A Coupled Oscillator Model of Ordered and Disordered Inter-limb Coordination

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Abstract

It has been assumed that neural networks referred to as central pattern generators (CPGs), possibly located at the spinal level, are responsible for generation of basic coordinated and alternating motor patterns during locomotion. In some vertebrates, the CPG can autonomously generate several rhythms of neural activities accompanied by different motor patterns depending on the intensity of descending signals that activate the CPG. In theoretical studies, CPGs are often simply modeled by coupled nonlinear oscillators because little is known about the detailed structure of CPGs[1]. In such models, each oscillator in the CPG represents the activities of a single neuron or a group of neurons innervating one limb. Thus the symmetry that the animal’s body has, for example, the left-right symmetry, is inherited in the CPG model. Moreover, each oscillator in the CPG model receives a control signal modeling a flow of descending signals from higher centers down to the CPG. Intensities of the control signals are often assumed to be common to each oscillator, leading to high degree of symmetry of the model. Such CPG models can phenomenologically reproduce several motor patterns representing the inter-limb coordination observed during the animal locomotion[1].

Meanwhile, in some neurological diseases of humans such as Parkinson’s disease, the motor coordination can be disordered and patients cannot successfully perform oscillatory movements with aimed inter-limb coordination. Although such coordination disorders have been extensively studied, less attention is given to relations between the disorders and CPGs despite the functional importance of the CPGs in the rhythmogenesis. We want to associate the disordered coordination with dynamics of the CPGs. To begin to study the relations, we ask the following question: “can a coupled-oscillator-type CPG model generate disordered as well as ordered motor patterns?” If so, how can we understand the mechanisms underlying the generation of such motor coordination?

In this study, we consider a simple half-center type hard-wired CPG model consisting of two oscillators (one for the right half-center and the other for the left) coupled symmetrically by reciprocal inhibition. Each of two oscillators in the model receives a control signal. We look mainly at the relative phase between two oscillators and the modulation of the amplitude of each oscillator for several conditions on the control signals. If the intensities of these two control signals are the same, the model has complete left-right symmetry. Golubitsky et al [2] have shown that symmetrically coupled oscillators can exhibit oscillations reflecting the symmetry of the model. Such symmetric oscillation patterns can break-down spontaneously when the model’s parameter values change but with keeping the symmetry of the model, generating less symmetric, possibly disordered oscillations. If, on the other hand, the intensities of these two control signals are different[3], the left-right symmetry of the model is lost. The difference between the intensities, referred to as the degree of asymmetry, could be an alternative source of the disordered coordination. We analyze the model’s asymptotic dynamics and its changes that may be observed when the intensity of each control signal and/or the degree of asymmetry changes. To this end, the bifurcation diagrams[4] of the
model are calculated. We then clarify the mechanism of the generation of the ordered and disordered coordination in the model based on the bifurcation structure of the model.

When the intensities of two control signals are the same and constant, the model shows the ordered coordination such as in-phase and anti-phase oscillations in which two oscillators oscillate with the same and constant amplitude and the relative phase, respectively, of 0° and 180°. We first show that the model with the complete left-right symmetry can show disordered coordination such as asymmetric periodic and chaotic oscillations for appropriate intensities of the control signals via a sequence of symmetry-breaking bifurcations. In the asymmetric periodic oscillations, the amplitudes of two oscillators are constant but not necessarily the same and the relative phase is locked at constant value but at neither 180° nor 0°. In the chaotic oscillations, the amplitude of each oscillator is modulated with the modulation period spanning several oscillation cycles and the relative phase fluctuates intermittently.

When the degree of asymmetry is non-zero, the model generates disordered coordination such as chaotic, quasi-periodic as well as asymmetric periodic oscillations in a wider range of the parameter space than the corresponding range in the model with the complete symmetry. The effect of the degree of asymmetry on the model’s dynamics is reflected in the dramatic changes in the bifurcation structure of the model.

Our model study suggests that coordination disorders in oscillatory movements could be a result of the interaction between the CPG and the higher motor center in the brain. We showed two possible mechanisms that generate the coordination disorders. Both of them are associated with a sequence of bifurcations occurring when the intensities of two control signals from the higher motor center change, but one is the spontaneous symmetry-breaking bifurcations in the model with the complete left-right symmetry and the other is due to the degree of asymmetry reflecting the difference in the two control signals. It is important to note that the coordination disorders in both cases are generated in the same hard-wired CPG model that has common parameter values including those of the coupling strengths. This fact is consistent with “the final common path” concept in the motor theory. That is, coordinated motor patterns, both ordered or disordered, emerge through a dynamics of the common spinal CPG circuitry, but they are either ordered or disordered depending on the intensity and symmetry of the driving control signal generated in the higher motor center. Finally, we show preliminary results of our joint research with clinical researchers on patients with Parkinson’s disease, which may provide a physiological implication of the model’s dynamics.

References