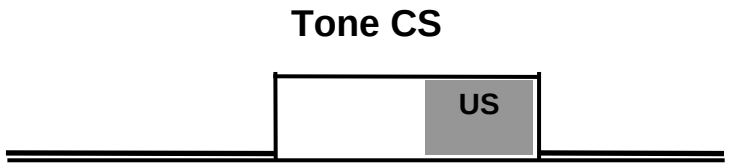
The mathematical model of trace conditioning

KRYUKOV V.I. (HEGUMEN THEOPHAN)
St. Daniel Monastery, Moscow, RUSSIA

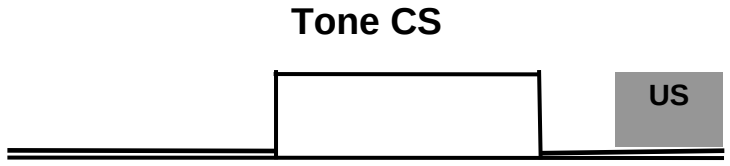
Short abstract: Based on Theta-Regulated-Attention Theory (Vinogradova, 2001) the model of memory and attention “Neurolocator” (Kryukov, 1991, 2008) has been applied to understand and integrate numerous data on trace conditioning by means of non-linear differential equation which describes the neurodynamics and behavior of the cognitive system.

Four basic paradigms of Pavlovian conditioning

A. Delay Conditioning

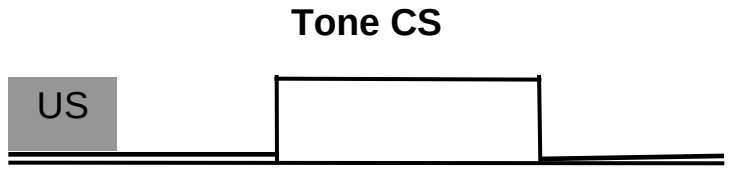


B. Trace Conditioning



C. Context Conditioning

D. Reverse Conditioning



Why trace conditioning is difficult to model ?

- It requires to fill in the seconds/minutes time gap between CS and US by means of neurons and synapses that are operating on a millisecond time scale
- It requires intact hippocampus, mPFC, cerebellum, and functional interaction between them (Kalmbach et al, 2009), by means of theta oscillations (Lesting et al, 2011; Wikgren et al, 2010)

- Trace but not delay conditioning requires attention (Han et al, 2003), that is a top-down control model

Previous trace conditioning models

1. Tapped delay-lines model (Desmond and Moore, 1991).
2. Temporal basis functions model (Ludvig et al, 2008).
3. Inherent ramp dynamics model (Rivest et al, 2009).
4. Phase transition model (Rodriguez and Levy, 2001;Levy et al, 2005a, 2005b)
5. Septo-hippocampal model (Yamazaki and Tanaka, 2005).
6. Pacemaker-accumulator model (Buhusi and Mec, 2005).
7. Attentional-associative model (Schmajuk et al, 1996; Larrauri and Schmajuk, 2008)

Main trace conditioning problems

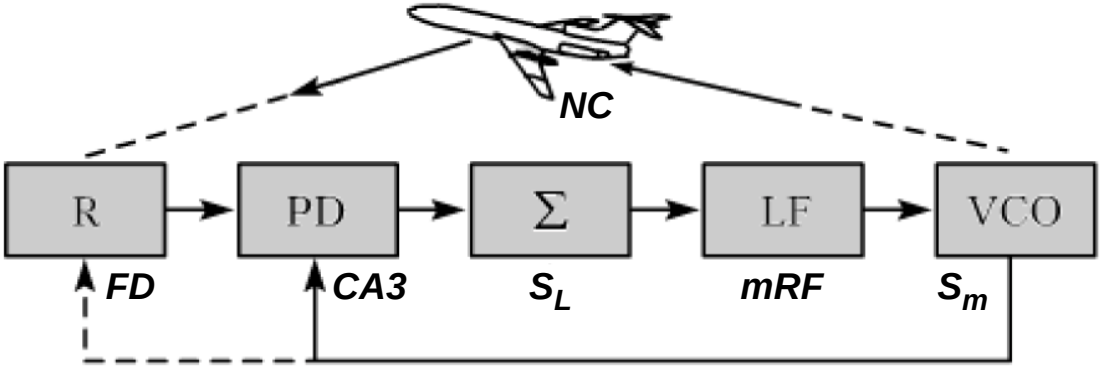
1. How can neurons and synapses operating on a millisecond time scale, encode information about trace intervals of order of seconds and minutes ?
2. What does hippocampus do during trace conditioning? What are specific roles of mPFC, amygdala, and cerebellum?
3. Where is the trace in trace conditioning?
4. The data on trace conditioning is enormous, and it is resembling a heap of sand. Can it be cemented by some sort of unified model?

The basics of Theta-Regulated Attention Theory

(Vinogradova, 2001)

- Hippocampal CA3-field acts as a comparator
- CA1-based limbic circle is used as a delay line
- Medial septum acts as a global pacemaker
- Theta rhythm plays a crucial organizing role in perception, attention and memory

“Neurolocator” model is a radar analogy (Kryukov, 1991)



Neocortex as a plant controlled by a phase-locked loop system and its neuronal counterparts

This model offers a solution to the problems: novelty detection, habituation, consolidation, role of LTP, persistency of LTM (Kryukov, 2008), and the general model of Pavlovian conditioning (Kryukov, 2011a, 2011b, 2012)

Key assumptions for "Neurolocator" model

1. Star-like architecture of cortical and subcortical oscillators
2. Hippocampus as (double) comparator
3. Unique PLL-like attentional system for all brain structures
4. New type of learning in oscillatory system - *Isolability Assumption*
5. Phase transition occurring at both local and global levels

Differential equation of the "Neurolocator" model, its reduction to trace conditioning and basic inequality

$$\frac{d\varphi_i}{dt} = \Lambda_{0i} - \left[\sum_{j=1}^{n} A_{0j} g_j(\varphi_j) + N_j(t)\right] F(p), \quad (i = 1,\ldots, n)$$

reduces to $$\frac{d\varphi}{dt} = \Lambda_0 - \left[A_t g_3(\varphi) F(p) + N(t)\right],$$

where $$A_t = A_{01} + A_{02} + A_{01}A_{02}g_1(t),$$

and $$g_1(t) = \int_0^t CS(t-x)US(x)dx / A_{01}A_{02}$$

whence $$g_{3min} < \frac{\Lambda_0}{A_{01}A_{02}K}\frac{ISI}{\tau_{CS}} < g_{3max}$$

Solution to the problem of long trace interval generation

- Computer simulation of metastable neuronal oscillators with very long periods and a good stability of period (Kirillov et al, 1989)
- Mathematical proof of phase transitions' existence and metastability in model network with integrate-and-fire neurons (Kryukov et al, 1990)
- Computer simulation of basic effects of metastability (Kryukov et al, 1990; Borisyuk and Cooke, 2007)
- Application of the metastable oscillator to trace conditioning (Kryukov, 2012) supported by the factual data (18 refs)

Specific role of different brain structures in trace conditioning

- Medial septum – a central pacemaker of variable theta frequency
- Hippocampus – a double (phase and time) comparator
- Septo-hippocampal system – a PLL controller
- mPFC – a “central executive” (leading oscillator and delay line)
- Amygdala – an emotional modulator (by arousal changes)

Where is the trace in trace conditioning?

- Some researchers consider it is in
  - mPFC (Quinn et al, 2008; Runyan et al, 2004; Pakaprot et al, 2000)
  - hippocampus and PFC (Runyan and Dash, 2005)
  - cerebellum (Woodruff-Pak and Disterhoft, 2008)
  - amygdala (Kwapis et al, 2011)

- “Neurolocator” model predicts
  - STM/LTM but not LTM – in all the above mentioned structures
  - LTM – in sensory and sensorimotor cortex

- This predictions supported by the data from
  - hippocampus (Beylin et al, 2001; McGlinchey et al, 2008; Matus-Amat et al, 2007)
  - mPFC (Simon et al, 2005; Lee and Kesner, 2003)
  - cerebellum (Gewirtz et al, 2008; Brown et al, 2010; Takatsuki et al, 2003)
  - amygdala (Raybuck and Lattal, 2011)
  - sensory cortex (Galvez et al, 2007; Miller et al, 2008, Chavez et al, 2009)

Main effects explained by the "Neurolocator" model:

7 hippocampal lesion effects (11 refs),

e.g. retrieval of memories is possible without hippocampus at short ISI (Chowdhury et al, 2005; Moyeret et al, 1990)

6 attentional effects (15 refs),

e.g. attention is the key trigger for plasticity in A1 (Fritz et al, 2007)

5 timing effects (15 refs),

e.g. Weber's law (Kehoe et al, 2010) and backward conditioning (Quinn et al, 2002)

7 learning effects (23 refs),

e.g. if training takes place during computer defined specific time intervals of theta activity the number of required trials is reduced by factor up to 4 (Griffin et al, 2004; Berry and Hoffman, 2011)

The main “Neurolocator” model predictions:

1. The trace and delay conditioning boundary is a wide region in space of model parameters. This explains some true but seemingly inconsistent data and suggests a unified model of conditioning.
2. The basic brain structures such as hippocampus, mPFC, amygdala, cerebellum, and sensory cortices each have new specific roles but they all are functionally integrated by means of theta/gamma synchronization.
3. The unified model of Pavlovian conditioning allows to replace multiple local memory systems theory by that of a single large-scale system which is orchestrated by septo-hippocampal hub.

Conclusions

- The “Neurolocator” model proposes solutions for four trace conditioning problems
- It provides self-consistent explanation for most trace conditioning effects, including some seemingly contradictory ones
- It predicts the existence of a unique brain-global oscillatory control system that can serve as a unified model of memory, attention and Pavlovian conditioning