Grid Cells and Theta as Oscillatory Interference: Electrophysiological Data From Freely Moving Rats

A. Jeewajee,^{1,2,3} C. Barry,^{1,3,4} J. O'Keefe,³ and N. Burgess^{1,5*}

ABSTRACT: The oscillatory interference model (Burgess et al. (2007) Hippocampus 17:801–812) explains the generation of spatially stable, regular firing patterns by medial entorhinal cortical (mEC) grid cells in terms of the interference between velocity-controlled oscillators (VCOs) with different preferred directions. This model predicts specific relationships between the intrinsic firing frequency and spatial scale of grid cell firing, the EEG theta frequency, and running speed (Burgess, 2008). Here, we use spectral analyses of EEG and of spike autocorrelograms to estimate the intrinsic firing frequency of grid cells, and the concurrent theta frequency, in mEC Layer II in freely moving rats. The intrinsic firing frequency of grid cells increased with running speed and decreased with grid scale, according to the quantitative prediction of the model. Similarly, theta frequency increased with running speed, which was also predicted by the model. An alternative Moiré interference model (Blair et al.,

The O cilla or In erference Model

· · · · · · · · · · · · · · · · · · ·		
$\cdots \cdots $		
('K , 1993; L, 2003) , E , L _ II , (H , (H ,), 2008).		
, 1993; B J L , 2000). 1D		
EEG (M)		
f ()94.9(8.(.)	(3)4.5.5(408.4 43.4	5,)-4.1)42())-48 ()5.38

(A , K , 1993).

(β

METHODS

Animal and S_sger

D,			L	Ε,			1	7),	
	L . F	I and go	(8 13;	250 4	470	<i>c</i> .	-
() ()),,,,,,,		`	•	<u> </u>	,. I			-
, (1	7) ,		-		. •	(F		•,
2007),		· · · · · ·				`			

64 × 64
× 2
······································
× 5

Ι			ere a		· · ·		· . · ·	EEG
4	(7	11 Н;	· · · · <u> </u>	(.,	F.	3),	•	
1	.	`e =	(f_{θ})	- , *		. A	•	· (*
	,		• • • • •		• . 	111111111111 1.1.1.1.1.1.1.1.1	_(f)	

(M)
(, (, (, (, (, (, (, (, (, (, (, (, (, (
, M
1.73) (1. F. 5). I
(B , 2008)
· · · · · · · · · · · · · · · · · · ·
Fr 5

(B , , 2002; 'K , , 2006), , B (2008)? I
(, , , , , , , , , , , , , , , , , , ,
· · · · · · · · · · · · · · · · · · ·
$= \left\{ \begin{array}{cccccccccccccccccccccccccccccccccccc$
β ,
, E. (6),
$f_{1}, \dots, f_{n}, \dots, \dots, \dots, f_{n}, \dots, \dots,$
$= (200.;, 3 \times 48)$

$\sim - \sim \sim \sim \sim$	and the second	•
M	i e ser e ser e	
	·····	,
	('K , 1993	;
L, 2003; M	., 2005; G ., 2007))