ROLE OF VELOCITY PERCEPTION ON PLACE FIELD SIZE AND DENSITY OF HIPPOCAMPAL PLACE CELLS

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ABSTRACT

Place field size is stable for a given neuron in a familiar environment, yet increases along the septotemporal axis of hippocampal CA1. It is suggested that place cell assemblies are velocity controlled oscillators (VCO), i.e., the place cell’s oscillation frequency is positively correlated with the running velocity. The VCO model has the potential assumption that the velocity is correctly perceived. However, the perception of velocity may not be faithful to the actual physical velocity in some pathological and behavioral conditions. In this study, we examine the scenario in which perceived velocity deviates from the actual value. Place field size and distribution density change with the precision of perceived velocity. Simulation studies verify that this model is in accordance with previous studies. Testable predictions are also proposed.

KEY WORDS

Velocity, theta rhythm, place cell, phase precession

1. Introduction

Hippocampal pyramidal cells fire according to the animal’s location and direction of movement [1, 2]. Place field size is stable for a given neuron in a familiar environment, serving as the spatial metric for the “cognitive map” [1]. Moreover, the place field sizes of pyramidal cells get progressively larger from the septal pole to the temporal pole and there is progressively smaller probability of recording a field, enabling the multiscale spatial coverage simultaneously [3].

At faster running velocity, place cells fire over fewer theta rhythm cycles yet oscillate at a higher frequency, producing more spikes per cycle. It is therefore suggested that place cell assemblies are velocity controlled oscillators (VCO)[4]. The velocity may be coded by velocity-modulation of entorhinal activity by sensory input via the head-direction system in anterior thalamus[5, 6] or simply “speed cells” recorded in hippocampus (yet thought to be the projection from other brain region) [7]. This may serve as the mechanism of the velocity perception. The VCO model was further extended to grid cells [8-10].

The previous studies on the VCO model have potentially assumed that the velocity is correctly expressed without any errors by regarding the physical velocity as the direct drive of place cell’s oscillation frequency. The direct conclusion of VCO model is that the place field size is not related to the running velocity, which is true in most conditions. However, the perception of velocity may not be faithful to the physical velocity in some pathological and behavioral conditions. For example, human studies suggest that a reduction in contrast leads to a reduction in perceived velocity [8-10], and drivers feel they are driving far more slowly in foggy weather conditions [11-13]. On the other hand, the perception of velocity is related to ambulatory, optic, and vestibular input and the impairment of these signals may also undermine the estimation of velocity [14].

In this study, we explicitly examine the scenario when perceived velocity deviated from the actual value. By utilizing the phase precession [15] and sequence compression studies [16, 17] on place cells, the perceived velocity is treated as an explicit variable. We show that the place field size for a given place cell changes with the ratio of the actual velocity over the perceived velocity. In addition, the density of the place fields is also changed. Simulation studies verify that this model is in accordance with previous studies.

2. The VCO model

First, we revisit the VCO model with terms and notations defined to facilitate the discussion on the role of velocity perception.

Hippocampal place cells of freely moving rats fire when they travel through a specific area (the place field) of their environment [4, 17-19]. In addition, the place cells fire at progressively earlier phase relative to the theta rhythm of the EEG as the rats traverse across the place field, a phenomenon called phase precession [1]. The phase precession phenomenon can be explained as the interference pattern between two oscillatory inputs [16, 17]. One input comes from the theta rhythm with frequency $f_\theta$ and another input has a frequency $f_\omega$ which increases the theta rhythm frequency with the running velocity $v$. The frequency difference between the two has been shown to be proportional to the running velocity [16, 20]

$$\Delta f = f_\omega - f_\theta = \beta v$$ (1)
where \( \beta \) is a positive constant for a given place cell and serves as a spatial parameter. Further, along the septotemporal axis of hippocampal CA1, place field sizes are gradually increasing. This means that \( \beta \) is decreasing gradually. To clarify, we define \( \beta_i \) (where \( \beta_1 > \beta_2 > \cdots \beta_n \)) that represents intrinsic property of pyramidal neurons at each location of the septotemporal axis of hippocampal CA1. \( \Delta f \), the frequency difference between place cell oscillation and theta rhythm, changes in proportional to the perceived velocity coded by the speed cells. When the velocity perception underestimates the true value as a result of, e.g., the impairment of one of the self-motion input signals \( \Delta f \) is also undermined.

\[ L_i = \frac{v}{\beta_i} \]

(4)

The place field size remains constant and is connected with the spatial parameter. This classical VCO model claims no impact of velocity misperception.

3. The Role of Velocity Perception

The above VCO model was based on a major potential assumption that the velocity is correctly perceived. However, animals must rely on certain signals to sense their self-motion relative to the environment to conduct path integration (dead reckoning). These signals include ambulatory, sensory flow (optic, olfactory, et al), and vestibular inputs [16, 17]. The impairment of these signal pathways may attenuate the correct perception of the actual running velocity, therefore giving rise to misleading results.

Here, the VCO model is extended (referred to as eVCO), in which, the perception of running velocity, as is referred to as \( v_p \) is treated as a variable, and is no longer taken granted to be equal to the actual value \( v \).

Note that the perception of velocity \( v_p \) is represented by the firing rate of some specific entorhinal neurons or the “speed cells”, it remains constant under
normal condition, but may change in response to the precision of velocity encoding.

3.1 Place field size

The VCO frequency is now directly dependent on the perceived velocity \( v_p \)
\[
\Delta f = \beta_i v_p \tag{5}
\]

In the above equation, \( \beta_i \) is still the intrinsic character of pyramidal neurons at septotemporal coordinates \( i \), and remains constant whenever \( v_p \) changes. To measure \( \beta_i \) of a specific neuron, the oscillation frequency of the neuron should be recorded from the rat in free roaming and with intact neural functions.

The place field size is measured in the real world by an experimenter as in (3)
\[
L_s = \frac{v}{\Delta f} \tag{6}
\]

However, because in our model, \( \Delta f \) has been related to the perceived velocity other than the real value, from (5) and (6)
\[
L_s = \left( \frac{v}{v_p} \right) \frac{1}{\beta_i} \tag{7}
\]

When the rat correctly perceived its velocity, the place field size is equal to the reciprocal of \( \beta_i \). The eVCO degenerates into the VCO. If the rat underestimates the velocity, i.e., \( v_p < v \), the place field size increases. On the contrary, if the rat overestimate the velocity, i.e., \( v_p > v \), the place field size decreases (Fig.2 A).

3.2 Place field spatial density

The “sequence compression ratio” has been defined as the ratio between the pairwise time lag of place cells firing within one theta cycle and the distance between the centers of the respective place fields [21]. Briefly, the compression factor is defined as
\[
c = \frac{\tau}{T_d} = \frac{\tau}{d_i} \tag{8}
\]

where \( T_d \) is the travelling time between neighboring place fields, \( \tau \) is the time lag between spiking of place cell pairs, \( d_i \) is the place field distance of neighboring place cells from neurons at the septotemporal coordinate \( i \).

The overall number of potential place cells on the same septotemporal coordinate may not change[4, 17-19]. Jung and colleagues [3] compared the spatial selectivity of CA1 neurons in the dorsal and ventral hippocampi of rats. A significantly smaller number of ventral hippocampus had "place fields" than in the dorsal hippocampus, and the average spatial selectivity was of significantly lower resolution. This indicates that the density of place fields is progressively lowered from septal to temporal axis of hippocampus.

In general, we can assume that, regardless of the precision of velocity perception, the number of place cells should remain unchanged. If the theta frequency remains constant, \( \tau \) remains resistant to the misperception of the velocity because the fixed number of place cells was compressed into the unchanged theta cycle. In normal conditions, \( d_i \) is also stable, and together with \( L_s \), gives stable place field distribution that constitute the ‘cognitive map’ of the exploring environment[22]. Thus, we may define a constant \( \alpha_i \) that is the property of
place cells at the septotemporal coordinate $i$, which reflects the distribution density of these place cells:

$$\alpha_i \equiv \frac{\tau}{d_i}$$  \hspace{1cm} (9)

Rewrite (8) as

$$c = \alpha_i v$$  \hspace{1cm} (10)

This means that $C$ is proportional to the running velocity with the constant factor $\alpha_i$.

For eVCO model, the velocity is also encoded by the speed cell. The equation (10) becomes

$$c = \alpha_i v_p$$  \hspace{1cm} (11)

However, we must note that despite the wrong encoding of the speed cell, the rat has to interact with the real world. The distance between pairs of place field centers is measured by the experimenter. From (8),

$$d_i = \frac{\tau}{c}$$

Combine the above equation and (11),

$$D_i = \frac{1}{d_i} = \frac{\alpha_i v_p}{\tau v}$$

where $D_i$ is the place field spatial density, defined as the reciprocal of $d_i$. For the place fields at the septotemporal coordinate $i$, $D_i$ is proportional to $v_p$ when the actual velocity remains unchanged (Fig. 2 B).

4. Simulations

4.1 The effects of varying place field density.

Fig. 3 demonstrates the concept of spatial coverage of place fields. In normal condition, place fields have the averaged distance $d$ between neighboring pairs and have stable size $L$ (Fig. 3 A). When the perceived velocity is lower than the actual one, the place field size increases, whereas we assume $d$ keeps unchanged (Fig. 3 B). Or, both $L$ and $d$ increase according to our eVCO model (Fig. 3 C). Numerical simulation is shown in (Fig. 3 D E). The place fields are randomly located in a unit square, with place field sizes (here defined as SD). Place fields are simulated as Gaussian functions. Mean coverage is defined as the averaged sum of all place fields at each spatial bin. An example coverage distribution is shown in (Fig. 3 D) where 100 place fields with SD being 0.1. The effect of varying density on the mean coverage is shown in (Fig. 3 E). The mean coverage for fixed place field density increases dramatically when place field size
increases. By contrast, the sparser density suggested by the eVCO makes the mean coverage relatively stable.

For a population of place cells in two dimensions, the overlap matrix can be used to reveal the extent of spatial scales [1]. Briefly, the firing rates of n neurons at m place bins form an n-by-m matrix. A column of this matrix forms the population vectors for a given place bin. The autocorrelation matrix gives the overlap matrix. The mean of the matrix value as a function over distance apart from the main diagonal can be calculated to estimate the overall overlapping of population firing (Fig. 4).

To facilitate comparison, the simulations parameters resemble the work done by Terrazas [3, 15]. In a unit-square environment, rats run on a circular track with a velocity. The perception of velocity may be one third or three times as large as the actual velocity.

4.2 Relevance to experimental data

We have considered the effects of perception error of self-motion velocity on the place field size and place field spatial density. We found that the place field size is inversely proportional to the ratio of the perceived velocity over the real velocity, and that the place field density is proportional to the ratio of the perceived

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Fig. 4 Numerical simulations of how place fields would distribute under different assumption. (A) Free walking as a control. (B) The perceived velocity is one third of the actual velocity. The place fields are assumed to be identical with in free walking, while the track radius is reduced to one third. (C) The perceived velocity is one third of the actual velocity. The place fields are distributed according to eVCO model. (D) The perceived velocity is three times as large as the actual velocity. The place fields are distributed according to eVCO model. The black circles in the first column represent the SD of the Gaussians in a unit-square environment. The red circles indicate the trajectories of the rat. The second column shows simulated place fields as in gray scale (black, 0). The y-axis is cell number and the x-axis is angular coordinate (in degree). The third and the fourth column show the population vector overlap matrices and mean overlap versus distance functions respectively.
velocity over the real velocity. This has been in agreement with the experimental studies [15]. In their study, the rats either ran freely on the circular track or were trained to drive a car on the same track. The place field size in car driving was found threefold of that in free running. To explain this, the authors conducted a numerical simulation in which the place field size was considered never changed and the animals were traveling in a smaller track with radius reduced to one third of the original one while keeping the duration of completing one lap constant. Therefore, the animals seemed to be running in a slower velocity. This explanation gives the insights of the underlying mechanism. In the eVCO language, the animals have unchanged mental place field size for given level place cells. The actual place field size may vary according to the precision of perceived velocity, shifting the place field size over septotemporal curve (Fig. 2) left (underestimate) or right (overestimate).

Numerical simulations of how place fields would distribute under different assumption. Free walking where the velocity is correctly perceived is taken as a control (Fig. 4A). One hundred Gaussian functions with random centers and standard deviation (SD) represent the place fields. The place field size is proportional to the standard deviation. SD was set to 0.1. The probability of a spike occurring at a location was made proportional to the height of the Gaussian. The constant of proportionality could be varied to simulate the firing rate changes.

5. Discussion

We have come to two main results. The first is that the place field size is inversely proportional to the perceived velocity. The second is that the place field spatial density is proportional to the perceived velocity.

5.1 Coverage of space

Consider the field of a place cell as the sensor (antenna) that samples the space. The place field size resembles the effective range within which signals can be detected. To cover an area, multiple antennae should be used. The number of antennae should be large enough to cover the space and small enough to avoid wasting resources. Localized antenna need to be densely distributed. On the contrary, long range antenna only requires sparse distribution. What differs the antenna system is that, in the rat, the space is represented at multiple spatial scales at the same time, which may have computational advantages to trade-off between spatial resolution and spatial contiguity [15].

5.2 Theta rhythm frequency

We have assumed that the theta rhythm frequency remains constant even for the misperception of velocity. However, there is report showing that the frequency is positively correlated with the velocity, although to a much less extent as compared to the place cell oscillation frequency [3]. Therefore, the equation (12) has to be modified to reflect the theta frequency-velocity relationship. For example, if the velocity perception is less than the real velocity, the place field density reduces even more than would be predicted by the equation.

5.3 Experimental relevance

Assume that the perceived velocity is one third of the actual velocity. Terrazas, et al postulated that the place fields for car driving are assumed to be identical with in free walking, while the track radius is reduced to one third [4]. The alternative explanation could be based on the proposed eVCO concept. Under the assumption that perceived velocity is one third of the actual velocity, the place field sizes and the averaged distances between pairs of place cell centers are threefold the original ones. On the other hand, increasing the amount of optic flow information available to the passively moved rats decreased their place field size while having no effect on the free walking rats[15]. This can be understood that the passive rats rely more on the optic flow to estimate their velocity while in free walking they rely more on the proprioception. When optic flow increased the velocity estimation increased which leads to decreased place fields size.

5.4 Internal representation of space

Although the early empiricists in UK proposed that all we knew about the world was derived from the sensory system, evidence from the past decades has indicated that place cells might be part of the preconfigured or semi-preconfigured brain system for representation and storage of self-location [23]. We have gained the knowledge that the place fields are formed mainly from the animal’s internal dynamics and are aligned to landmarks and borders [24]. In this study, the misperception of velocity alone can cause the shift in place field size and density, which, we would argue, have supported the knowledge.

5.5 eVCO model in grid cells

Grid cells in medial entorhinal cortex (MEC) were shown to exhibit sharply tuned spatial firing in multiple firing fields. The MEC serves as the direct input into hippocampus [25, 26]. Researches have proposed that grid fields of different spacing generates place field in the hippocampus [27]. Further, the VCO has been applied to the MEC [28-30]. Therefore, the eVCO may also be applied to the MEC grid cells. The velocity perception error may also affect the grid field size and spacing.
5.6 Limitations

We have extended the VCO model to emphasize the possibility of velocity encoding error that might occur in some pathological and behavioral conditions. However, the exact mechanism of how speed cell firing regulates the place cell oscillation has remained unanswered.

6. Conclusion

We have built a model that explicitly acknowledges the possibility of misperception of self-motion velocity. The place field size and density shift along with the precision of velocity perception (probably in the form of speed cell’s firing rate) such that the space coverage by place fields remains sufficient and economic.

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