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The role of chaotic resonance in cerebellar learning

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ABSTRACT

According to the cerebellar learning hypothesis, the inferior olive neurons, despite their low firing rates, are thought to transmit high-fidelity error signals to the cerebellar cortex. "Chaotic resonance", via moderate electrical coupling between inferior olive neurons, has been proposed to realize efficient transmission of the error signal by desynchronizing spiking. Here, we first show that chaotic resonance is a robust phenomenon, as it does not depend upon the details of the inferior olive neuronal model. Second, we show that chaotic resonance enhances learning of a neural controller for fast arm movements. Furthermore, when both coupling and noise are considered simultaneously, we found that chaotic resonance widens the range of noise intensity within which efficient learning can be realized. We suggest that, from an energetic viewpoint, the spiking activity induced by chaos can be more economical than that induced by noise.

1. Introduction

The anatomy and the physiology of the cerebellum make it ideally suited to learn how to refine motor commands (Albus, 1971; Ito, 1970; Ito, Sakurai, & Tongroach, 1982; Kawato & Gomi, 1992; Marr, 1969; Schweighofer, Spoelstra, Arbib, & Kawato, 1998; Shidara, Kawano, Gomi, & Kawato, 1993) or to learn sensory predictions from motor commands (Miall, Christensen, Cain, & Stanley, 2007; Miall, Weir, Wolpert, & Stein, 1993; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). The Purkinje cells, the sole output neurons of the cerebellar cortex, receive two major types of synaptic inputs: (i) numerous parallel fibers that relay information from much of the cerebral cortex and spinal cord, and (ii) a single climbing fiber, which is an axon from an inferior olive (IO) neuron, that has been shown to transmit error signals (Gilbert & Thach, 1977; Kitazawa, Kimura, & Yin, 1998). When conjointly activated with parallel fibers, IO spikes modify cerebellar input–output transformations, in agreement with the known long-term depression (LTD) at the parallel fiber–Purkinje cell synapse (Ito et al., 1982).

Two apparently contradictory constraints must be met, however, for the cerebellum to realize efficient adaptive motor control or prediction. First, the IO must transmit error signals with high temporal resolution despite its low firing rate. Second, IO neurons must fire at a low firing rate so that complex spikes encoding error signals do not interfere with simple spikes carrying motor control commands or predictions (Kawato & Gomi, 1992; Kobayashi et al., 1998). We previously proposed that these two constraints are simultaneously met via low-rate IO chaotic spike firing (Schweighofer et al., 2004). Such chaotic behavior leads to the generation of IO spikes at different timings at each trial. Specifically, we showed that electrical coupling via gap junctions can provide the source of disorder that induced a "chaotic resonance" (Nishimura, Katada, & Aihara, 2000) in IO networks. Here, chaotic dynamics is not supplied externally but it originates internally from complex interaction among the neurons. This resonance leads to an increase in information transmission in IO neurons by distributing high-frequency components of the error inputs over the sporadic, irregular, and non-phase-locked spikes. Desynchronization is indeed necessary for scattering the spike timings of each neuron to increase the time resolution of the population rate coding (Masuda & Aihara, 2002, 2003). Purkinje cells can then reconstruct the complete error signal via spatio-temporal integration because functionally related Purkinje cells and IO cells are grouped in "microcomplexes" (Ito, 1990; Schweighofer, 1998).

The direct effect of electrical coupling in enhancing cerebellar learning has yet to be shown, however. Furthermore, the robustness of chaotic resonance is unclear for two reasons. First, chaos does not always imply destruction of synchrony, since synchronization between chaotic oscillators has been commonly observed in a variety of physical or biological systems (Pikovsky, Rosenblum, & Kurths, 2001). Second, in our original study, we used a rather

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complicated compartment model (Schweighofer, Doya, & Kawato, 1999), and many physiological parameters can be chosen rather arbitrarily in this model. Finally, it is unclear whether chaos is indispensable to desynchronize IO neurons and to realize efficient information transmission, since neural noise can also desynchronize IO neurons.

Here, we develop a simple model of IO neurons to test the hypothesis that chaotic spiking induced via electrical coupling in IO neurons robustly enhances the learning of complex motor commands compared to non-chaotic or noise-induced jittered spiking. In our simulations, the IO neurons provide error signals to an idealized model of the cerebellar cortex that learns, via feedback error learning (Kawato, Furukawa, & Suzuki, 1987; Kawato & Gomi, 1992), to control a simplified model of the human arm in rapid reaching movements.

2. Methods

2.1. Inferior olive model

The dynamical properties of the IO neuron can be summarized as follows. (i) Under an isolated condition, a single IO neuron generates a limit cycle oscillation (Manor, Rinzel, Segev, & Yarom, 1997). (ii) Through gap-junction connections with other neurons, the IO neuron gives rise to more complex spike patterns (Lang, Sugihara, & Llinas, 1996; Makarenko & Llinas, 1998; Schweighofer et al., 2004). The μ-model is a simplified two-dimensional neuronal model that satisfies these dynamical characteristics (Fujii & Tsuda, 2004; Tsuda, Fujii, Tadokoro, Yasuoka, & Yamaguti, 2004). In particular, when embedded in a one-dimensional chain, complex spiking patterns such as chaotic itinerancy can be generated (Tsuda et al., 2004). The dynamics of a one-dimensional chain of μ-neurons is given by

$$\begin{aligned} \eta_1 \frac{\mathrm{d}x_i}{\mathrm{d}t} &= -y_i - \mu_i x_i^2 \left(x_i - \frac{3}{2}\right) + I + J_i + \xi_i, \\ \eta_2 \frac{\mathrm{d}y_i}{\mathrm{d}t} &= -y_i + \mu_i x_i^2, \end{aligned} \tag{1}$$

where

$$J_i = \begin{cases} g(x_2 + x_N - 2x_1) & (i = 1) \\ g(x_{i+1} + x_{i-1} - 2x_i) & (i = 2, \dots, N-1) \\ g(x_1 + x_{N-1} - 2x_N) & (i = N), \end{cases} \tag{2}$$

x_i and y_i represent the membrane potential and ion channel activity of the ith neuron ($i = 1, 2, \dots, N$), N is the total number of the neurons, μ is a system parameter, η_1 and η_2 are time constants, g is the coupling strength of the gap junctions, and I is an external input. An advantage of using this model is its weak dependence on the parameter value, since μ is the only parameter that controls the qualitative dynamics of the neuron; the time constants, which are set equal in this study ($\eta_1 = \eta_2$), do not change the qualitative dynamics of the neuron. Furthermore, because the parameter dependence on the neural dynamics has been thoroughly analyzed (Fujii & Tsuda, 2004), the proper parameter value for μ to generate spiking dynamics is also well understood.

Real neurons are subject to various kinds of noise. Since noise can destroy synchronous firing activity in a similar way as chaos, it is natural to consider that noise can also enhance information transfer in the IO. To take into account such a noise effect, we added independent white *Gaussian* noise $\xi_i(t)$ to the original μ-model, with $E[\xi_i(t)] = 0$, $E[\xi_i(t)\xi_j(s)] = 2D\delta(t-s)\delta(i-j)$, where D is the noise intensity, as in Collins, Chow, and Imhoff (1995).

The spiking activity of the kth IO neuron is defined as a membrane potential that exceeds a threshold value of x_{th}. In the case of noise-free simulations ($D = 0$), Eq. (1) is integrated by the fourth-order Runge–Kutta algorithm started from a random initial condition. In the presence of noise, Eq. (1) becomes a stochastic differential equation, which is simulated by Euler's algorithm (Fox, Gatland, Roy, & Vemuri, 1988). In the following experiments, five simulations were run to compute the average quantities so that the dependence of the neural dynamics on the random initial conditions is weakened.

2.2. Mutual information

As a basic study to evaluate the information transmission of the IO network, we measured the mutual information (Rényi, 1970) between an input signal and the spike responses. As an input signal, we used chaotic signals from the Rössler equations ($\mathrm{d}x/\mathrm{d}t = -y - z$, $\mathrm{d}y/\mathrm{d}t = x + 0.36y$, $\mathrm{d}z/\mathrm{d}t = 0.4x - (4.5 - x)z$) (Rössler, 1979). The y-variable is injected to all neurons in the same manner as $I = I_0 + \beta \cdot y$ ($I_0 = 0.01$ and $\beta = 0.002$). The output $S(t)$ represents a time sequence of a number of spikes generated from the population of neurons within a time interval of 0.02. Then the mutual information between input $I(t)$ and output $S(t)$ is computed, where the signals are discretized into 25 bins for calculating the probability distributions.

It is noted that the chaotic input signal has been utilized merely as a typical example of complex signal in the brain. The same results can be obtained when a periodic or noisy signal is used as the input.

2.3. Synchrony

For the IO neurons with low firing frequency to transmit information efficiently, synchronous activity is not desired, because in this condition the network becomes equivalent to a single neuron. As an index to detect such synchronized activity of the neurons, the order parameter R (Kuramoto, 1984) has been utilized. The order parameter is defined as $R\exp(\mathrm{i}\Phi) = (1/N)\Sigma_{j=1}^{N}\exp(\mathrm{i}\phi_j)$, where ϕ_j represents phase of the jth neuron given by angle $\phi_j = \arctan\left(\frac{x_j(t-0.2)}{x_j(t)}\right)$. The order parameter takes a real value between 0 and 1, where a large value close to $R = 1$ implies strong mutual synchronization and a small value close to $R = 0$ implies desynchronization.

2.4. Chaos

We quantified the strength of chaotic activity of the IO neurons with the Lyapunov exponents, computed as in Shimada and Nagashima (1979). From the Lyapunov exponents ordered in a descending manner $\lambda_1 \geq \lambda_2 \geq \cdots \geq \lambda_{2N}$, the Lyapunov dimension is defined as $D_L = k + \sum_{i=1}^{k}\lambda_i/|\lambda_{k+1}|$, where k is the maximal value of j such that $\sum_{i=1}^{j}\lambda_i \geq 0$ (Kaplan & Yorke, 1970). The Lyapunov dimension represents an effective dimension of the chaotic dynamics in the $2N$-dimensional state space. A larger Lyapunov dimension implies more complex dynamics of IO neurons. In the scenario of chaotic resonance, the information transmission is expected to be maximized in the regime where the Lyapunov dimension takes the largest value.

2.5. Feedback error learning

The IO neurons are supposed to provide error signals to an idealized model of the cerebellar cortex. Here, we assume that the cerebellum learns an inverse model of an arm via feedback error learning (Kawato et al., 1987; Kawato & Gomi, 1992; Schweighofer et al., 1998; Shidara et al., 1993). In feedback error learning, supervised learning of a feedforward controller occurs using a feedback control signal as the error signal. As the feedforward controller improves, the reliance on the feedback controller decreases. Note that our purpose here is to show that chaotic resonance of IOs with very low firing rates can enhance the learning of complex mappings, such as an inverse model for arm control; thus other complex mappings such as forward models would have been possible as well. We therefore do not model the cerebellum in great detail, but instead we model a simple network composed of granule cells that project to Purkinje