Theoretical Foundations of Potential Traveling Wave Effects

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Contents

1 Summation of phase delayed activities lead to a lower population-wide frequency

It is almost confirmed (Harvey Nature 2009) that LFP frequency is slightly lower that intracellular filtered Vm frequency, thus giving rise to the phenomenon of phase precession. Geisler PNAS 2010, though with caveats, showed that the summation of phase-delayed place cell activities lead to an LFP with slightly lower frequency. Having a spontaneously generated LFP with lower frequency than intracellular oscillation, phase precession could be achieved without a reference oscillator. A reference oscillator would refer to most model papers where phase is calculated relative to a fixed LFP frequency (like 8Hz) .

1.1 Literature review - Geisler PNAS 2010

1.1.1 Model Setup

This is a rate based model without connections. The firing rate of place cell N is denoted as $R_n(t)$.

$$R_n(t) = [1 + e^{i2\pi f_0(t-\tau_n)}]\frac{1}{\sqrt{\pi}\sigma}e^{-(t-T_n)^2/\sigma^2} \tag{1}$$

Summation:
Roughly speaking, summation of place cell activities lead to LFP, denoted as $R(t)$. Each cell contributed equally to LFP. Cell density is denoted as $\frac{1}{\delta} = \frac{1}{\Delta T} = \frac{c}{\Delta\tau}$ where ΔT refers to difference between adjacent place fields divided by a constant velocity, $\Delta\tau$ refers to difference between phase delays.

$$R(t) = \frac{1}{\sqrt{\pi}\sigma}\frac{\Delta\tau}{c}\sum_n(1 + e^{i2\pi f_0(t-\tau_n)})e^{-(t-T_n)^2/\sigma^2} \tag{2}$$

When $\Delta\tau \to 0$ (i.e. $n \to \infty$), the summation becomes an integral. Moreover, the discrete variables become continuous: $\tau_n \to \tau$ and $T_n \to \frac{\tau}{c}$:

$$R(t) = \frac{1}{\sqrt{\pi}\sigma}\frac{1}{c}\int_{-\infty}^{\infty} d\tau(1 + e^{i2\pi f_0(t-\tau)})e^{-(t-\frac{\tau}{c})^2/\sigma^2} \tag{3}$$

If we check the common integrals in quantum integral theory (`https://en.wikipedia.org/wiki/Common_integrals_in_quantum_field_theory`), it is easy to compute the above integration with the knowledge that $\int_{-\infty}^{\infty} e^{-\frac{1}{2}ax^2} = \sqrt{\frac{2\pi}{a}}$ and $\int_{-\infty}^{\infty} e^{-\frac{1}{2}ax^2+iJx} = \sqrt{\frac{2\pi}{a}}e^{-\frac{J^2}{2a}}$. After integration, $R(t)$ could be expressed as follows:

$$R(t) = 1 + e^{i2\pi f_0(1-c)t}e^{-(\pi f_0 c\sigma)^2} \tag{4}$$

Therefore, the population activity is oscillating at a frequency of $f_0(1-c)$ (lower than f_0) and amplitude of $\mid e^{-(\pi f_0 c\sigma)^2} \mid$.

1.1.2 Caveats of the model

This model directly described the firing rate of place cell as a bell-shaped curve modulated by theta oscillation. Summation of cells whose activities oscillate at different phases lead to a population activity with slightly lower frequency (i.e. LFP). This model did mention phase delays. But if we observe more carefully, the phase delay exists in the firing rate of individual place cell **instead of LFP measurements across the dorsal-ventral axis**. Equation 4 doesn't include a phase delay term of the LFP activity. Subsequent investigations could be made to refine the phase delay.
Revised at 03/08/19: According to Figure 4 of Patel Neuron 2012, phase delay exists both in the firing rate of individual place cells and local LFP measurements along dorsal-ventral axis.

2 Modulate the learning of replay

Theodoni Elife 2018 set up a rate-based recurrent network of place cells with STDP learning rule and a slow-decaying depression variable. They rigorously proved that the frequency of LFP influence the speed to reach replay. Therefore, it is also possible that the phase of LFP would also influence the replay learning speed.
Tracing back into literature, **Romani Hippocampus 2016** first introduced the slow-decaying depression variable to produce replay.
Moreover, **Drieu Science 2018** showed that interrupting theta precession would eliminate replay during the subsequent sleep. I believe phase offset would also influence the time to reach theta precession emergence since weights must evolve enough to become asymmetric.

2.1 Literature review - Theodoni Elife 2018

Rate-based recurrent neural network with STDP learning rule and slow-decaying depression variable.

2.1.1 Model Setup

Recurrently connected rate model with STDP learning rule.

$$\tau \dot{r_i} = -r_i + \Phi(\frac{1}{N}\sum_{j=1}^{N} \tilde{w_{ij}} r_j x_j + I_i(t)) \tag{5}$$

The external current input $I_i(t)$ is place-specific (θ_i) and modulated by theta oscillation.

$$I_i(t) = I_0 + I_{PF} cos(\theta_i - vt)(1 + I_{theta} cos(2\pi f t)) \tag{6}$$

The slow decaying depression variable $x_i(t)$ is key to replay activity (Romani Hippocampus 2015).

$$\dot{x_i} = \frac{1 - x_i}{\tau_x} - U_0 x_i r_i \tag{7}$$

Weight modification follows conventional STDP rule with constant weight inhibition $\tilde{w_{ij}} = w_{ij} - w_I$.

$$\dot{w_{ij}} = \int_{-\infty}^{\infty} dT K(T) r_i(t) r_j(t+T) \tag{8}$$

where $K(T)$ is the conventional plasticity window follows (Song Nature Neuroscience 2002).

2.1.2 Mathematical analysis

The key to solving the above dynamic system is to calculate the integration in Equation 8. To achieve this, authors made two important assumptions as observed in the simulation results:

- **Scale separation:** weight changes much slowly than firing rate dynamics.
  This assumption simplifies $\dot{w}(\theta, \theta')$ into $\langle \dot{w}(\theta, \theta') \rangle_t$. In this way, some t related functions could be ignored.
  For example, when $r(\theta, t) = t_0 + rPFcos(\theta - vt)$:

$$\begin{aligned} \langle r(\theta,t) r(\theta', t+T) \rangle_t &= (r_0 + rPFcos(\theta - vt))(r_0 + r_{PF} cos(\theta' - vt - vT)) \\ &= r_0^2 + \langle r_0 r_{PF} (cos(\theta - vt) + cos(\theta' - vt - vT)) \rangle_t \\ &+ r_{PF}^2 \langle cos(\theta - vt) cos(\theta' - vt - vT) \rangle_t \end{aligned} \tag{9}$$

  Perform summation of t in a period (i.e. $T = \frac{2\pi}{v}$):

$$\begin{aligned} \langle cos(\theta - vt) + cos(\theta' - vt - vT) \rangle_t &= 0 \\ \langle cos(\theta - vt) cos(\theta' - vt - vT) \rangle_t &= \frac{1}{2} \langle cos(\theta + \theta' - 2vt - vT) + cos(\theta - \theta' + vT) \rangle_t \\ &= \frac{1}{2} \langle cos(\theta - \theta' + vT) \rangle_t \end{aligned} \tag{10}$$

  Therefore, $\langle \dot{w}(\theta, \theta') \rangle_t$ could be expressed as below:

$$\langle \dot{w}(\theta, \theta') \rangle_t = \int_{-\infty}^{\infty} dT K(T) (r_0^2 + \frac{r_{PF}^2}{2} (cos(\theta - \theta') cos(vT) - sin(\theta - \theta') sin(vT))) \tag{11}$$

- **Mode isolation:**
  There are clearly two modes (a cos mode and a sine mode) in Equation 11. Therefore, we could rewrite the equation as:

$$\begin{aligned} \langle \dot{w}(\theta, \theta') \rangle_t &= \langle \dot{w}(\theta - \theta') \rangle_t \\ &= \langle \dot{w_{even}}(\theta - \theta') \rangle_t cos(\theta - \theta') + \langle \dot{w_{odd}}(\theta - \theta') \rangle_t sin(\theta - \theta') \end{aligned} \tag{12}$$

Note that under these two assumptions, weight change depends only on place field difference ($\langle \dot{w}(\theta - \theta') \rangle_t$). Therefore, in the paper, the authors plotted weights against $\Delta\theta$.
Importantly, the learning time to replay emergence depends on the w_{even}. **In contrast, in the ring attractor paper by Kechen Zhang, the bump movement (sequential firing) depends on the odd mode of weights.**

- **Effect of theta modulation:** With theta modulation, the firing rate could be expressed as:

$$\begin{aligned} r(t) &= r_0 + r_{PF}cos(\theta - vt)(1 + r_{theta}cos(2\pi ft)) \\ &= r_0 + r_{PF}cos(\theta - vt) + \frac{r_{PF}r_{theta}}{2}(cos(\theta - v_+t) + cos(\theta - v_-t)) \end{aligned} \tag{13}$$

where $v_+ = v + 2\pi f$ and $v_- = v - 2\pi f$. Since $v << 2\pi f$, then $v_+ \approx 2\pi f$ and $v_- \approx -2\pi f$. Since we are averaging over time, all cos terms with t inside could be eliminated. Then the cross correlation between neurons are:

$$\begin{aligned} \langle r(\theta, t)r(\theta', t+T) \rangle_t &= r_0^2 + \frac{r_{PF}^2}{2}cos(\theta - \theta' + vT) \\ &+ \frac{r_{PF}^2 r_{theta}^2}{8}(cos(\theta - \theta' + v_+T) + cos(\theta - \theta' + v_-T)) \\ &= cos(\theta - \theta')(\frac{r_{PF}^2}{2}cos(vT) + \frac{r_{PF}^2 r_{theta}^2}{4}cos(2\pi fT)) \\ &+ sin(\theta - \theta')(\frac{r_{PF}^2}{2}sin(vT)) \end{aligned} \tag{14}$$

2.1.3 Caveats of the model

- Replay occurred before the emergence of theta precession (maybe not true, get the phase-position plot)
- Very arbitrary inhibition part
- Experimental evidence cannot support model prediction

2.1.4 Generalization of the model

- **Firing rate with phase delay** (x)
The external current in this case is

$$I_i(t) = I_0 + I_{PF}cos(\theta_i - vt)(1 + I_{theta}cos(2\pi ft + \pi x_i)) \tag{15}$$

$$\begin{aligned} r(\theta, x, t) &= r_0 + r_{PF}cos(\theta - vt)(1 + r_{theta}cos(2\pi ft - x)) \\ &= r_0 + r_{PF}cos(\theta - vt) + \frac{r_{PF}r_{theta}}{2}(cos(\theta_+ - v_+t) + cos(\theta_- - v_-t)) \end{aligned} \tag{16}$$

where $\theta_+ = \theta + x$, $\theta_- = \theta - x$, $v_+ = v + 2\pi f$ and $v_- = v - 2\pi f$. Then the cross correlation between two neurons are:

$$\begin{aligned} \langle r(\theta, x, t)r(\theta', x', t+T) \rangle_t &= r_0^2 + \frac{r_{PF}^2}{2}cos(\theta - \theta' + vT) \\ &+ \frac{r_{PF}^2 r_{theta}^2}{8}(cos(\theta_+ - \theta'_+ + v_-T) + cos(\theta_- - \theta'_- + v_+T)) \end{aligned} \tag{17}$$

The weight growth rate could be attributed to six mode: $cos(\theta - \theta'), sin(\theta - \theta'), cos(\theta - \theta' + x - x'), sin(\theta - \theta' + x - x'), cos(\theta - \theta' - x + x'), sin(\theta - \theta' - x + x')$. The tricky part is how to tease these affects apart. Or do I need to separate these modes?

- **Firing rate with phase delay and conductance delay**

2.2 Literature Review: Romani Hippocampus 2015

Rate-based recurrent neural network with fixed weights and slow-decaying depression variable.

2.2.1 Model Setup

The firing rate dynamics of neuron i could be expressed as follows:

$$\tau \dot{r_i} = -r_i + \Phi(\frac{1}{N}\sum_{j=1}^{N} W_{ij} r_j x_j + I_i(t)) \tag{18}$$

The external current input $I_i(t)$ is place-specific (θ_i) and modulated by theta oscillation. Note that the expression of external current is slightly different from that in **Theodoni Elife 2018**.

$$I_i(t) = I_0 + I_\Theta cos(2\pi f_\Theta t) + I_L cos(\theta_i - \theta_L(t)) \tag{19}$$

The slow-decaying depression variable $x_i(t)$ evolves as follows:

$$\dot{x_i}(t) = \frac{1 - x_i(t)}{\tau_R} - U x_i(t) m_i(t) \tag{20}$$

The connection weights are fixed as follows:

$$W_{ij} = J_1 cos(\theta_i - \theta_j) - J_0 \tag{21}$$

where $\theta_i \in [0, 2\pi]$; so $\theta_j - \theta_i \in [-2\pi, 2\pi]$. Under this definition of connections, the weight range spans two period of the cosine function.

2.2.2 Characteristics of the model

- **Spontaneous bursting activity**
  When $I_i(t) = I_0$, the above model setup and fixed connections could lead to spontaneous bursting activity. This kind of periodic bursting could be interpreted as an oscillatory instability of the dynamic system determined by Equation 18 and Equation 20. It shouldn't be too hard to solve the parameter space of the oscillatory dynamics of $m_i(t)$ and $x_i(t)$. In other words, the solution to nullclines is a pair of complex number with negative real part. **(Try to do it after ECE272A)**. Generally speaking, M and X act as two nodes with reciprocal inhibition. The inhibition from X to M is slow. In this way, the oscillation behavior emerges.

- **Phase Precession**
  The paper concluded that, under above settings, phase precession could emerge in recurrent network without asymmetric connections (Tsodyks Hippocampus 1996).

3 A STDP learning model with traveling wave and delayed conductance

3.1 Recurrent neural network with uniform inhibition

3.1.1 Model Setup

W_{ij}: connection weight from neuron j to neuron i; W_I: uniform inhibition weight; $\theta_i \in (0,1)$: the preferred firing location of neuron i; $x_i \in (0,1)$: the anatomical location of neuron i from dorsal to ventral in hippocampus (dorsal end: $x_i = 0$; ventral end: $x_i = 1$). θ_i and x_i are randomly assigned to neurons and independent of each other. f_0 : frequency of theta oscillation; N: neuron number; r_i: firing rate of neuron i; In the simulation, these equations are integrated using Euler's method and $dt = 1ms$.

$$
\begin{aligned}
I_i &= I_0 + [I_2 cos(2\pi(\theta_i - vt))]_+ (1 + I_1 cos(2\pi f_0 t + \pi x_i)) \\
\tau_m \dot{r_i} &= -r_i + \phi(\frac{1}{N}\sum_{j=1}^{n}(W_{ij} - w_I) r_j(t - \tau_{ij}) + I_i), \\
\phi(x) &= \alpha \log(1 + \exp(\frac{x}{\alpha})) \approx [|x|]_+, \quad \tau_{ij} = \frac{|\Delta x_{ij}|}{\tau} \\
\dot{W_{ij}} &= \int_{-\infty}^{\infty} dT K(T) r_i(t - \tau_{ij}) r_j(t+T)
\end{aligned}
\tag{22}
$$

For the model without conductance delay, $\tau_{ij} = 0$ for any i and j.

3.1.2 Weight dynamics with wave-mediated synaptic input:

The most important assumption is time scale separation between weight dynamics and firing rate dynamics

The firing rate of neuron (θ, x)could be approximated by the following equation. To simplify calculation, let consider a circular track where the preferred firing location of place cell is represented by $\theta \in (0,1)$. v is the moving velocity of a mouse and f is the theta oscillation frequency in hippocampus. The place cell's anatomical location from dorsal to ventral is represented by $x \in (0,1)$.

$$
\begin{aligned}
r(\theta, x, t) &= r_0 + r_{PF} cos(2\pi(\theta - vt))(1 + r_\theta cos(2\pi f t + \pi x)) \\
&= r_0 + r_{PF} cos(2\pi(\theta - vt)) + \frac{r_{PF} r_\theta}{2}(cos(\theta_+ - v_- t) + cos(\theta_- - v_+ t)) \\
&= r_0 + r_1 cos(2\pi(\theta - vt)) + r_2(cos(\theta_+ - v_- t) + cos(\theta_- - v_+ t)) \\
\theta_+ &= 2\pi\theta + \pi x, \theta_- = 2\pi\theta - \pi x; v_- = 2\pi v - 2\pi f, v_+ = 2\pi v + 2\pi f
\end{aligned}
\tag{23}
$$

According to conventional STDP rule, the weights are updated through the following equation. $W_{\theta,\theta'}$: connection from neuron (θ, x) to neuron (θ', x').

$$
\dot{W_{\theta,\theta'}} = \int dT K(T) r(\theta, x, t) r(\theta', x', t+T)\rangle_t \tag{24}
$$

By the assumption of scale separation, we could average the cross correlation over t and then perform the integral:

$$
\begin{aligned}
\langle r(\theta, x, t) r(\theta', x', t+T)\rangle_t = r_0^2 &+ \cos(2\pi v T)(\frac{r_1^2}{2}\cos(2\pi\Delta\theta)) + \sin(2\pi v T)(-\frac{r_1^2}{2}\sin(2\pi\Delta\theta)) \\
&+ \cos(2\pi f T)(r_2^2 \cos(2\pi\Delta\theta)\cos(\pi\Delta x)) + \sin(2\pi f T)(r_2^2\cos(2\pi\Delta\theta)\sin(\pi\Delta x))
\end{aligned}
\tag{25}
$$

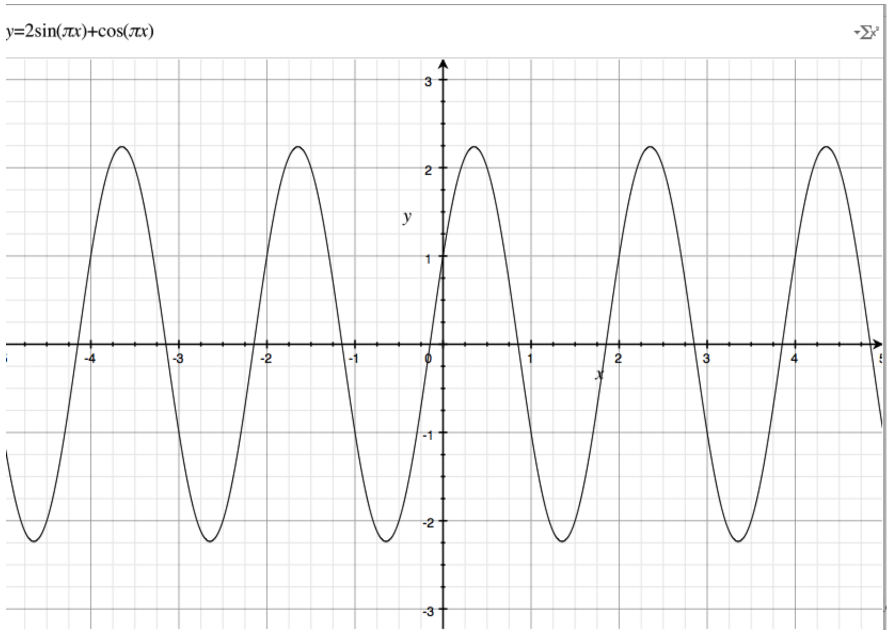

Figure 1: Curve of dW relative to Δx

If we integrate the terms related to T in Equation 25 with the STDP time window $K(T)$. We got the following coefficients: The numbers are calculated with $A_+ = 0.1; A_- = 0.1/3, \tau_+ = 0.02, \tau_- = 0.06, v = 0.1, f = 8$.

$$\begin{aligned}
&\int dTK(T)\cos(2\pi vT) \approx A_+\tau_+ - A_-\tau_- = 0(\frac{2\pi}{2\pi v} = 10second) \\
&\int dTK(T)\sin(2\pi vT) = \frac{A_+\tau_+^2(2\pi v)}{1+(2\pi v)^2\tau_+^2} + \frac{A_-\tau_-^2(2\pi v)}{1+(2\pi v)^2\tau_-^2} = 0.0001 = \alpha \\
&\int dTK(T)\cos(2\pi fT) = \frac{A_+\tau_+}{1+(2\pi f)^2\tau_+^2} - \frac{A_-\tau_-}{1+(2\pi f)^2\tau_-^2} = 0.0008 = \beta(\frac{2\pi}{2\pi f} = 0.125second) \\
&\int dTK(T)\sin(2\pi fT) = \frac{A_+\tau_+^2(2\pi f)}{1+(2\pi f)^2\tau_+^2} + \frac{A_-\tau_-^2(2\pi f)}{1+(2\pi f)^2\tau_-^2} = 0.0016 = \gamma
\end{aligned} \tag{26}$$

Therefore, the weight change could be further simplified into:

$$\begin{aligned}
dW_{(\theta,x)\to(\theta',x')} &= \alpha(-\frac{r_1^2}{2}\sin(2\pi\Delta\theta)) + \gamma(r_2^2\cos(2\pi\Delta\theta)\sin(\pi\Delta x)) + \beta(r_2^2\cos(2\pi\Delta\theta)\cos(\pi\Delta x)) \\
&\approx \gamma(r_2^2\cos(2\pi\Delta\theta)\sin(\pi\Delta x)) + \beta(r_2^2\cos(2\pi\Delta\theta)\cos(\pi\Delta x))
\end{aligned} \tag{27}$$

The relationship between dW and Δx is shown Figure 3.1.2. ($\frac{1}{\tau} = 0.03$). This equation also agrees with simulation results of the weight dynamics.

3.1.3 Weight dynamics of wave-mediated synaptic input and conductance delay

$W_{\theta,\theta'}$: connection from neuron (θ, x) to neuron (θ', x'). The learning rule is conventional STDP and the neuron's firing rate could be represented by this:

$$\dot{W_{\theta,\theta'}} = \int dTK(T)\langle r(\theta,x,t-\tau')r(\theta',x',t+T)\rangle_t, \quad \tau' = \frac{|\Delta x|}{\tau} \tag{28}$$

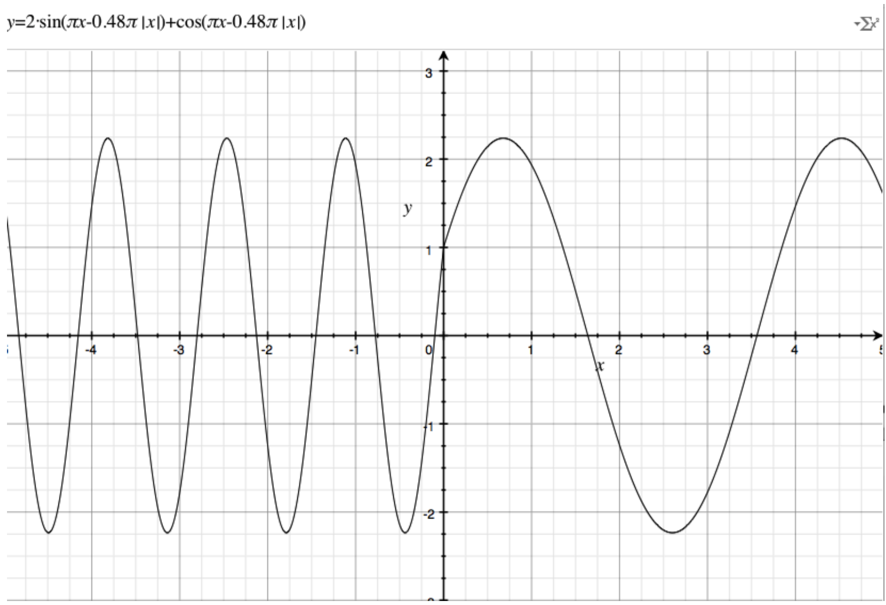

Figure 2: Curve of dW relative to Δx

We could then average the cross correlation from neuron (θ, x) to neuron (θ', x') over time. The terms in the form of $cos(xt)$ or $sin(xt)$ will be cancelled out.

$$
\begin{aligned}
\langle r(\theta,x,t-\tau')r(\theta',x',t+T)\rangle_t &= r_0^2 + \frac{r_1^2}{2} cos(2\pi\Delta\theta + 2\pi v(\tau' + T)) \\
&+ \frac{r_2^2}{2} cos(2\pi\Delta\theta + \pi\Delta x - 2\pi f(T + \frac{|\Delta x|}{\tau})); (v_- \approx -2\pi f) \\
&+ \frac{r_2^2}{2} cos(2\pi\Delta\theta + \pi\Delta x + 2\pi f(T + \frac{|\Delta x|}{\tau})); (v_+ \approx 2\pi f) \\
&= r_0^2 + \frac{r_1^2}{2} [cos(2\pi\Delta\theta + B)cos(2\pi vT) - sin(2\pi\Delta\theta + B)sin(2\pi vT)]; (B = 2\pi v\frac{|\Delta x|}{\tau}) \\
&+ r_2^2 \cos(2\pi\Delta\theta)[\cos A \cos(2\pi fT) + \sin A \sin(2\pi fT)]; (A = \pi\Delta x - 2\pi f\frac{|\Delta x|}{\tau}) \\
&= r_0^2 + \cos(2\pi vT)(\frac{r_1^2}{2}\cos(2\pi\Delta\theta + B)) + \sin(2\pi vT)(-\frac{r_1^2}{2}\sin(2\pi\Delta\theta + B)) \\
&+ \cos(2\pi fT)(r_2^2\cos(2\pi\Delta\theta)\cos(A)) + \sin(2\pi fT)(r_2^2\cos(2\pi\Delta\theta)\sin(A))
\end{aligned} \tag{29}
$$

So the increase of weight under this scenario is: where $A = \pi\Delta x - 2\pi f\frac{|\Delta x|}{\tau}$

$$
\begin{aligned}
dW_{(\theta,x)\to(\theta',x')} &= \alpha(-\frac{r_1^2}{2}\sin(2\pi\Delta\theta + B)) + \gamma(r_2^2\cos(2\pi\Delta\theta)\sin(A)) + \beta(r_2^2\cos(2\pi\Delta\theta)\cos(A)) \\
&\approx \gamma(r_2^2\cos(2\pi\Delta\theta)\sin(A)) + \beta(r_2^2\cos(2\pi\Delta\theta)\cos(A))
\end{aligned} \tag{30}
$$

I want to know the effect of Δx on weight change. So fix $\Delta\theta$, then the weight change would solely depends on $Z = -\beta\sin(A) + \gamma\cos(A)$and $A = \pi\Delta x - 2\pi f\frac{|\Delta x|}{\tau}$. Let $\frac{1}{\tau} = 0.03$, the relationship between Z and Δx would be like Figure 3.1.3. Therefore, connection from dorsal to ventral ($\Delta x < 0$) is smaller than connections from ventral to dorsal ($\Delta x > 0$).

3.1.4 Rate dynamics under equilibrium:

Then I want to investigate that under weight equilibrium, what is the distribution of rate constant r_0, r_1 and r_2 in equation 23. Set Equation 30 to zero and set the rate constants dependent on (θ, x).

3.2 Recurrent neural network with E/I balance and Dale's principle

3.3 Recurrent neural network with short-term depression

4 Self-generated travelling wave:

4.1 Phase-locked, weakly coupled oscillators

4.2 Swim rhythm arise from spinal cord oscillators

5 Phase-offset ring attractor