# A PHYSIOLOGICAL MECHANISM FOR PHASE DECODING: INFORMATION EXCHANGE BETWEEN RHYTHMICALLY COUPLED NETWORKS.

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Background

Introduction

Analysis of hippocampal place cell firing in rats has revealed the existence of a phase code: the phase of firing of place cells with respect to the ongoing theta rhythm carries information about the rat's position. Brain regions downstream of the hippocampus must have a neural mechanism which can decode the phase information. In order to explore neural mechanisms for phase decoding, we have implemented two networks of spiking neurons: an 'encoder' (the hippocampus) and a 'decoder' (a region which the hippocampus projects to, e.g. enthorinal or cingulate cortex). Even though the aim of the model is to account for networks in the hippocampal region, the principles of information exchange might apply in general to brain networks which shows temporary phase-locking.

Phase coding: theta phase precession

The firing of hippocampal place cells show a systematic phase precession: as a rat enters a place field, firing occur late in the theta phase. As the rat passes through the place field the phase of firing advances systematically.
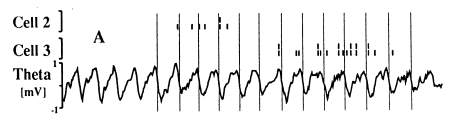
Example illustrating the phase precession of two place cells. The markers indicate single spikes. The lower trace is the field of the theta rhythm. The vertical lines indicates the onset of each theta period. Adapted from O'Keefe and Recce (1993):

The phase precession suggests that the phase of firing with respect to the theta rhythm provides spatial information in addition to firing rate: a phase code.

In evidence for a phase code, Jensen and Lisman (submitted) have recently shown that the reconstruction of a rats position from place cell firing is improved by taking the theta phase of firing into account.

Several biophysical models which can explain the phase precession (phase encoding) have been proposed. So far no models have been proposed for how to read the phase code. The aim of this work is to construct a physiological realistic phase decoder, and discuss its implications for information exchange between rhythmically coupled networks.

The Network

Sequence generator/phase encoder

The phase precession can be explained by a mechanism in which representations of future locations (0 - 1 sec ahead) are read-out as sequences. (e.g. Jensen and Lisman 1996; Tsodyks et al. 1996 Skaggs et al. 1996). Hence the hippocampus has representations for the current location, but it also **predicts** upcoming locations. Previously we have constructed a biophysical model of the CA3 which can produce such sequences (Jensen and Lisman 1996). The sequence read-out is timed by externally imposed theta oscillations (medial septum) and internally generated gamma oscillations which are produced by an inhibitory feedback. It is the asymmetric synaptic feedback connections (recurrent collaterals) of the CA3 which produces the sequence read-out in each theta cycle, In each theta cycle a sequence of about 5-7 representations of locations is produced.
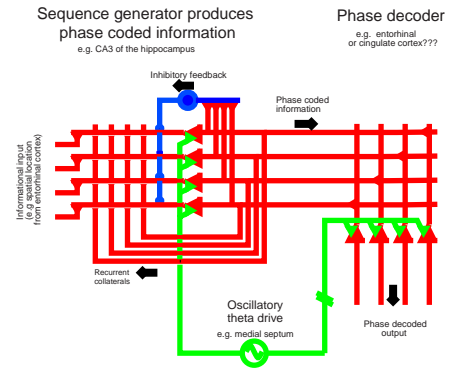
Phase decoder

The phase decoder (right) receives the output of the sequence generator and the oscillatory theta drive. **Neurons in the phase decoder will fire if they are sufficiently depolarized by the theta drive and a subset of the neurons in the sequence generator.**

The networks have been implemented by spiking integrate-and-fire neurons and simulated on a computer. We have constructed the simplest possible model. The networks can easily be extended with more neurons without loss of the main properties.

Simulation Results

A) Maze:

B) Sequence generator/encoder

C) Phase Decoder
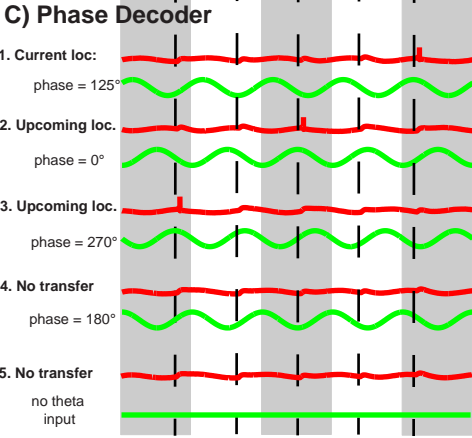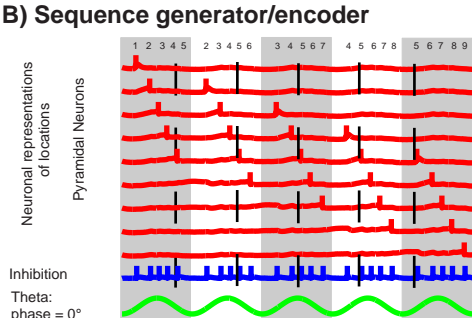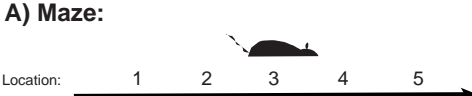
Simulation results:

A) A rat is running on a linear maze and passes location 1 to 5. We assume that the path of locations has been stored as a sequence in the synapses of CA3.

B) When the rat is at location 1 a sequence of future locations (2 to 5) is produced by the network. In the next theta cycle the rat has moved to location 2 and sequence 3 to 5 is produced, etc. The firing of e.g. the cell representing location 5 advances in every theta cycle: phase precession. This is reproduced from Jensen and Lisman (1996).

C) The phase decoder receives input mainly from the cell representing location 5 and the theta input with an adjustable phase delay.
Phase delay 125°: information about current location is retrieved, i.e. location 5.
Phase delay 0°: upcoming location 5 is predicted at location 3, i.e. two theta cycles ahead (0.3 sec).
Phase delay 270°: upcoming location 5 is predicted at location 1, i.e. four theta cycles ahead (0.6 sec).
Anti-phase: No information is transferred. Also no information is transferred when the decoder does not receive an oscillatory input.

In summary: When firing from early theta phases of the encoder is transferred, information about current position is extracted. When firing from late theta phases is transferred information about upcoming locations is obtained. Information transfer is blocked when the decoder receives no oscillatory input, or an oscillatory input in anti-phase with the encoder.

Implications

We have constructed a simple neuronal decoder which can extract phase coded information. **It is essential that the decoder receives an oscillatory input which is coherent with the oscillatory signal in the encoder** (sequence generator). By changing the phase of the oscillatory input to the decoder, different information is transferred: for instance upcoming locations or current location. When the decoder receives no oscillatory input, no information is transferred. In the rat, enthorinal, periform and cingulate cortices show (occasional) coherent theta oscillations with the hippocampus. It is therefore possible that one or more of these regions function as a decoder for hippocampal phase coded information. An important prediction is that the firing of the neurons in the decoder is coupled to the theta rhythm, but will not show phase precession.

These principles might extend beyond the hippocampus. We propose, that if two regions oscillate coherently, it signifies transfer of phase coded information. The coherency does not necessarily have to be persistent. Intermittent coherent oscillations have been observed in a number of systems and frequency bands. A few examples are 7-12 Hz coherency between rat whiskers and somato sensory cortex (Nicolelis et al. 1995) and 20 Hz coherence between muscles and motor cortex (Hari and Salenius 1999).