Medical Hypotheses 81 (2013) 592–600

Contents lists available at SciVerse ScienceDirect

Medical Hypotheses

journal homepage: www.elsevier.com/locate/mehy

Are fast/slow process in motor adaptation and forward/inverse internal model two sides of the same coin?

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ARTICLE INFO

Article history:
Received 9 January 2013
Accepted 3 July 2013

ABSTRACT

Motor adaptation is tuning of motor commands to compensate the disturbances in the outside environment and/or in the sensory-motor system. In spite of various theoretical and empirical studies, mechanism by which the brain learns to adapt has not been clearly understood. Among different computational models, two lines of researches are of interest in this study: first, the models which assume two adaptive processes, i.e. fast and slow, for motor learning, and second, the computational frameworks which assume two types of internal models in the central nervous system (CNS), i.e., forward and inverse models. They explain motor learning by modifying these internal models.

Here, we present a hypothesis for a possible relationship between these two viewpoints according to the computational and physiological findings. This hypothesis suggests a direct relationship between the forward (inverse) internal model and the fast (slow) adaptive process. That is, the forward (inverse) model and fast (slow) adaptive process can be two sides of the same coin. Further evaluation of this hypothesis is helpful to achieve a better understanding of motor adaptation mechanism in the brain and also it lends itself to be used in designing therapeutic programs for rehabilitation of certain movement disorders.

Introduction

Motor adaptation is referred to modifying motor commands to compensate disturbances either in the external environment or in the motor system [1]. This adaptation mechanism may use prediction of action consequences or sensory information which enables us to perform accurate and robust movements [2]. Different computational models have been proposed for the mechanisms underlying motor adaptation. Computational models can help to understand complex biological data and also they are particularly useful in designing of new behavioral and neurophysiological experiments [3]. Although computational models have significantly improved our understanding of the mechanisms involved in motor adaptation, the architecture of these mechanisms has not been well understood [4]. This study considers two viewpoints of these models as follows:

1. The models considering two adaptive processes, i.e., fast and slow, for motor adaptation: most of the models of trial-to-trial motor adaptation proposed till 2006 had a single adaptation time constant. They could accurately predict motor responses to novel force fields and other forms of disturbance and quantify the patterns of generalization [5–8]. However, most of these models were unable to explain some of the observations such as the phenomenon of savings, spontaneous recovery, anterograde interference, rapid unlearning and rapid downscaling [1]. In 2006, Smith et al. [1] introduced a two-state model in which two processes provide motor output: fast process which learns strongly from performance errors and leads to a motor memory with poor retention (fast component), and slow process which learns weakly from performance errors and leads to a motor memory with good retention (slow component).
2. The computational frameworks including internal forward and inverse models in the CNS: these studies suggest that acquisition of a motor skill is probably obtained through learning an internal model of the task dynamics in the brain. It has been proposed that there are two types of internal models: Forward Models (FMs) which enable the CNS to predict the sensory consequences of motor commands, and Inverse Models (IMs) which produce motor commands to achieve a desired state.

To the best of our knowledge, relationship between these two viewpoints has not been investigated so far. In the following sections, the architecture, neural substrate, and other characteristics of the fast and slow adaptive processes are reviewed, the same

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http://dx.doi.org/10.1016/j.mehy.2013.07.009

characteristics of internal models are summarized and finally similarities between two viewpoints are collectively compared. We suggest that the forward (inverse) model and fast (slow) adaptive process might be two sides of the same coin. This article explains the basis of this hypothesis and reviews evidences that support this idea.

Hypothesis

Our hypothesis states that there are similarities between forward/inverse internal model and fast/slow adaptive process. It is proposed based on some of the existing theoretical and experimental studies which are investigated in the following sections.

Two state model and its characteristics

Savings is a fundamental property of memory which can occur in a motor adaptation task [9]. Some motor adaptation characteristics such as savings, anterograde interference, rapid unlearning, and rapid downscaling have not been explained by most of the models proposed for trial-to-trial motor adaptation. Smith et al. [1] were the first to present evidence that within a timescale of minutes, motor adaptation would be derived by two different processes: fast-learning–fast-forgetting and slow-learning–slow-forgetting. They proposed an innovative linear two-state model which was capable to explain the above mentioned motor adaptation characteristics. Some features of these two processes are reviewed in the following sub-sections.

Architecture

The following equations describe structure of the proposed model in [1]:

$$\begin{aligned} x_1(n+1) &= A_f \cdot x_1(n) + B_f \cdot e(n) \\ x_2(n+1) &= A_s \cdot x_2(n) + B_s \cdot e(n) \\ x &= x_1 + x_2 \\ B_f &> B_s, A_s > A_f \end{aligned} \tag{1}$$

where, subscripts *f* and *s* refer to fast and slow states; x_1 and x_2 represent two internal states and $x(n)$ is overall motor output in step n. A and B are retention and learning factors respectively. Holding the mentioned conditions insures different learning rates and retention capacities for the two states.

Different internal organizations can lead to the same input–output behavior. A possible architecture is parallel organization in which two learning components (fast and slow) independently adapt from error, and their outputs are combined to produce the overall motor output (Fig. 1a). Another possibility is a cascade organization in which error rapidly tunes the fast component, and then the slow component adapts using output of the first stage (Fig. 1b). A combination of behavioral experiments, neurophysiological and lesion studies are needed to clarify the real architecture of this system. Results of some experiments [10] suggested the cascade model while later on Lee and Schweighofer [4] evaluated different serial and parallel architectures of fast and slow processes by simulating motor adaptation in different experimental paradigms. They showed that the architecture in which a "one-state fast process" was parallel with a "multiple-states slow process", could describe all simulated data [4].

Neural bases

Another question is whether the fast and slow processes have different neural basis [11] or result from multiple time-scales in the synaptic plasticity of single neurons [12]. Achieved data in [2] proposed that fast and slow components of motor memory may be anatomically distinct from each other. Based on the observations reported by Medina et al. [10] during eye-blink conditioning in rabbits, Smith et al. [1] proposed that the cerebellar nuclei and cerebellar cortex may act similar to the slow and fast learning components, respectively. They also suggested that the learning components may also depend on other motor areas other than those of the cerebellum, e.g. the memory cells in motor cortex [1].

It has also been observed that application of anodal cerebellar tDCS (transcranial direct current stimulation) enhanced motor acquisition (movement error reduction was faster), but had no effect on retention. In contrast, applying anodal tDCS over M1 (primary motor cortex) had no effect on acquisition, but enhanced retention of the recently acquired visuomotor transformations [13]. These observations were also consistent with other studies [14,15]. Anodal direct current stimulation of cerebellum can augment cerebellar excitability [15] and increase the adaptation rate in a reaching task [13]. In a walking adaptation task, it has been shown that applying anodal tDCS over the cerebellum accelerates the adaptive process while cathodal cerebellar stimulation decreases the adaptation rate [16]. The idea of M1 involvement in the retention (but not the acquisition) of new motor memories has also been suggested in some other studies [17,18]. Considering terminology, fast (slow) process is possibly responsible for acquisition of motor memories (retention of newly acquired motor memories); therefore the results of the above mentioned studies confirm cerebellum (M1) involvement in fast (slow) adaptive process. These studies also provide more evidences that neural substrates of these processes are distinct.

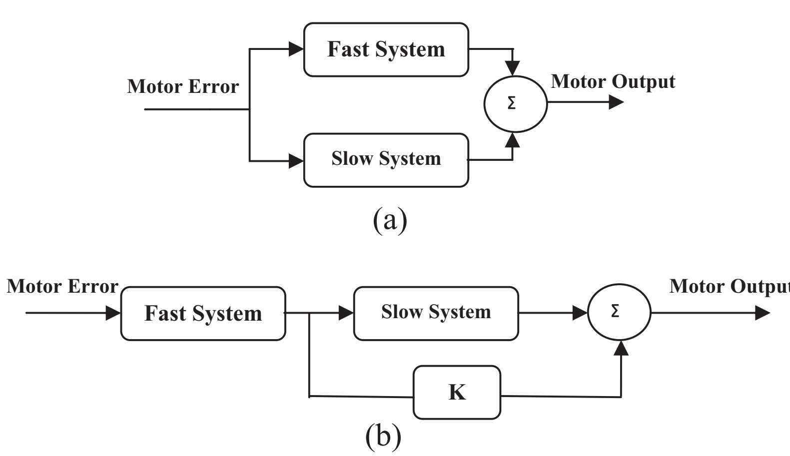

Fig. 1. Two possible realizations for the model with fast and slow internal states: (a) parallel and (b) cascade [1].