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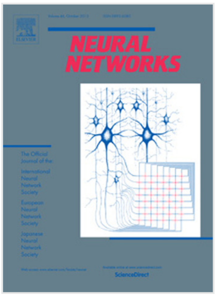

A theory of cerebellar cortex and adaptive motor control based on two types of universal function approximation capability

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A theory of cerebellar cortex and adaptive motor control based on two types of universal function approximation capability

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Abstract

Lesions of the cerebellum result in large errors in movements. The cerebellum adaptively controls the strength and timing of motor command signals depending on the internal and external environments of movements. The present theory describes how the cerebellar cortex can control signals for accurate and timed movements. A model network of the cerebellar Golgi and granule cells is shown to be equivalent to a multiple-input (from mossy fibers) hierarchical neural network with a single hidden layer of threshold units (granule cells) that receive a common recurrent inhibition (from a Golgi cell). The weighted sum of the hidden unit signals (Purkinje cell output) is theoretically analyzed regarding the capability of the network to perform two types of universal function approximation. The hidden units begin firing as the excitatory inputs exceed the recurrent inhibition. This simple threshold feature leads to the first approximation theory, and the network final output can be any continuous function of the multiple inputs. When the input is constant, this output becomes stationary. However, when the recurrent unit activity is triggered to decrease or the recurrent inhibition is triggered to increase through a certain mechanism (metabotropic modulation or extrasynaptic spillover), the network can generate any continuous signals for a prolonged period of change in the activity of recurrent signals, as the second approximation theory shows. By incorporating the cerebellar capability of two such types of approximations to a motor system, in which learning proceeds through repeated movement trials with accompanying corrections, accurate and timed responses for reaching the target can be adaptively acquired. Simple models of motor control can solve the motor error vs. sensory error problem, as well as the structural aspects of credit (or error) assignment problem. Two physiological experiments are proposed for examining the delay and trace conditioning of eyelid responses, as well as saccade adaptation, to investigate this novel idea of cerebellar processing.

Keywords: cerebellum, recurrent inhibition, threshold, spillover, mGluR2, timing

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1. Introduction

The book “The cerebellum as a neuronal machine” (Eccles et al., 1967) has promoted theories of the cerebellum. Eccles (1967) developed the idea that the cerebellum, which continually receives numerous diverse signals from receptors and cortical motor centers, performs “piecemeal and provisional integration” of the feedback information, and transmits the efferents to the integrational mechanisms of the spinal cord and to the cerebral cortex, which contain “corrective” information when a movement is “off target,” thus allowing the completion of coherent and smooth movements. In response to this idea, Marr (1969) and Albus (1971) independently proposed perceptron-type models, in which distinct roles are given to mossy fiber (MF) and climbing fiber (CF); signals of MFs from numerous receptors are discriminated to represent the context information of current movements, and if the cerebellar output (Purkinje cell) is incorrect, learning is accomplished under the supervisor signal of CF to achieve better movement performance.

Ito (1970) suggested a more concrete neural machine-like role of the cerebellum, a computer-aided feedforward control of movement, and outlined the “flocculus hypothesis” for the vestibulo-ocular reflex system. He further described an idea according to which cerebello–cerebral interactions are considered a reference model for adaptive control systems (Ito, 1970, 1984), which is consistent with the computationally developed concepts of internal forward models (Miall & Wolpert, 1996; Wolpert et al., 1998; Kawato, 1999; Lisberger, 2009). Ito et al. (1982) discovered the most prominent plasticity, the long-term depression (LTD) of synapses from parallel fibers (PFs) to Purkinje cells (PCs). Later, the presynaptically expressed long-term potentiation (LTP) of these synapses was found by Sakurai (1987) and the postsynaptically expressed one, which is exactly inverse to the LTD, was found by Lev-Ram et al. (2002). Fujita (1982) developed an adaptive filter model of the cerebellum by restructuring the perceptron-type Marr and Albus models to explain the results of VOR adaptation experiments, although it does not have a universal computational capability because of the hypothesized limited capacity of pre-filter subsystems in the Golgi–granule cell system.

Without adhering to concrete neural computation that the cerebellar cortex might perform, Kawato et al. (1987) proposed a computational approach to the role of the cerebellum in motor learning; the cerebellum plays the role of an inverse model of a controlled object and feedforwardly performs voluntary movement control by taking a desired trajectory signal. From this

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