A unifying theory on the relationship between spike trains and EEG based on the spectral noise shaping neural coding hypothesis

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1. Introduction

To clarify the long running controversial arguments on the relationship between signal and noise in both spike train and EEG (Ferster 1996, Arieli *et al* 1996, Leung 1998), we present a novel concept that gamma oscillation in vivo results from the noise shaping neural coding that has been proposed to explain efficient neural code observed in the brain (Shin 2001a, Shin 2001b). The noise shaping neural coding hypothesis supports the suggestion (Bland 1986) that low frequency, astropine-sensitive (Type II) theta activity is produced during alert immobility to provide the motor system with a readiness or priming signal and high frequency theta (Type I), once locomotion is triggered, appears which reflects the activation and consequences of the locomotor pattern itself. To test predictions from the noise shaping neural coding hypothesis, we conducted behavioral and electrophysiological experiments using rats trained to perform spontaneous locomotion in both linear track and wheels and performed biomechanical analysis.

2. Method and Materials

Eight male Long Evans rats between 220 g and 350 g were used. Pairs of 80 u varnish-isolated stainless-steel wires have been placed to the CA1 region (4.2 mm posterior bregma, 2 mm lateral to midline, 2.5 and 3.0 mm ventral to dura). After surgery, rats were mildly water deprived for 23 hours and trained to run continuously in a wheel (see Shin & Talnov 2001, Shin *et al* 2001 for detail method). 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 and Discussion

We found that the frequency of hippocampal theta rhythm is related to stride frequency and the amplitude of hippocampal theta rhythm is correlated with stride length. In addition, we confirmed the positive relationship between theta frequency and gamma frequency and found the negative relationship between gamma oscillation strength and gamma oscillation frequency similar to gamma oscillation in cortex (Herculano-Houzel *et al* 1999), which has been predicted by the noise shaping neural coding hypothesis. Our results strongly support the suggestions that hippocampal theta rhythm codes actual/imagined motor

behaviors (Bland 1986) and may be engaged in path integration (Maaswinkel *et al* 1999), sensory-motor integration (Wolpert *et al* 1995), encoding and retrieval of episodic memories (Borisyuk *et al* 2001, Louie & Wilson 2001), and motor representations of space (Rosetti 1998, O'Keefe & Burgess 1999).

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