Amphibians: Neurons that count & Ultrasonic communication in frogs

Franz Srambical

Overview

- Introduction
- Long-term temporal integration in the anuran auditory system (Rose et al. 1998)
- Auditory midbrain neurons that count (Rose et al. 2002)
- Ultrasonic communication in frogs (Shen et al. 2006)

Introduction

- species of frogs:
  - R. pipiens
  - H. regilla
  - A. tormotus
  - O. livida
  - P. nigromaculata

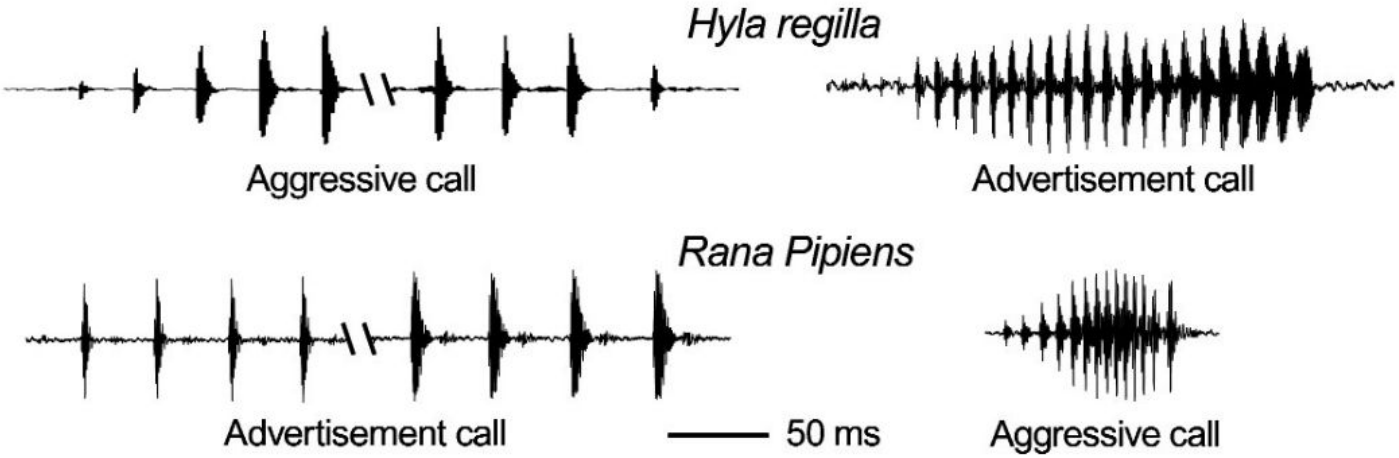
Introduction

- frog call types:
  - advertisement calls
  - aggressive calls

Vocal communication in frogs, Kelley 2004

Introduction

- frog call characteristics:



Auditory midbrain neurons that count, Rose et al 2002

Long-term integration

- biologically relevant information often in temporal structure
- discrimination between calls differing in temporal pulse density
    - they likely use temporal integration

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- recordings in auditory midbrain of R. pipiens & H. regilla
- 109 neurons of 25 male frogs
- 67/109 neurons tuned for AM rate
- 44/67 neurons: response latency < 40ms (excited best by AM rates < 60 Hz)
- 23/67 neurons: response latency 45-150ms (excited best by AM rates > 60Hz)
    - these cells are studies further

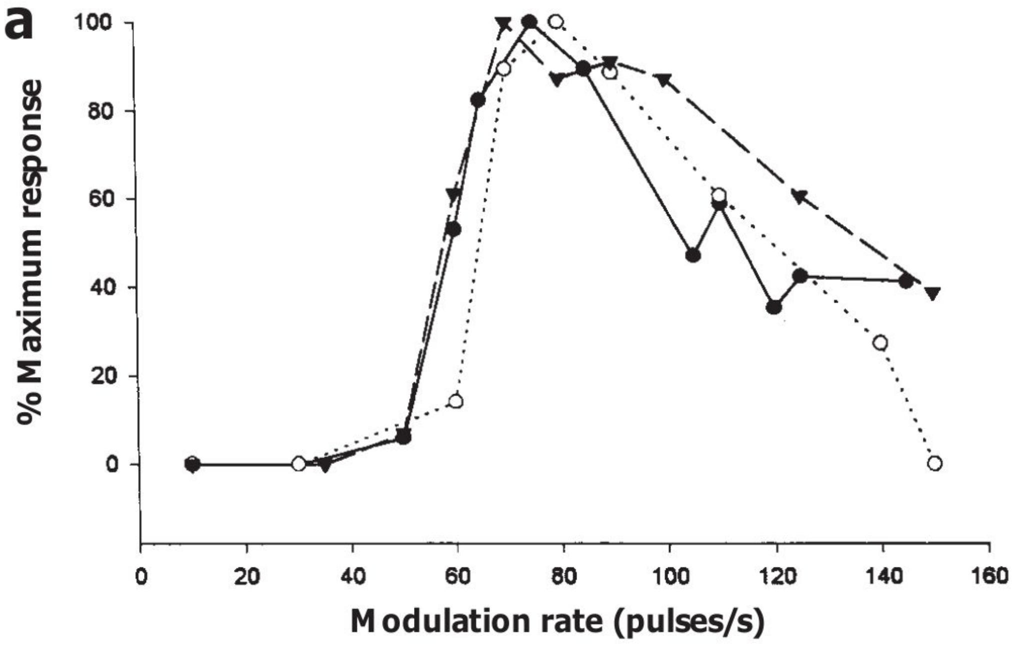
Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- these neurons were clustered in medial torus
- little response to AM rates < 50 Hz
- in H. regilla: respond to advertisement calls (in R. pipiens: aggressive calls)
- selectivity independent of whether AM sinusoidal or ‘natural’

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration



Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- fail to respond to tone bursts or slow rates of AM (with same stimulus energy)
  - => selectivity not from integration of stimulus intensity

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- hypothesis 1: tuning to high AM rate because of sensitivity to duration and rise-time of pulses
  - stimulus pulses (with 10ms duration & natural shape) excite neurons at high rep. rates, but not at low rep. rates
  - => hypothesis can be ruled out
- hypothesis 2: tuning to high AM rate because individual pulses are integrated when in appropriate temporal pattern

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- hypothesis 2:
  - number of pulses per stimulus presentation varied
  - min 8 pulses at 80 pulses/s required to elicit spike
  - => integration with time constant > time required to conduct signals to this area of the brain
  - => evidence of integration process
  - but what is being integrated?

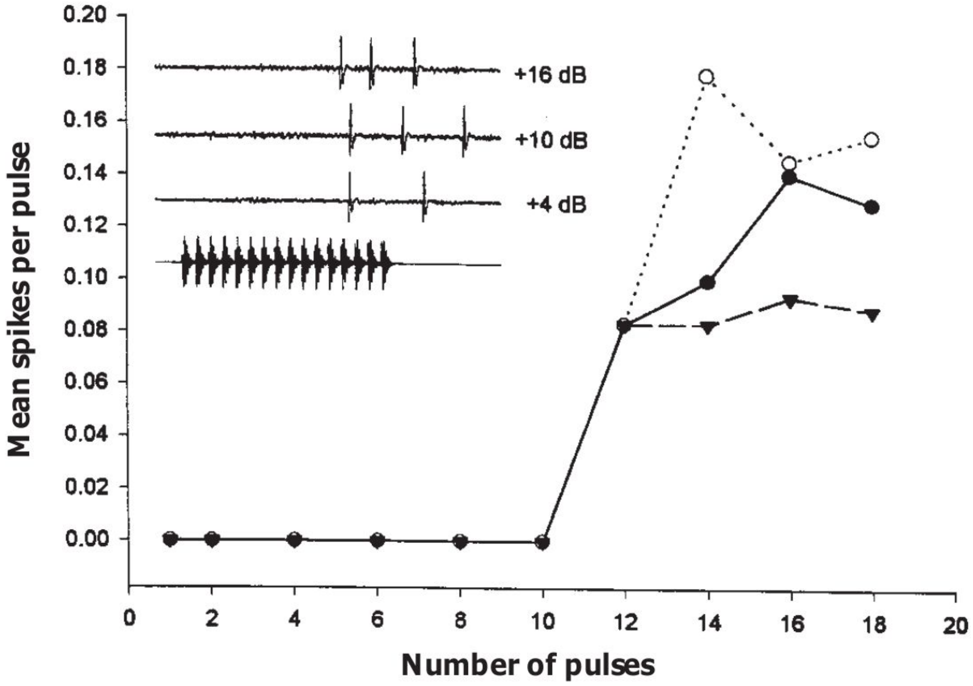
Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- hypothesis 1: stimulus intensity distributed in specific temporal pattern
  - pulse amplitude varied while repetition rate constant
  - fewer pulses should be needed to elicit spike when intensity is increased
  - but: is not the case

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration



Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

- hypothesis 2: information about number and temporal density of pulses
  - findings indicate that cell responded to threshold number of stimulus pulses within a particular time window
  - but: increases in stimulus peak amplitude may not translate into proportionally greater activity levels in afferents to neuron (dynamic range limits)

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Long-term integration

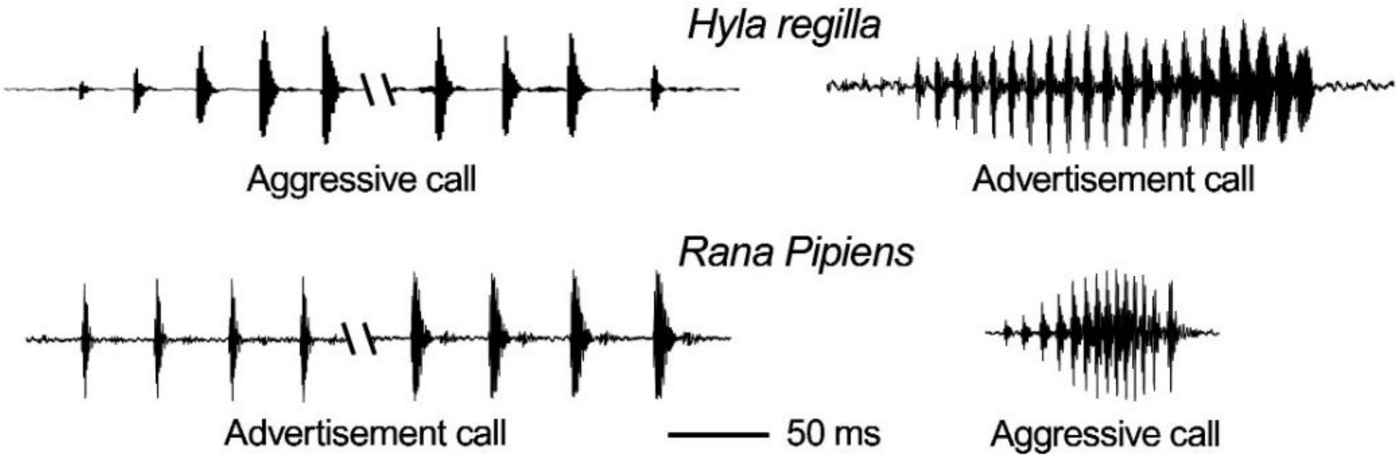
- hypothesis 2: information about number and temporal density of pulses
  - varied duty cycle (pulse duration / interpulse interval)
  - number of pulses required independent of duty cycle
  - selectivity for PRR almost independent of duty cycle
- => these (PI) neurons integrate information about number & temporal density of pulses, not simply stimulus intensity

Long-term temporal integration in the anuran auditory system, Rose et al 1998

Auditory midbrain neurons that count

Auditory midbrain neurons that count

- anuran vocalization



Auditory midbrain neurons that count

- temporal patterning required for call recognition
- pulse-integrating (PI) neurons might be neural substrate
- authors found that PI neurons need:
  - threshold number of pulses to fire
  - respond to any presentation of a stimulus with at least one more than the threshold number of pulses
- question: require a certain number of IPI or a certain average pulse rate?

Auditory midbrain neurons that count, Rose et al 2002

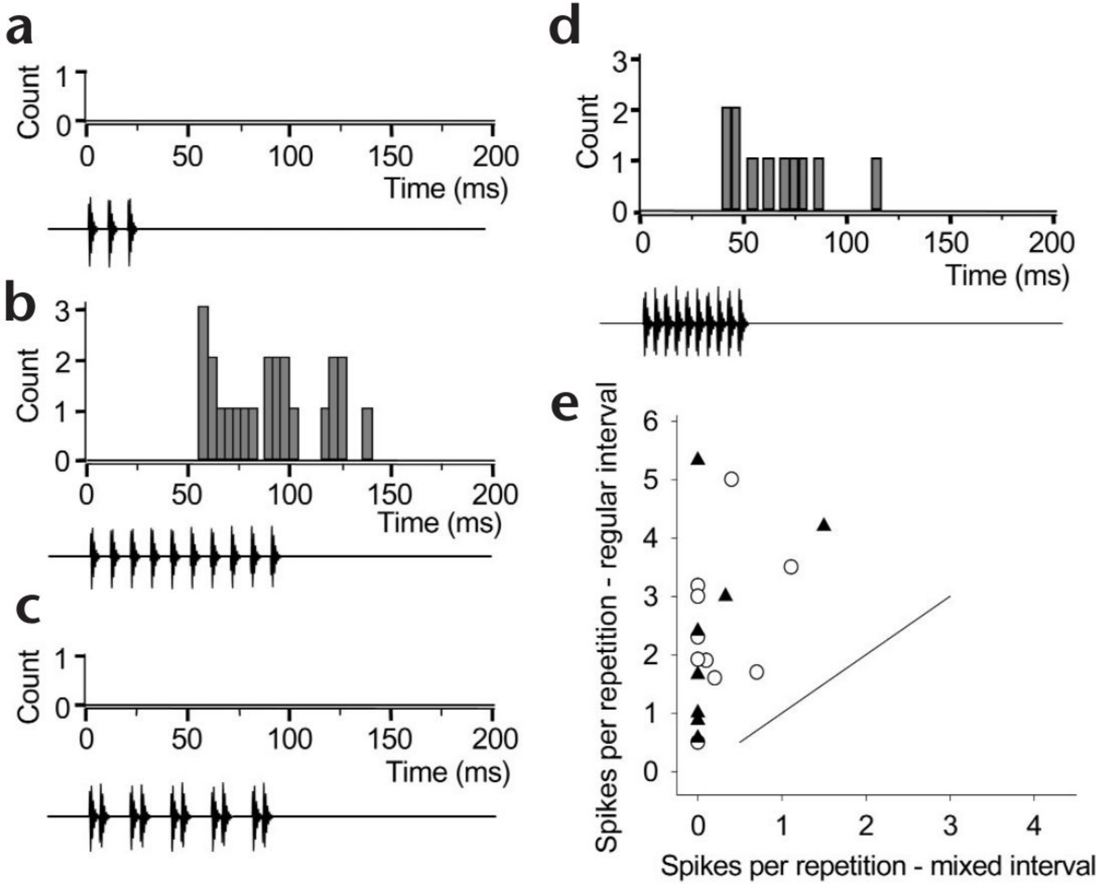
Auditory midbrain neurons that count

- recording from 33 PI neurons
- stimuli with different pulse-interval distributions
- response if > 5 pulses presented at 100 pulses/s
- strong, tonic response if 10 pulses presented at 10ms IPI
- across neurons: responses to constant-interval stimulus ranged from phasic to tonic
- no response to mixed-interval stimulus (10ms - 5ms) with same average pulse rate as constant-time interval stimulus
- repeated IPIs of 5ms effective, but not optimal in exciting neuron

Auditory midbrain neurons that count, Rose et al 2002

Auditory midbrain neurons that count

- ⇒ mixed-interval stimulus was not simply composite of ineffective IPIs



Auditory midbrain neurons that count, Rose et al 2002

Auditory midbrain neurons that count

- experiment: single long interval in series of optimal IPIs
  - neuron required 8 consecutive optimal intervals for response
  - interval >= 30ms already reset integration process
  - after such long interval, 8 additional optimal intervals were needed for response
  - 30ms interval is similar to that seen in encounter calls of species

Auditory midbrain neurons that count, Rose et al 2002

Auditory midbrain neurons that count

- experiment: two neurons with similar reset time but different integration times
  - across cells: no significant relation between integration time and reset time
- question: are these cells…
  - counting the number of consecutive intervals shorter than particular duration?
  - counting those of a specific duration?

Auditory midbrain neurons that count, Rose et al 2002

Auditory midbrain neurons that count

- neurons with ‘narrow’, and neurons with ‘broad’ interval tolerance
- in neurons with ‘narrow’ interval tolerance:
    - difference of ~2ms was enough for reset
- ⇒ neurons were counting number of consecutive IPIs within some tolerance

Auditory midbrain neurons that count, Rose et al 2002

Auditory midbrain neurons that count

- mechanism underlying interval-counting process
  - whole-cell recordings in vivo
  - complex interplay between activity-dependent excitation and inhibition contributes to counting process
  - single pulses primarily elicit inhibition
  - cells become progressively depolarized with additional pulses with optimal interval, and finally spike on threshold

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The numerical abilities of anurans and their neural correlates: insights from neuroethological studies of acoustic communication, Rose 2017

Ultrasonic communication in frogs

Ultrasonic communication in frogs

- ultrasound: frequency > 20 kHz
- among vertebrates: only microbats, bats, cetaceans were known to produce and detect ultrasounds for communication/ echolocation
- here: evidence of ultrasonic communication in amphibians (A. tormotus from Huangshan Hot Springs in China)

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- A. tormotus:
  - males produce bird-like melodic calls (often contain spectral energy in ultrasonic range)
- question: communication via ultrasound to avoid masking by wideband noise of fast-flowing streams, or by-product of sound production mechanism?

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- acoustic playback experiments:
  - in frog's natural habitat
  - recording of vocalization pattern of 8 male frogs under 3 experimental conditions:
    - 1. NS (no sound) period
    - 2. US (ultrasound) period
    - 3. AUD (audible) period
  - in each period: playback of components of prerecorded conspecific vocal signals

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

a Evoked vocal responses

Frog no.	NS	US	AUD
*531 - 1	0	11	10 (2)
*531 - 2	2	6	–
*601 - 2	6	18 (4)	–
*531 - 3	0	0	18
*601 - 5	6	6	14
601 - 4	0	1	1 (1)
602 - 1	3	5 (1)	1
602 - 2	0	0	1

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

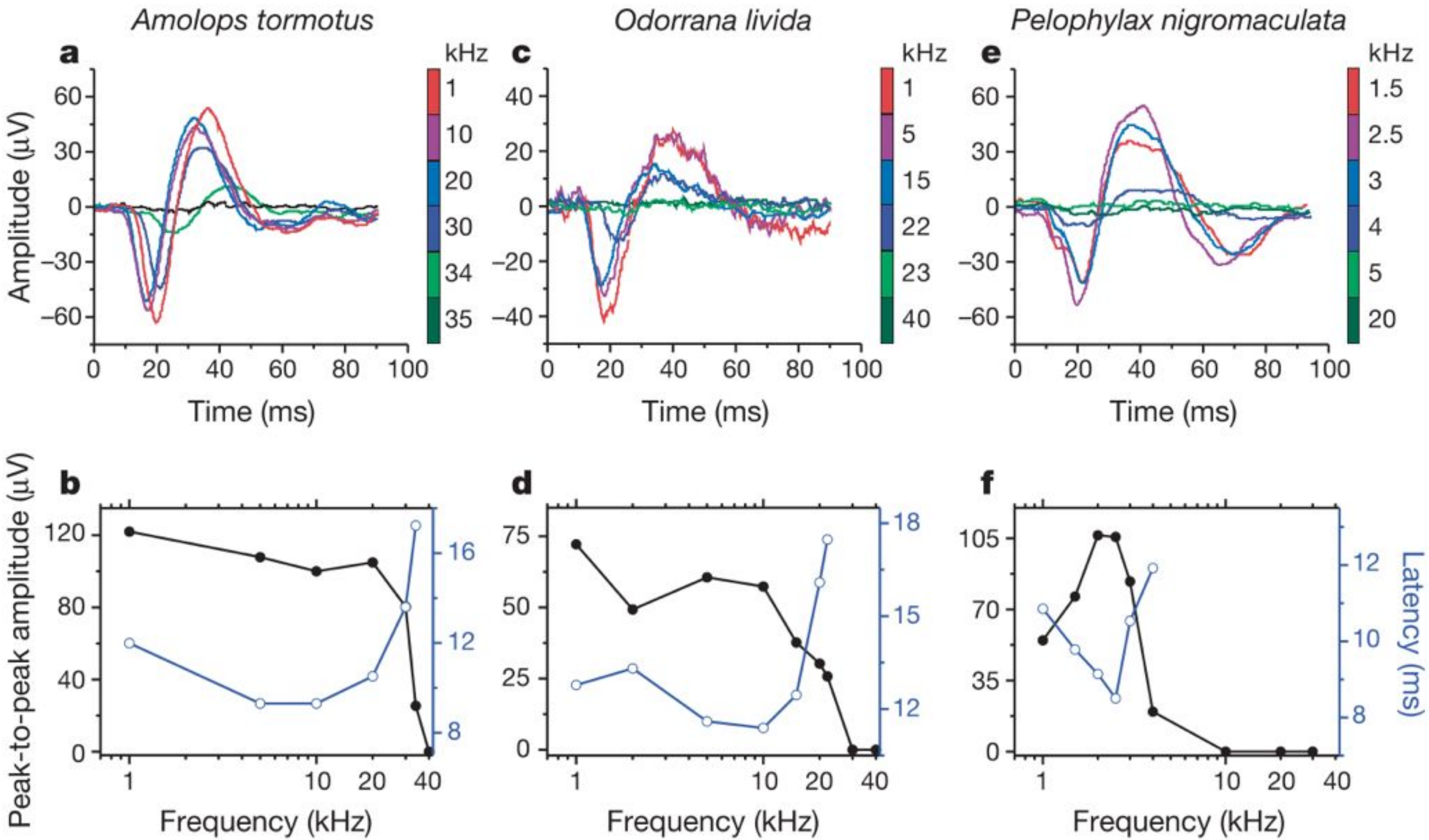
- in 5 frogs: male’s calling rate increased during AUD or US compared to NS period
- in 3 frogs: no overt evoked vocal response to any playback stimulus
- authors state that this shows that males of A. tormotus detect and respond to ultrasound

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- to validate the ultrasonic sensitivity physiologically, authors recorded auditory-evoked potentials (AEPs) from torus semicircularis
    - AEPs consistently observed in response to tone bursts at 89 dB from 1 to 34 kHz
    - no AEP detectable for stimuli > 34 kHz
    - peak-to-peak AEP amplitude inversely correlated with latency

Ultrasonic communication in frogs, Feng et al 2006



Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- experiment: isolated 30 cells from torus semicircularis of 16 frogs & observed tone-burst responses
    - 12/30 cells: respond to tone-bursts over wide frequency range (including > 20 kHz)

- ⇒ demonstrates ultrasonic sensitivity of A. tormotus

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- background noise from Huangshan Hot Springs has broad energy spectrum
- hypothesis: extension of call-frequency as adoption to prevent masking by background noise

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- Do sympatric frog species also show ultrasonic sensitivity?
- recorded AEPs from O. livida
    - could detect ultrasound up to 22 kHz
- recorded AEPs from P. nigromaculata
    - could not detect ultrasound

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- authors conjecture that ultrasound hearing is:
  - limited to species living in noisy environments
  - probably not due to artifacts in acoustic system

Ultrasonic communication in frogs

- experiment: determine whether frog's ear is responsible for ultrasonic sensitivity in A. tormotus:
  - AEP recording of torus semicircularis under:
    - 1. intact condition (both ears unobstructed)
      - AEPs had clear evidence of ultrasonic sensitivity
    - 2. occluded condition (modeling clay covering openings of ear canals)
      - abolished AEPs
- ⇒ ultrasonic sensitivity in A. tormotus mediated by acoustic stimulation of ear

Ultrasonic communication in frogs, Feng et al 2006

Ultrasonic communication in frogs

- Arch et al. state that three ultrasound-detecting species have converged on small-scale functional modifications of the basilar papilla
  - reduced BP chamber volume
  - reduced tectorial membrane mass
  - reduced hair bundle length
  - reduced hair cell soma length

Inner ear morphological correlates of ultrasonic hearing in frogs, Arch et al 2012

Ultrasonic communication in frogs

- Feng et al questioned whether ultrasonic sensitivity is sexually dimorphic
- Later, Shen et al showed that females of A. tormotus do not exhibit ultrasonic sensitivity

Ultrasonic frogs show extraordinary sex differences in auditory frequency sensitivity, Shen et al 2011

Thank you!