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Modular neuromuscular control of human locomotion by central pattern generator

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ABSTRACT

The central pattern generators (CPG) in the spinal cord are thought to be responsible for producing the rhythmic motor patterns during rhythmic activities. For locomotor tasks, this involves much complexity, due to a redundant system of muscle actuators with a large number of highly nonlinear muscles. This study proposes a reduced neural control strategy for the CPG, based on modular organization of the co-active muscles, i.e., muscle synergies. Four synergies were extracted from the EMG data of the major leg muscles of two subjects, during two gait trials each, using non-negative matrix factorization algorithm. A Matsuoka's four-neuron CPG model with mutual inhibition, was utilized to generate the rhythmic activation patterns of the muscle synergies, using the hip flexion angle and foot contact force information from the sensory afferents as inputs. The model parameters were tuned using the experimental data of one gait trial, which resulted in a good fitting accuracy (RMSEs between 0.0491 and 0.1399) between the simulation and experimental synergy activations. The model's performance was then assessed by comparing its predictions for the activation patterns of the individual leg muscles during locomotion with the relevant EMG data. Results indicated that the characteristic features of the complex activation patterns of the muscles were well reproduced by the model for different gait trials and subjects. In general, the CPG- and muscle synergy-based model was promising in view of its simple architecture, yet extensive potentials for neuromuscular control, e.g., resolving redundancies, distributed and fast control, and modulation of locomotion by simple control signals.

1. Introduction

During the last four decades, much advances have been made in our understanding of the neuromuscular mechanisms involved in producing basic rhythmic activities such as walking, chewing, etc., in humans and animals. It has been shown that the central nervous system controls such activities in a hierarchical fashion. The lower-level controller (in the spinal cord) generates the basic rhythmic patterns of the motor program, and the higher-level controller (in the motor cortex, cerebellum, and basal ganglia) selects, initiates and modulates the motor programs according to the environmental conditions (Rybak et al., 2002).

The lower-level controller of rhythmic activities is often attributed to the Central Pattern Generator (CPG), a complex, distributed network of interneurons in the spinal cord (Duysens et al., 1998). It is thought that the CPG can generate rhythmic motor patterns to produce rhythmic activities with no need to rhythmic inputs from a higher-level controller, as well as sensory feedbacks from the peripheral nervous system (Grillner and Zangger, 1979). Nevertheless, it receives descending commands from the supra-spinal centers, to initiates the appropriate motor program, and interacts with the proprioceptive signals, which provide the necessary correction of the motor patterns to maintain the activity in a proper relationship to the environment (Rossignol et al., 1988).

The previous studies on the neural mechanisms involved in the control of rhythmic activities have often focused on the interplay between the CPG, reflex circuits, and feedback and feed-forward modulatory signals (McCrea and Rybak, 2008; Nassour et al., 2014). There are also several reports of CPG-based simulation of the neuromuscular interactions in simplified musculoskeletal models with a very limited number of muscle actuators and joints (Taga, 1995, 1998; Ogihara and Yamazaki, 2001; Markin, 2010). In order to control complex locomotor tasks, the CPG needs to provide coordinated motor patterns for a redundant system of muscle actuators,

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with a large number of highly nonlinear muscles, and several joints with many degrees of freedom. Moreover, it should account for the convolutions caused by bi-articular muscles and dynamic coupling between the body segments. Obviously, the control of locomotion through the interaction of the CPG with such complex musculoskeletal system is difficult and would need sophisticated models of the CPG and reflex circuity. There are a few recently published reports of such models, consisting of extended two-level CPG models and complicated neural reflex circuits, that allow for generating the complex activity patterns of nine single- or bi-articular muscles per leg during gait, using the length-sensitive spindle afferents of individual muscles and the foot-contact tactile information (Aoi et al., 2008; Markin et al., 2016).

In order to simplify the control of the musculoskeletal system by the central nervous system, a modular or hierarchical organization of motor control has been proposed by several researchers (Bernshteĭn, 1967; Berkinblit et al., 1986; Mussa-Ivaldi et al., 1994; Neptune et al., 2009; Allen and Neptune, 2012). In this approach, the activation levels of a number of co-active muscles, i.e., muscle synergies or modules, are considered as the basic neural control element. As a result, the control of the musculoskeletal system during complex activities is reduced into the control of a limited number of control elements, rather than each individual muscle. It has been shown that for locomotion, each of these modules is associated with one or more biomechanical subtasks, e.g., body support, forward propulsion and leg swing (Neptune et al., 2009; McGowan et al., 2010; Allen and Neptune, 2012). Furthermore, the activation patterns of muscles across a wide range of walking speeds, levels of body weight support and other combined movements have been explained by this modular organization (d'Avella et al., 2003; Ivanenko et al., 2005; Cappellini et al., 2006). It has been suggested that the relative consistency of the timing and composition of muscle activity comprising each module, regardless of the factorization algorithm used to identify the modules (Ivanenko et al., 2005; Cappellini et al., 2006; Tresch et al., 2006), provides confidence that the identified modules do indeed reflect the basic elements of neural control (Neptune et al., 2009).

The CPG-based neuromuscular control of the complex locomotor tasks can be obviously simplified if such modular or hierarchical organization of motor control is considered (Aoi et al., 2010, 2013). The objective of the present study was to investigate the feasibility of a simple CPG- and muscle synergy-based model for reproducing the complex activity patterns of the principal leg muscles during locomotion. A Matsuoka's four-neuron CPG model with mutual inhibition is utilized to generate the rhythmic activation patterns of four muscle synergies, with the hip flexion angle and foot contact force information from the sensory afferents as inputs. The EMG signals are recorded from eight lower extremity muscles of two subjects, during two gait trials each. The muscle synergies extracted from the EMG data of one trial are used to tune the parameters of the CPG. The predictions of the CPG model for the activation patterns of the leg muscles are then compared with the experimental results of the same trial, as well as those of the other trial and subject.

2. Methods

2.1. Experiments

Two healthy men (age, 24 and 28 yr; mass, 75 and 80 kg; stature, 178 and 180 cm) volunteered for the experiments. Subjects read and signed informed consent before participation and the procedures were approved by the university ethics committee. During experiments, reflective markers were fixed onto the subjects' anatomical landmarks, based on the guidelines described in Plug-in-Gait Marker Placement Protocol (Vicon Motion Systems, Oxford, UK). Also pairs of bipolar Ag-AgCl surface electrodes (1 cm^2 area) were attached bilaterally to eight muscles of each lower extremity, including soleus (SOL), tibialis anterior (TA), medial gastrocnemius (MG), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), gluteus maximus (GMax) and gluteus medius (GMed).

During the tests, the subjects were instructed to walk at the self-selected speed on a level surface, along a 10 m walkway. Five trials were recorded using a six-camera motion analysis system (Oqus, Qualisys, Gothenburg, Sweden), a force plate (Kistler Instrument AG, Switzerland) and a telemetry electromyograph (Myon, Switzerland), at a sample rate of 120, 240 and 1000 Hz, respectively. All measurements were synchronized using a trigger interface.

Among the recorded trials of each subject, two with the most complete data (with no missing markers and/or stepping off the force plate) were selected for analysis. The tracking data were filtered through a recursive low-pass digital Butterworth filter with a cut-off frequency of 4 Hz and the joints' kinematics were obtained based on Euler-Cardan method. The EMG signals were first high-pass filtered using a zero lag fourth-order Butterworth filter (40 Hz cut-off frequency), and then demeaned, rectified, and smoothed by a zero lag fourth-order low-pass (4 Hz cut-off frequency). Considering the sensitivity of the EMG signals to the external conditions such as electrode placement, skin impedance, and inter-subject differences, the EMG of each muscle was normalized against its highest value throughout the gait cycle, in order to become comparable for different trials and subjects. Finally, the EMG, ground reaction force, and kinematic data were time normalized to 100% of the gait cycle. All data processing was performed using a custom-made code in Matlab (Mathworks, Inc., Natick, MA, USA).

2.2. Extracting muscle synergies

The non-negative matrix factorization (NNMF) algorithm (Lee and Seung, 1999; Tresch et al., 1999), was employed to extract the muscle synergies during walking. At first, an EMG matrix (M_0) was constructed in which each vector represented the normalized activation data of one muscle during the gait cycle. The dimension of this matrix was $m \times t$, where m corresponded to the number of the muscles and t indicated the total number of EMG time samples during a gait cycle. The EMG matrix was then decomposed into a linear combination of the synergy patterns by using NNMF algorithm:

$$M_0 \approx W \times C \tag{1}$$

where W is a $m \times n$ matrix, representing the contribution of each of m muscles in each of n synergies, and C is a $n \times t$ matrix, expressing the activation timing of the n synergies. The multiplication of these two matrices, M_r, attempts reconstructing the muscle activations throughout a complete gait cycle. In NNMF, an optimization algorithm is utilized to minimize the sum of the square errors between M_r and M_0.

For implementing the NNMF algorithm, it was required to specify the number of the modules. In order to find the minimum number of modules that could reconstruct the muscle activations with sufficient accuracy, a trial-error procedure was employed. Starting from one module, the variability accounted for, VAF, of each muscle was determined as (Chvatal and Ting, 2013):

$$VAF = 1 - \frac{(M_0 - M_r)^2}{M_0^2} \tag{2}$$

The number of modules was considered adequate if the VAF of all muscles was larger than 90%, and that of the EMG matrix larger than 75%, throughout the gait cycle. It was found that four modules could reconstruct the muscle activation patterns during gait with sufficient accuracy, in agreement with previous studies (Neptune et al., 2009; Clark et al., 2010).

2.3. CPG modeling

The Matsuoka oscillator model (Matsuoka, 1985, 1987) was utilized to simulate the CPG's interaction with the musculoskeletal system, reduced into a four muscle synergy system (Fig. 1). The model was considered to be consisted of four neurons with mutual inhibition, a_{ij}, each belonging to a muscle module, M_i. The inputs of the model, u_i, were assumed to be constructed form the foot contact force and the hip flexion angle, to generate its outputs as the activation level of each synergy at each instant of the gait cycle.

The governing equations of the oscillator are as follows:

$$\dot{x}_i + x_i = \sum_i^j a_{ij} y_j + u_i - b_i f_i \quad (i = 1, \ldots, 4) \tag{3}$$

$$T_i \dot{f}_i + f_i = y_i \tag{4}$$

$$y_i = \max(0, x_i) \tag{5}$$

where x_i and y_i are the inner state and the output of the ith neuron, respectively.