

Is hippocampal gamma band activity in vivo the signal-dependent noise?

Jonghan Shin

RIKEN Brain Science Institute, 2-1 Hirosawa, Saitama, Japan; Computation and Neural Systems, Caltech, Pasadena, USA; Korea Advanced Institute of Science & Technology, Seoul, South Korea
shin@corpus.brain.riken.go.jp

1. Introduction

It is widely agreed that identifying the origin and functional role of neural noise (or on-going activity) (Ferster 1996; Arieli et al. 1996; Freeman 2000) may reveal something new and fundamental about how the brain works. Recently, Harris and Wolpert (1998) proposed a significant new perspective on neural noise in that they assumed signal-dependent noise in the brain and demonstrated that it can be involved in motor planning. Their model suggests that neural noise can be actively engaged in cognitive process such as optimal path planning in eye and arm movements. However, renewal process such as Poisson spike train does not agree with the condition of signal-dependent noise whose standard deviation increases linearly with the absolute value of the signal (Harris 2001). On the other hand, the noise shaping neural coding hypothesis (Shin 2002a) has successfully contributed to resolve several key issues in the brain information processing (e.g., visual contrast adaptation (Shin, Koch, & Rodney 1999; Shin 2001a), the relationship between spike trains and EEG (Shin 2002b), and the mechanism of deep brain electrical stimulation in patients with Parkinsonian, Epilepsy, or chronic pain (Shin 2002c)). Based on the noise shaping neural coding hypothesis, I propose a new concept on the relationship between hippocampal theta and gamma oscillations: hippocampal theta oscillation is a signal to code motor behavior and hippocampal gamma oscillation is signal-dependent noise. To test this concept, behavioral and electrophysiological experiments were conducted using rats trained to perform spontaneous locomotion in both linear track and wheels.

2. Method and Materials

Eight male Long Evans rats between 220 g and 350 g were used. A pair of 80 μ m varnish-isolated stainless-steel wires has been placed to the CA1 stratum oriens (4.2 mm posterior bregma, 2 mm lateral to midline, 2.5 and 3.0 mm ventral to dura) for unipolar recording of hippocampal local field potentials (see Shin & Talnov 2001 for detail). After surgery, rats were mildly water deprived for 23 hours and trained to run continuously in a wheel. A circular encoder recorded running speed and concurrently a digital video recorder recorded rats' behavior. Up to three drops of water were provided if rats run the wheel for 10 sec continuously. Uninterrupted 6 sec running period was selected as a single trial for analysis. In a second behavioral task, rats were trained to run a linear track (wide 1.5 m and width 15 cm). Kinematics analysis was performed for one hindlimb in animals. In these analyses, a stride is defined as the locomotion sequence starting with elevation of the foot from the ground, forward movement of the foot off the ground (swing phase), and placement upon the ground until the next elevation of the same foot (stance phase). Elevation of the foot was defined as the point at which the toes were no longer flexed or off the ground.

3. Results

It was found that the frequency of hippocampal theta oscillation is related to stride frequency and the amplitude of hippocampal theta oscillation is correlated with stride length. In addition, the hypothesis (Shin & Talnov 2001) that variations in locomotion between linear track and wheels may account for differences in the connection between theta frequency and speed of locomotion is supported using the biomechanical analysis. I also confirmed the characteristics of "theta modulation of gamma waves" (Bragin et al. 1995) and the negative

relationship between hippocampal gamma oscillation strength and frequency similar to cortical gamma oscillations (Herculano-Houzel et al. 1999), which has been predicted by the noise shaping neural coding hypothesis. Finally, it was found that the noise variance of hippocampal EEG is linearly proportional to the amplitude of hippocampal theta oscillations (i.e., motor command efference copy). Therefore, noise in hippocampal EEG agrees with the condition of signal-dependent noise suggested by Harris and Wolpert (1998).

3. Discussion

Given the interdependent relationship between covert/overt motor functions and cognitive functions (e.g., memory and perception) (Shin 2001b), our results support the suggestions that hippocampal theta oscillations are related to motor behaviors and may be engaged in path integration (Maaswinkel et al. 1999), sensory-motor integration (Bland & Oddie 2001), encoding and retrieval of episodic memories (Louie & Wilson 2001; Caplan et al. 2001), motor representations of space (O'Keefe & Burgess 1999), and novelty detection (Borisyuk et al. 2001). Finally, based on the relationship between hippocampal theta and gamma band activities in vivo, I suggest that in-vivo gamma band activity in hippocampal formation can be the signal-dependent noise resulting from the noise shaping neural coding and may be engaged in optimal trajectory planning for spatial navigation. It should be noted that this suggestion (i.e., gamma band activity as the signal-dependent noise) does not exclude previous suggestions related to gamma band activity in vivo.

Acknowledgements

J. Shin thanks A. Talnov for help with the experiments.

References

- Arieli A, Sterkin A, Grinvald A, Aertsen A (1996), "Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses" *Science*, 273, 1868-1871.
- Bland BH, Oddie SD (2001), "Theta band oscillation and synchrony in the hippocampal formation and associated structures: the case for its role in sensorimotor integration" *Behavioral Brain Res.*, 127, 119-136.
- Borisyuk R et al. (2001), "Oscillatory model of novelty detection" *Network: Comput. Neural Syst.*, 12, 1-20.
- Bragin A, Jando G, Nadasdy Z, Hetke J, Wise K, Buzsaki G (1995), "Gamma (40-100 Hz) oscillation in the hippocampus of the behaving rat" *J. of Neuroscience*, 15, 47-60.
- Caplan JB, Madsen JR, Raghavachari S, Kahana MJ (2001), "Distinct patterns of brain oscillations underlie two basic parameters of human maze learning" *J. Neurophysiol.*, 86: 368-380.
- Ferster D (1996), "Is neural noise just a nonsense?" *Science*, 273, 1812.
- Freeman W (2000), "Brains create macroscopic order from microscopic disorder by neurodynamics in perception" *Disorder Versus Order in Brain Function* (Eds. Arhem P, Blomberg C, Liljenstrom H), World Scientific, Singapore, pp. 205-219.
- Harris CM, Wolpert DM (1998), "Signal-dependent noise determines motor planning" *Nature*, 394, 780-784.
- Harris C (2001), "Temporal uncertainty in reading the neural code (multiplicative noise)" *Proc. of 4th Neural Coding Workshop*, Plymouth, UK 10-15 Sept. pp.10-13.
- Herculano-Houzel S, Munk MH, Neuenschwander S, Singer W (1999), "Precisely synchronized oscillatory firing patterns require electroencephalographic activation" *J. of Neuroscience*, 19, 3992-4010.
- Louie K, Wilson MA (2001), "Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep" *Neuron*, 29, 145-156.
- Maaswinkel H, Jarrard LE, Whishaw IQ (1999), "Hippocampectomized rats are impaired in homing by path integration." *Hippocampus*, 9, 553-561.
- O'Keefe J, Burgess N (1999), "Theta activity, virtual navigation and the human hippocampus" *Trends in Cognitive Science*, 3, 403-406.

- Shin J, Koch C, Douglas R (1999), "Adaptive neural coding dependent on the time-varying statistics of the somatic input current" *Neural Computation*, 11, 1893-1913.
- Shin J (2001a), "Adaptation in spiking neurons based on the noise shaping neural coding hypothesis" *Neural Networks*, 14, 907-919.
- Shin J (2001b), "The context-update model of P300: Is it related to the cognitive map theory", *Proc. of 1st World Congress on Neuroinformatics (CD-ROM version)*", Sept. 24-29, Vienna, Austria, 2001
- Shin J, Talnov A (2001), "A single trial analysis of hippocampal theta frequency during nonsteady wheel running in rats" *Brain Res.*, 897, 217-221.
- Shin J (2002a), "The spectral noise shaping neural coding hypothesis: A brief history and physiological implications" *Neurocomputing*, to be appeared.
- Shin J (2002b), "A unifying theory on the relationship between spike trains and EEG based on the spectral noise shaping neural coding hypothesis" *Biosystems*, in revision.
- Shin J (2002c), "From the noise shaping neural coding hypothesis to brain disorders" in preparation.