Henriette Walz - Thesis

7.1.1 Nervous system - Signal encoding

1. single neurons are the building blocks of the nervous system (Cajal 1899)
2. encoding of information in spike frequency - rate code(first description(?) Adrian 1928) also find examples! (light flash intensity Barlow et al. 1971,)
3. encoding info in inter spike intervals (Singer and Gary 1995)
4. encoding time window (Theunissen and Miller 1995) "This time window is the time scale in which the encoding is assumed to take placewithin the nervous system
5. encoding is noisy (Mainen and Sejnowski 1995, Tolhurst et al 1983, Tomko and Crapper 1974 -¿ review Faisal et al 2008) in part because of stimulus properties but also cell properties (Ion channel stochasticity (van Rossum et al.,2003))
6. noise can be beneficial to encoding -¿ "stochastic resonance" (weak stimuli on thresholding devices like neurons, noise allows coding of sub threshold stimuli) (Benzi et al., 1981)
7. single neurons are anatomically and computationally independent units, the representation and processing of information in vertebrate nervous systems is distributed over groups or networks of cells (for a review, see Pouget et al., 2000)
8. It has been shown that the synchrony among cells carries information on a very fine temporal scale in different modalities, from olfaction (Laurent, 1996) to vision (Dan et al., 1998)
9. In the electrosensory system it was shown before that communication signals change the synchrony of the receptor population (Benda et al., 2005, 2006) and that this is read out by cells in the successive stages of the electrosensory pathway (Marsat and Maler, 2010, 2012; Marsat et al., 2009).

10. An advantage of rate coding in populations is that it is fast. The rate in single neurons has to be averaged over a time window, that is at least as long as the minimum interspike interval. In contrast, the population rate can follow the stimulus instantaneous, as it does not have to be averaged over time but can be averaged over cells (Knight, 1972a).

11. In a population of neurons subject to neuronal noise, stochastic resonance occurs even if the stimulus is strong enough to trigger action potentials itself (supra-threshold stochastic resonance described by Stocks, 2000; see Fig. 1.1 B

12. Cells of the same type and from the same population often vary in their stimulus sen- sitivity (Ringach et al., 2002) as well as in their baseline activity properties (Gussin et al., 2007; Hospedales et al., 2008)

13. Heterogeneity has been shown to improve information coding in both situations, in the presence of noise correlations, for example in the visual system cells (Chelaru and Dragoi, 2008) or when correlations mainly originate from shared input as in the olfactory system (Padmanabhan and Urban, 2010)

14. A prerequisite to a neural code thus is that it can be read out by other neurons (Perkel and Bullock, 1968).

15. Development and evolution shape the functioning of many physiological systems and there is evidence that they also shape the encoding mechanisms of nervous systems. For example, the development of frequency selectivity in the auditory cortex has been shown to be delayed in animals stimulated with white noise only (Chang and Merzenich, 2003). Also, several encoding mechanisms can be related to the selective pressure that the energetic consumption of the nervous system has exerted on its evolution (Laughlin, 2001; Niven and Laughlin, 2008). These finding conformed earlier theoretical predictions that had proposed that coding should be optimized to encode natural stimuli in an energy-efficient way (Barlow, 1972). -¿ importance of using natural stimuli as the coding and nervous system could be optimized for unknown stimuli features not contained in the artificial stimuli like white noise.

7.1.2 electrosensory system - electric fish

1. For decades, studies examining the neurophysiological systems of weakly electric fish have provided insights into how natural behaviors are generated using relatively simple sensorimotor circuits (for recent reviews see: Chacron et al., 2011; Fortune, 2006; Marsat and Maler, 2012). Further, electrocommunication signals are relatively easy to describe, classify and simulate, facilitating quantification and experimental manipulation. Weakly electric fish are therefore an ideal system for examining how communication signals influence sensory scenes, drive sensory system responses, and consequently exert effects on conspecific behavior.

2. The weakly electric fish use active electroreception to navigate and communicate under low light conditions (Zupanc et al., 2001).

3. In active electroreception, animals produce an electric field using and electric organ (and this electric field is therefore called the electric organ discharge, EOD) and infer, from changes of the EOD, information about the location and identification of objects and conspecifics in their vicinity (e.g. Kelly et al., 2008; MacIver et

al., 2001). However, perturbations result not only from objects and other fish, but also from self-motion and other factors. All of these together make up the electrosensory scene. The perturbed version of the fish's own field on its skin is called the electric image (Caputi and Budelli, 2006), which is sensed via specialized receptors distributed over the body surface (Carr et al., 1982).

4. In A. leptorhynchus, the dipole-like electric field (electric organ discharge, EOD) oscillates in a quasi-sinusoidal fashion at frequencies from 700 to 1100 Hz (Zakon et al., 2002) with males emitting at higher frequencies than females (Meyer et al., 1987).

5. The EOD of each individual fish has a specific frequency (the EOD frequency, EODf) that remains stable in time (exhibit- ing a coefficient of variation of the interspikes intervals as low as $2 * 10^{-4}$; Moortgat et al., 1998).

6. During social encounters, wave-type fish often modulate the frequency as well as the amplitude of their field to communicate (Hagedorn and Heiligenberg, 1985).

7. Communication signals in A. leptorhynchus have been classified into two classes: (i) chirps are transient and stereotyped EODf excursions over tens of milliseconds (Zupanc et al., 2006), while (ii) rises are longer duration and more variable modulations of EODf, typically lasting for hundreds of milliseconds to sec- onds (Hagedorn and Heiligenberg, 1985; Tallarovic and Zakon, 2002). (OLD INFO ? RISES NOW OVER MINUTES/HOURS)

7.1.3 P-Units encoding

1. In baseline conditions (stimulus only own EOD), they fire irregularly at a certain baseline rate. Action potentials occur approximately at a certain phase of the EOD cycle, they are phase-locked to the EOD, but only with a certain probability to each cycle. The baseline rate differs from cell to cell (compare the two example cells in Fig. 2.2 A and B, Gussin et al., 2007)

2. Since tuberous receptors are distributed over the whole body and the EOD spans the whole surrounding, all P-units of a given animal are stimulated with a similar stimulus (see Kelly et al. (2008) for an exact model of the EOD). Their noise sources are, however, uncorrelated (Chacron et al., 2005b).

3. In response to a step increase in EOD amplitude, P-units exhibit pronounced spike frequency adaptation (Benda et al., 2005; Chacron et al., 2001b; Nelson et al., 1997; Xu et al., 1996).

7.1.4 Chapter 4 - other models

1. Kashimori et al. (1996) built a conductance-based model of the whole electroreceptor unit and were able to qualitatively reproduce the behaviour of different types of tuberous units.

2. Nelson et al. (1997) constrained a stochastically spiking model by linear filters of the previously determined P-unit frequency tuning.

3. Kreiman et al. (2000) used the same frequency filters to stimulate a noisy perfect integrate-and-fire neuron with which they investi- gated the variability of cell responses to random amplitude modulations (RAMs).

4. To reproduce the probabilistic phase-locked firing and the correlations of the ISIs, Chacron et al. (2000) used a noisy leaky integrate-and-fire model with refractoriness as well as a dynamical threshold.

5. Benda et al. (2005) used a firing rate model with a negative adap- tation current to reproduce the high-pass behaviour of P-units.

References

Benda, J. and Herz, A. V. (2003). A universal model for spike-frequency adaptation. *Neural computation*, 15(11):2523–2564.

Benda, J., Longtin, A., and Maler, L. (2005). Spike-frequency adaptation separates transient communication signals from background oscillations. *Journal of Neuroscience*, 25(9):2312–2321.

Chacron, M. J., Longtin, A., and Maler, L. (2001a). Negative interspike interval correlations increase the neuronal capacity for encoding time-dependent stimuli. *Journal of Neuroscience*, 21(14):5328–5343.

Chacron, M. J., Longtin, A., and Maler, L. (2001b). Simple models of bursting and non-bursting p-type electroreceptors. *Neurocomputing*, 38:129–139.

Chacron, M. J., Longtin, A., and Maler, L. (2005a). Delayed excitatory and inhibitory feedback shape neural information transmission. *Physical Review E*, 72(5):051917.

Chacron, M. J., Maler, L., and Bastian, J. (2005b). Electroreceptor neuron dynamics shape information transmission. *Nature neuroscience*, 8(5):673–678.

Gussin, D., Benda, J., and Maler, L. (2007). Limits of linear rate coding of dynamic stimuli by electroreceptor afferents. *Journal of neurophysiology*, 97(4):2917–2929.

Nelson, M., Xu, Z., and Payne, J. (1997). Characterization and modeling of p-type electrosensory afferent responses to amplitude modulations in a wave-type electric fish. *Journal of Comparative Physiology A*, 181(5):532–544.

Ratnam, R. and Nelson, M. E. (2000). Nonrenewal statistics of electrosensory afferent spike trains: implications for the detection of weak sensory signals. *Journal of Neuroscience*, 20(17):6672–6683.

Walz, H. (2013). *Encoding of Communication Signals in Heterogeneous Populations of-Electroreceptors*. PhD thesis, Eberhard-Karls-Universität Tübingen.

Xu, Z., Payne, J. R., and Nelson, M. E. (1996). Logarithmic time course of sensory adaptation in electrosensory afferent nerve fibers in a weakly electric fish. *Journal of neurophysiology*, 76(3):2020–2032.