

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

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**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.,



... I ... (B ... 2008) ...

### The Oscillator Inference Model

... ID ... (K ... 1993; L ... 2003) ... E ... L ... II ... (H ... 2008) ...

... ( ... ) ... (K ... 1993; B ... 1994; ... 1996; J ... L ... 2000) ... ID ...

...  $f()$  ... EEG ... (M ...) ...  $f()$  ...

...  $f$  ... ( )94.9( 8.(.1( 3 ... )4.5.5( 408.4 43.5, )-4.1 )42( )-)-48 ( )5.38

... (A ... K ..., 1993). ...  
M ...

(β

## METHODS

### Animal and Surgery

Dorsal skin was shaved and the L<sub>1</sub>/E<sub>12</sub> region (Fig. 1, 7) was prepared. L<sub>1</sub>/H<sub>12</sub> (Fig. 1, 8, 13; 250–470 mg) was prepared (1, 7). The skin was removed and the muscle was removed (Figs. 1, 2007).

64 × 64  
8 × 8  
2  
× 2  
5  
× 5



F  
F  
F

In the case of the EEG (Fig. 3), the results are similar to those of the ECG (7-11 Hz; Fig. 3), with the frequency  $(f_0)$  being in the range of 7-11 Hz. A similar result is obtained for the EEG (Fig. 3), with the frequency  $(f_0)$  being in the range of 7-11 Hz.

Figure 5 shows the results of the calculations. The results are presented in two columns. The left column shows the results of the calculations for the case of a homogeneous material. The right column shows the results of the calculations for the case of a material with a longitudinal layer. The results for the case of a homogeneous material are presented in the top row of the left column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the left column. The results for the case of a homogeneous material are presented in the top row of the right column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the right column. The results for the case of a homogeneous material are presented in the top row of the left column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the left column. The results for the case of a homogeneous material are presented in the top row of the right column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the right column.

Figure 5. The results of the calculations for the case of a homogeneous material and for the case of a material with a longitudinal layer. The results are presented in two columns. The left column shows the results of the calculations for the case of a homogeneous material. The right column shows the results of the calculations for the case of a material with a longitudinal layer. The results for the case of a homogeneous material are presented in the top row of the left column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the left column. The results for the case of a homogeneous material are presented in the top row of the right column. The results for the case of a material with a longitudinal layer are presented in the bottom row of the right column.







(B... 2002; 'K... 2006),  
B... (2008)? I...

(... 1973; L... 2008)?

0.5  
H  
E (6)

E (6)  
G  
 $f$   
 $f_0$   
 $\beta$   
48  
 $\beta$   
(200... 3 x 48  
=

... (K... 1993; L... 2003; M... 2005; G... 2007)

