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Adjustable primitive pattern generator: A novel cerebellar model for reaching movements

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Abstract

Cerebellum has been assumed as an array of adjustable pattern generators (APGs). In recent years, electrophysiological researches have suggested the existence of modular structures in spinal cord called motor primitives. In our proposed model, each "adjustable primitive pattern generator" (APPG) module in the cerebellum is consisted of a large number of parallel APGs, the output of each module being the weighted sum of the outputs of these APGs. Each spinal field is tuned by a coefficient, representing a descending supraspinal command, which is modulated by *i*th APPG correspondingly. According to this model, motor control can be interpreted in terms of the modification of these coefficients. Vector summation of force fields implies that the complex nonlinearities in neuronal behavior are eliminated, causing our model to be simple and linear. The force field vectors, derived from motor primitives, depend on the state of movement and its derivative and the time that causes different repertoire of movement. This is physiologically plausible. Our model agrees with virtual trajectory hypothesis, stating that dynamics are not computed explicitly in central nervous system, but the desired trajectory, is fed into the spinal cord. We think that the dysmetria and the ataxia seen in some cerebellar diseases may be the result of local disruption of some APPGs. Accordingly, determining the exact location of related motor primitives in human spinal cord and stimulating them by functional neurostimulation may provide a good management for these clinical signs. Surely, experimental researches and clinical trials are needed to validate our hypothesis.

Keywords: Reaching movement; Cerebellum; Modeling; Adjustable pattern generator, Motor primitive

Highly regular structure of the cerebellum has been in the core of attention in theoretical and computational modeling. In their primary models, both Marr [7] and Albus [1] predicted that motor learning occurs in the synapses of parallel fibers on Purkinje dendrites, which is mediated by concurrent climbing fiber inputs. However, the mechanism of climbing fiber's effect differed between these two models; Marr predicted the facilitation of synapses while Albus noted the inhibition. Experimental results suggest that synaptic inhibition is the mechanism of the learning, because otherwise synapses quickly become saturated.

Houk assumed the cerebellum as an array of adjustable pattern generators (APGs) [5]. Each APG generates an elemental burst command with an adjustable intensity and duration.

Other computational models have been proposed for the role of cerebellum in motor learning based on the internal models theory [10,11]. In these models, cerebellum is assumed to acquire an inverse model of the motor apparatus. These models are mostly discussed and applied in robotics.

In the last decade, electrophysiological researches on the spinal cord of frogs, rats, and cats suggested a modular structure in spinal cord that is the output stage of the motor system [2,4,6]. These modular structures are called "motor primitives".

The first section of this article deals with the early APG model of cerebellum as well as motor primitives. In the second section, we propose a novel and integrated model of cerebellum based on the APG model and motor primitives that we call it 'adjustable primitive pattern generator' (APPG). Finally, the advantages of the proposed model will be discussed.

In APG model, it is assumed that there are modules of APG in cerebellum that learn how to control the movements [5].

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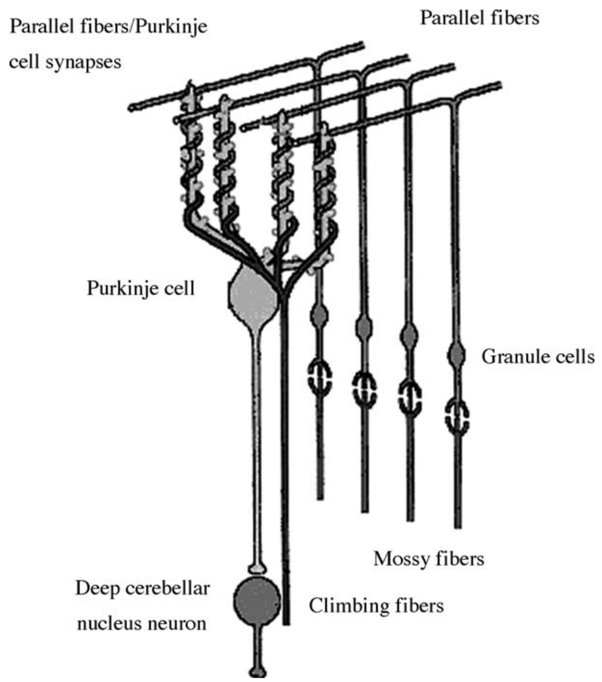

Fig. 1. The circuit of the cerebellar cortex.

Each module includes a positive feedback loop between a cerebellar nucleus cell (N) and a motor cortical cell. Each nucleus cell receives inhibitory input from a specific set of Purkinje cells (PCs). Each set of PCs receives a private climbing fiber training input originating from inferior olive, and a convergent input from an array of parallel fibers (PFs) which are the axons of the granule cells (GCs). GCs encode the sensory information received from the mossy fibers (Fig. 1).

The advantage of the APG model is its ability to explain the learning process during the reaching movement: at the beginning of a motor action, a positive feedback starts with sensory inputs to the motor cortex or red nucleus, thus causing the initiation of redundant elemental commands. The output of each APG eliminates the unnecessary commands and adjusts the intensity of the command. The termination of movement occurs when a large number of PCs fire strongly and cease the positive feedback.

In another work by Fagg et al. [3] it is supposed that each array of APGs drives a muscle synergy rather than a single muscle. Although this was a novel idea, but the synergies were supported by few physiological evidences and were invariant to time, state of movement, and gradient of states.

Some studies indicate that the electrical stimulation of the inter-neuronal circuitry in the lumbar spinal cord of frogs and rats impose a specific balance of muscle activation. Hence, motor primitives are modules assumed to be functional units in the spinal cord, generating a specific motor output by selecting a specific pattern of muscle activation.

An efficient result of these studies is that the simultaneous stimulation of two motor primitives results in vector summation of force fields arised from their separate stimulation [2,9]. Different levels of activation in each primitive cause different repertoire of movements.

The existence of primitives in the spinal cord suggests that there might be the same modular primitives in the higher neural centers such as cerebellum. It seems that the APG model is more consistent with the existence of these primitives in cerebellum,

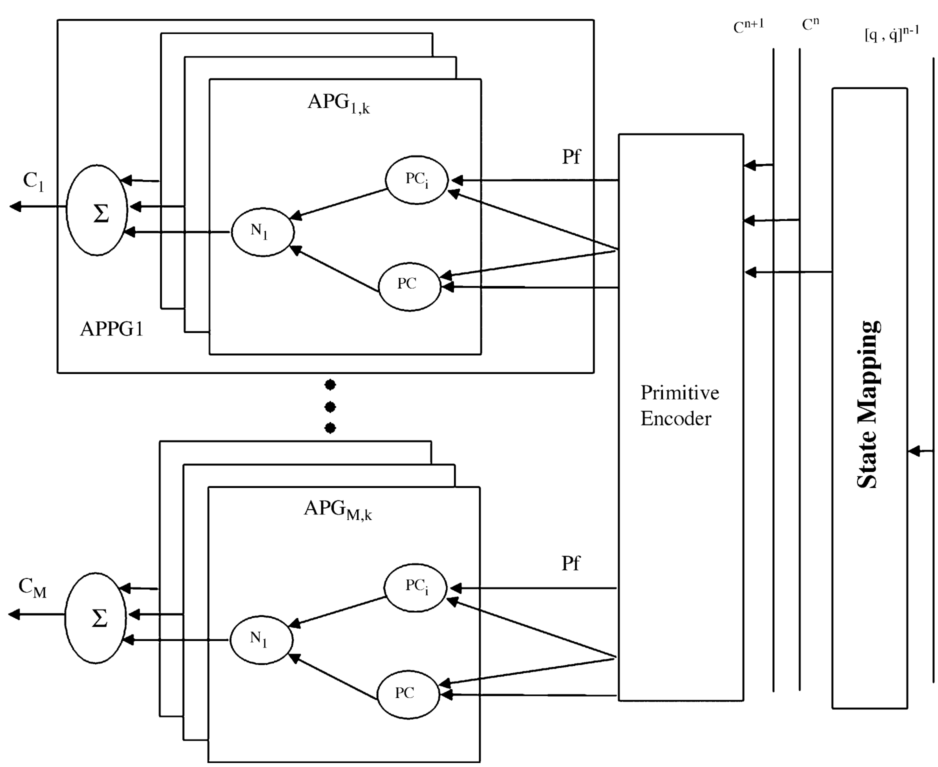

Fig. 2. The schematic representation of the proposed cerebellar APPG model.

because in this case, a set of parallel arrays of APG can drive each motor primitive module in the spinal cord. Therefore, in the proposed model, it is assumed that each APPG module is consisted of a large number of parallel units of APG, the output of each module being the weighted sum of the outputs of these APGs.

The fields generated by focal activation of the spinal cord are nonlinear functions of position, velocity and time, $\phi_i(q, \dot{q}, t)$. The torque function is obtained by superposition of spinal fields [8]:

$$\tau(t) = \sum_{i=1}^{k} c_i \phi_i(q, \dot{q}, t) \tag{1}$$

where $q, \dot{q}, \ddot{q}$ represent the limb configuration vector of joint angle and its first and second time derivatives, respectively. The term $\tau(t)$ is the vector of joint torque at time t. Each spinal field is tuned by a non-negative and scalar coefficient, c_i, representing a descending supraspinal command which is modulated by ith APPG correspondingly.

According to this model, motor control can be interpreted in terms of the modification of these coefficients. When cerebellar modules learn the appropriate coefficients, smoother movements will be generated.

Fig. 2 illustrates the scheme of our proposed model for cerebellar learning based on APPG modules. Primitive encoder represents the Granule cells, which provide cerebellum with sparse expansive encoding of the coefficients of primitives (c_i) from the spinal cord and motor cortex. A map transforms a low dimensional variable $q(t)$ into a multi-dimensional control signal; input of this transformation is the proprioceptive information of the motor apparatus and the output represents the mossy fiber. This process is performed in "state mapping" block shown in Fig. 2. The C^n represents the current coefficient of motor primitive that corresponds to the efferent copy of motor information coming from spinal cord to the cerebellum. C^{n+1} represents the information from motor cortex to the cerebellum (equivalent to next motor coefficient). $[q, \dot{q}]^{n-1}$ represents the proprioceptive information from the limbs (the previous state of the limb).

Vector summation of force fields eliminates the complex nonlinearities (the interactions both among neurons and between neurons and muscles), making the APPG a simpler linear model.

The force field vectors derived from motor primitives, depend on the state of movement and its derivative and the time that causes different repertoire of movement. This is more physiologically plausible and covers the movement planning with more degrees of freedom.

This model agrees with virtual trajectory hypothesis, stating that dynamics are not computed explicitly in central nervous system, but the momentary primitive coefficients (c_i), representing the desired trajectory, are fed into the spinal cord as motor commands. This will be straightforward and much simpler in comparison with internal models of movement control.

Some potential clinical benefits may be assumed for our hypothesis. As an example, it seems that the dysmetria and the ataxia seen in some cerebellar diseases may be the result of local disruption of some APPGs. Accordingly, determining the exact location of related motor primitives in human spinal cord and their selective stimulation by functional neurostimulation (FNS) may provide a good management for these clinical signs. Surely, experimental researches and clinical trials are needed to validate our hypothesis.

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