

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

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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.

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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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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.

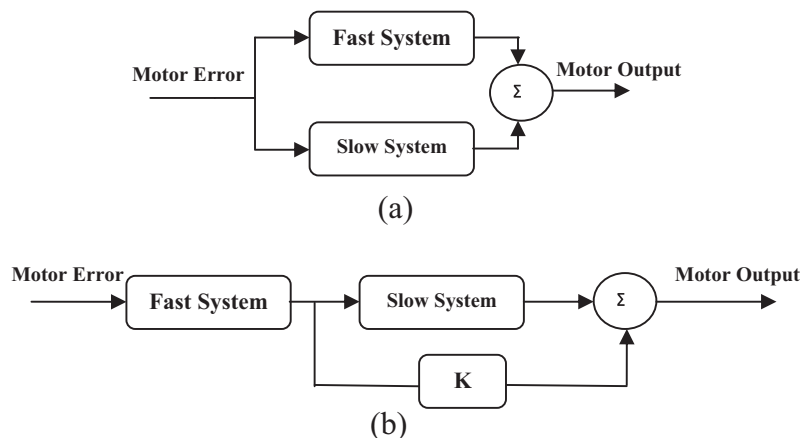


Fig. 1. Two possible realizations for the model with fast and slow internal states: (a) parallel and (b) cascade [1].

Theory suggests that fast process is preferentially employed when the motor system faces large errors (caused by abrupt perturbations) [2] which typically make subjects aware of the perturbations [19]. Also behavioral and functional imaging results have indicated that in the early phases of motor training (when fast component is dominant), high-level strategic, attentional, and working memory processes are active, but they are not involved in the later stages of motor adaptation [2]. This is consistent with the fact that except in the initial phase of practice, we are able to do a motor skill unconsciously [20]. There are related studies which compare learning performance in subjects using two types of perturbation introduction: gradual (producing small errors) and abrupt (producing large errors and awareness). These studies offer evidences about the independency of neural basis for adapting to gradual and abrupt perturbations which are supposedly related to the slow and fast process, respectively. Some of these studies are briefly reviewed in the following:

- It has been shown that patients with severe degeneration of the cerebellum have serious problems in motor adaptation during reaching movements in the presence of large, sudden perturbations (which engage fast process). But, when a gradually increasing perturbation with the same final amplitude was introduced during several trials (engaging slow process), the patients had obvious improvements in reaching movements [21,22].
- Kagerer et al. [23] applied a 90° visual feedback rotation to two groups of healthy subjects in two forms: gradual and abrupt. When subjects of gradual group reached the 90° rotation, they performed faster movement with less spatial error, and showed larger after-effects compared to the subjects who practiced under constant 90° visual feedback rotational disturbance.
- Gradual introduction of perturbation during adaptation to force fields, resulted a better retention [24,25] and different generalization patterns [19,25,26].
- It has been shown that adaptation to step (abrupt) and ramp (gradual) perturbations had different dependency on the cerebellum [27], e.g. in non-human primates inactivation of dentate nucleus, blocks adaptation to ramp (gradual) visuomotor distortion, whereas adaptation to step (abrupt) visuomotor perturbations was spared. Therefore, it seems that the lateral cerebellum may be involved selectively in adaptation to gradual but not abrupt distortions [27].
- Another recent report [28] found that adaptation to an abrupt perturbation during reaching movement changed cerebellar excitability; but these changes were not observed when the perturbations were introduced gradually.
- Based on the experiments in [29], it seems that people with hereditary cerebellar ataxia qualitatively do not have an initial fast-adaptive part, but the slow-adaptive component is more protected. This was observed in both adaptation and deadaptation phases of the task. They suggested that the cerebellar pattern could be an indicative of a specific deficit in faster process.

These studies and also observations in [2,21] suggest that neural substrate related to fast and slow components of motor memory are distinct and cerebellum plays an important role in the memory component generated by the fast process.

On the other hand some evidences suggest that M1 is involved in the slow component of memory. A number of these studies are summarized as follows:

- Some of neurophysiological studies have highlighted changes in the primary motor cortex (M1) during learning of force field or visuomotor rotation studies [30,31]. They have found that changes in M1 do not happen during the initial phase of

adaptation (i.e., when errors are large and the fast process is the dominant component). Instead these changes take place later, when performance errors are small (i.e., when the slow process drives motor output).

- Orban de Xivry et al. [32] observed that during adaptation to a force field, disruption of M1 using TMS (transcranial magnetic stimulation) did not affect the rapid adaptation stage; but reduced adaptation of motor commands at the plateau of performance error, i.e., when motor commands tend to repeat [32]. After some practice in a new environment, subject's motor performance becomes better and he/she learns to generate the appropriate motor commands for compensating the perturbation. Smaller trial-to-trial changes in motor commands results in more repetition. Considering the definition of fast and slow processes in [1], it can be concluded that after some practice, slow process is the dominant component in driving motor output. Therefore, the observations in [32] may suggest that M1 is the neural substrate for slow process.
- Muellbacher et al. [33] reported that stimulation of M1 using low-frequency, repetitive TMS immediately after practicing a thumb flexion task caused obvious retention deficits. This can be an evidence for the role of M1 in retention of newly acquired motor memories.

Generalization patterns

Another interesting observation about fast and slow processes is the generated generalization pattern. Motor memories resulted from fast process are effector-independent and can be generalized to untrained hand [34], while those produced by slow process are not [19]. In the study by Malfait and Ostry [19] it has been shown that when awareness of subjects about the perturbation was removed (e.g. by gradual introduction of the force field instead of abrupt), they could still learn how to compensate it; however no inter-limb transfer was observed. These results support effector-dependency of memories produced by slow process. Coordinate system of adaptation depends on how the perturbation is introduced. Abrupt presentation of a force field results in adaptation in an extrinsic coordinate system that can transfer to the other arm, suggesting that subjects learn something about the force field [19,34]. Gradual and implicit presentation of force fields cause adaptation in intrinsic arm coordinates that does not transfer to the other arm, suggesting that the internal model of the arm is adapted [19].

All the above properties about adaptive fast and slow processes are summarized in Table 1.

Internal forward and inverse models

It is now relatively well accepted that the CNS relies on some knowledge about the task and dynamical states of moving organ in the brain, called internal models. Based on current systemic view adopted from control engineering, these models are categorized as mechanisms that mimic (1) the input–output transformation of a body organ or a tool (internal forward models or predictors) [35–37], and (2) inverse of this transformation (internal inverse models or controllers) [38–42].

Some evidences for existence of forward models in human movement control were presented in [35,43]. These models have been used in motor learning [37,44], state estimation [35], and motor control [45–48]. Since forward model mimics the dynamics of the plant, it can be used to predict changes in the plant states (e.g. position and velocity) using an efferent copy of the motor commands. Existence of delayed feedbacks in a closed loop control system (e.g. delays in the neural pathways) can cause instability [39,49–51] (Fig. 2a). Using a forward model in control of

Table 1

Similarities between characteristics of FM (IM) and Fast (Slow) process. Results of some studies with the same view are summarized in each cell. Conclusion of the statements in each cell is shown in **bold**. Adjacent cells may have no direct relation. (Notations: \leftrightarrow is related to; \nleftrightarrow is not related to; **Related to FM or Fast Process**; **Related to IM or Slow Process**).

	Fast and slow processes	Internal forward and inverse models
Neural structure of each of two processes and internal models	<p>Based on the observations in [10], Smith et al. [1] proposed that the cerebellar nuclei and cerebellar cortex may act similar to the slow and fast learning components, respectively. Their function may also depend on other motor areas other than the cerebellum, for example the memory cells in motor cortex [1].</p> <p>cerebellar nuclei\leftrightarrowslow learning component</p> <p>cerebellar cortex\leftrightarrowfast learning component</p> <p>An enhancement of motor acquisition by anodal cerebellar tDCS and enhancement of retention by anodal M1 tDCS has been observed [13–15]</p> <p>M1 is involved in the retention (but not the acquisition) of new motor memories [17,18]</p> <p>Motor acquisition and retention are related to fast and slow learning components, respectively</p> <p>M1\leftrightarrowslow learning component</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>Adaptation to gradual visuomotor distortions and not sudden visuomotor perturbations is blocked by inactivation of the dentate nucleus [27]</p> <p>Theory suggests that slow process is preferentially employed when the motor system faces small errors (caused by gradual perturbations)</p> <p>Dentate nucleus (cerebellar nuclei)\leftrightarrowslow learning component</p> <p>Anodal tDCS over the cerebellum can increase the adaptation rate [13,16]</p> <p>Considering terminology, fast process is possibly responsible for acquisition of motor memories</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>Fast process is engaged when there are large errors that produce awareness about the perturbation [2,19]</p> <p>Patients with severe degeneration of the cerebellum have serious problems in adapting their motor commands during reaching movements in response to large and sudden perturbations [21,22]</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>Adaptation in response to an abrupt (and not gradual) schedule of perturbation produced changes in cerebellar excitability [28]</p> <p>Fast process is preferentially employed when the motor system faces large errors (caused by abrupt perturbations) [2]</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>Disruption of M1 using TMS did not affect the rapid adaptation stage; but reduced adaptation of motor commands at the plateau phase of adaptation, i.e., when motor commands tend to repeat. This phase could be related to slow learning component [32]</p> <p>M1\leftrightarrowslow learning component</p> <p>During the initial phase of adaptation (i.e., when errors are large and the fast process is the dominant component) there were no changes in M1. In contrast, changes in M1 happen in late phases, when performance errors are small (i.e., when the slow process drives motor output) [30,31]</p> <p>M1\leftrightarrowslow learning component</p> <p>Observations in [13,21] suggest that cerebellum plays an important role in the memory component generated by the fast process.</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>The cerebellar patients qualitatively do not have an initial fast-adaptive part, but the slow-adaptive component is more protected [29]</p> <p>Cerebellum\leftrightarrowfast learning component</p> <p>Stimulation of M1 using TMS immediately after practicing a thumb flexion task resulted in significant retention deficits [33]</p> <p>Considering terminology [1] slow process is possibly responsible for retention of newly acquired motor memories</p>	<p>Developmental damage or temporary disruption of the cerebellum impairs ability to accurately predict sensory consequences of motor commands (which is the function of forward model) [22,71,72].</p> <p>cerebellum\leftrightarrowforward model</p> <p>IF learning of forward models occurs in the cerebellum (and they are not the only way for learning the appropriate motor commands [22,69]), THEN there should be some cases in which damage to the cerebellum impairs learning of FMs and not IMs. A proof to this hypothesis is observation in [21]. During adaptation to a gradual perturbation people with cerebellar damage could generate approximately the correct motor output</p> <p>Cerebellum\leftrightarrowforward model</p> <p>Based on the results in [22], cerebellar patients and healthy subjects had comparable inverse models after adapting to a gradual disturbance. In contrast, their results suggested that cerebellum was critical for formation of forward models</p> <p>Cerebellum\leftrightarrowforward model</p> <p>Experiments by Nowak et al. [74] provide another evidence for importance of cerebellum in formation of predictor or forward model</p> <p>Cerebellum\leftrightarrowforward model</p> <p>Forward models are required to compute optimal motor commands [70] Some studies show that cerebellar patients are not able to produce optimal motor commands [21] Although in [32] it was observed that in spite of disruption of the motor cortex by TMS, subjects were able to compute the optimal trajectory to the target</p> <p>Forward model\leftrightarrowcerebellum</p> <p>forward model\leftrightarrowmotor cortex</p> <p>In over-trained monkeys, Purkinje cells in the cerebellar cortex code for kinematic (i.e., sensory state, the same space as output of the forward model) and not dynamic information (i.e., muscle commands causing muscle tensions, the same space as the output of the inverse model) [29,75] In contrast, cells in the motor cortex and other frontal motor areas show strong sensitivity to task dynamics [17,76]</p> <p>Cerebellum\leftrightarrowforward model</p> <p>motor cortex\leftrightarrowinverse model</p> <p>In [77] it was suggested that neural computation of mapping from desired sensory states of arm to the required force (i.e. the inverse model), was implemented using a set of bases whose properties were consistent with the activity fields of cells in the motor cortex and the cerebellum</p> <p>Motor cortex and the cerebellum\leftrightarrowinverse model</p> <p>Observation of task related (dynamic or muscle-like) cells in M1 [76,77].</p> <p>M1\leftrightarrowComputing the internal model</p> <p>Assigning feedback gain to the proprioceptive states by primary motor cortex and mapping the internal belief about states into motor commands [70].</p> <p>Primary motor cortex\leftrightarrowsensorimotor mapping from internal belief about states into motor commands (similar to definition of inverse model)</p> <p>Some researchers have suggested the cerebellum as an inverse model which generates the motor commands [62,67,68].</p> <p>Cerebellum\leftrightarrowInverse model</p> <p>Significant activation levels changes were observed in visuomotor areas of the lateral and vermal cerebellum in an eye–hand tracking task. Since the coordination between the eyes and the hand in the examined task was dependent on forward model, the changes in cerebellum activity could represent a predictive signal [73]</p>

(continued on next page)

Table 1 (continued)

	Fast and slow processes	Internal forward and inverse models
Effector-independency/ dependency of learning	M1↔slow learning component Motor memories resulted from fast process are effector-independent and generalized to untrained hand [34] unlike those produced by slow process [19]	Lateral and vermal cerebellum↔forward model Information about novel forces acquired via observation is represented in an effector-independent coordinate framework [81] Effect of movement observation on motor performance improvement might be through modification of forward models [95] Viewing hand movements in a visuomotor rotation paradigm will change perceived location of the arm [84]. This could also be a result of change in forward model
Conscious performance of actions	Fast process↔Effector-independent slow process↔Effector-dependent Fast process is preferentially employed when the motor system faces large errors (caused by abrupt perturbations) [2] which typically make subjects aware of the perturbations [19]	Change in a forward model↔Effector-independency of motor learning by observation During initial stages of skill learning, the cerebellum develops a forward model which provides predictions related to rapid, skilled movements at a conscious level [78,79]. y continuing practice, the inverse control model is established and the behavior can be performed without conscious input [12]
Adaptation rate	Fast process↔awareness of the perturbation Fast Adaptive process precedes the slow one [1]	Inverse model↔automatic movements & after continuing practice forward model↔conscious level & initial phase of learning Forward model adapts approximately five times faster than inverse model when there are very large errors in performance [50] The acquisition of forward model precedes learning of the inverse model (motor controller) [54,60,61].

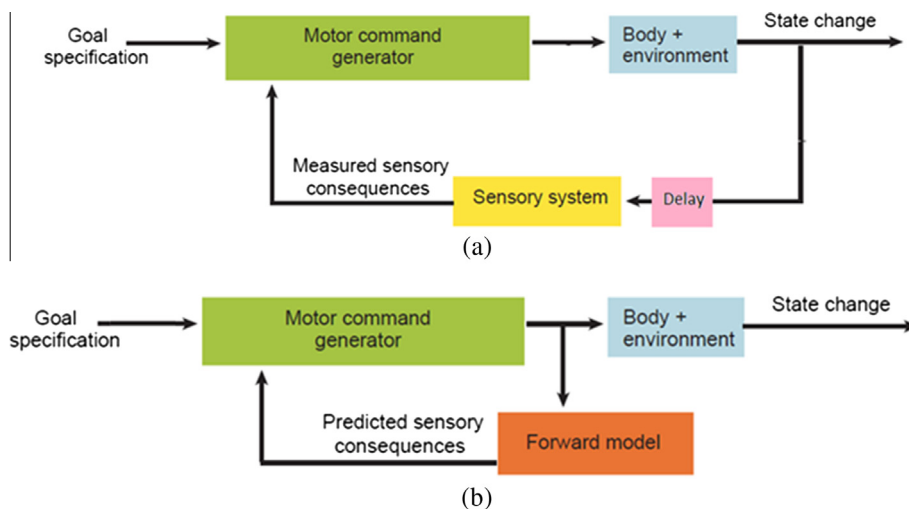


Fig. 2. Comparison between closed-loop control systems with and without forward model. (a) Delays in the neural pathways of sensory feedback can make the closed loop control system unstable. (b) A forward model predicts the consequences of motor commands with no delay and eliminates the threat of system instability (this figure is a modified version of Fig. 1.1 in [53]).

movements, which predicts the consequences of motor commands with no delay, eliminates this threat [29,35,46,51,52] (Fig. 2b).

The inverse model is an inverse mapping of the plant's input–output relationship. This model transforms desired states of the plant into motor commands and therefore can be directly used as the controller in the forward (input to output) path (Fig. 3).

In the following sub-sections some features of FMs and IMs are explained.

Architecture

To study that whether the CNS may employ just one of these internal models or both, Bhushan and Shadmehr [50] investigated

a number of control systems with different architectures using a human arm model as the plant. Some dynamical features of subjects' movements were compared to those of simulated systems. They found that dynamics of control architecture with both forward and inverse models (rather than just one of them) was remarkably similar to that observed in their experimental data. Co-existence of internal forward and inverse models has also been proposed by other researchers [39,48,54–59]. For example, Kawato [39] suggested a framework containing both types of internal models to explain some human movements including arm reaching movement while holding an object in hand. An efferent copy of the arm motor command (i.e., inverse model output) was used as

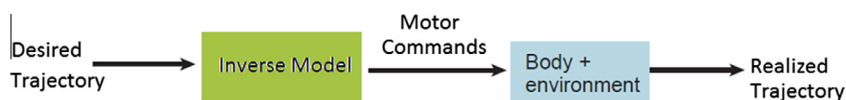


Fig. 3. Inverse model as controller in series with the plant (this figure is a modified version of Fig. 1 in [39]).

the input to the forward model to predict the arm movement in advance. Thus subjects could generate appropriate motor commands for the hand to grab the object precisely.

Rate of adaptation

Bhushan and Shadmehr [50] also estimated adaptation rates of the forward and inverse models using data collected from human subjects. They showed that adaptation of forward model was approximately five times faster than inverse model in presence of very large performance errors [50]. This is in accordance with other studies which suggest that forward model acquisition is faster than the formation of the motor controller (inverse model) [54,60,61].

Neural bases

The neural structures involved in the formation of internal models have not been known clearly; some computational studies proposed that adaptation is achieved by modifying internal models within the CNS and specifically within the cerebellum [35,62–64]. Involvement of cerebellum in motor adaptation has also been shown in various experimental studies. Individuals with cerebellar damage have adaptation problems in reaching, walking, and eye movements [21,29,65,66]. However it is not clear whether forward or inverse models are formed in cerebellum during motor adaptation. Some researchers suggest that the cerebellum acts as an inverse model and generates the motor commands [62,67,68], while others suggest it as a forward model or predictor [22,35,36,69,70]. On the other hand, there are evidences that both kinds of internal models are probably formed in the cerebellum [54].

Here some studies about the cerebellum role in forward models and involvement of M1 in inverse models are reviewed:

- Developmental damage or temporary disruption of the cerebellum impairs ability to accurately predict sensory consequences of motor commands (which shows a problem in forward model function) [22,71,72].
- If forward models are formed in the cerebellum and they are the only way for learning the appropriate motor commands [22,69], then, at least in some cases, damage to the cerebellum should only impair the learning of FMs. In contrast it should have no effect on the ability to learn the correct motor commands. Observations in [21] confirm this idea. Patients with cerebellar damage were able to generate approximately the correct motor output in adapting to a gradual perturbation [21].
- Miall and Jenkinson [73] have done an fMRI study on subjects who performed an eye–hand tracking task. They reported significant changes of activation levels in visuomotor areas of the lateral and vermal cerebellum. They suggested that coordination between the eyes and the hand in the examined task was dependent on an internal forward model (predictor). Therefore, changes in cerebellum activity could represent a predictive signal used for error correction.
- Izawa et al. [22] designed an experiment to see whether the cerebellum is involved in the learning of forward or inverse models. They compared performance of cerebellar patients and healthy control subjects in a reaching task. In order to provide a condition in which both groups could adapt to the disturbance, a gradual visual perturbation was applied. They designed two innovative tasks to discriminate effects of forward and inverse models. Based on the results, they concluded that patients and healthy subjects had comparable inverse models. On the other hand, the cerebellum seemed to have a critical role in the formation of forward models and prediction of sensory consequences of motor commands.
- A simple experiment was used by Nowak et al. [74] to investigate the role of cerebellum as forward model. Subjects grabbed a force transducer (while a basket was hanged from it) to mea-

sure grip force. One subject was a patient with no cerebellum. A ball was dropped in the basket by the experimenter or by subject himself. When experimenter dropped the ball both healthy group and the patient showed comparable delayed responses. In contrast, when the subject dropped the ball himself, healthy individuals anticipated correct time of increase in downward force caused by ball impact. On the other hand, the cerebellar patient was unable to make the same anticipatory adjustment. This experiment highlights importance of the cerebellum in formation of predictor (forward model).

- Experiments showed that the cerebellar damage impairs adaptation to kinematic [29] and force [66] perturbations. One way to explain these observations is to assume that internal forward models are located in the cerebellum [70].
- Theoretically accurate forward models are required to compute optimal motor commands [70]. Some studies show that cerebellar patients are not able to produce optimal motor commands. In [21] it was found that the severely affected cerebellar patients were unable to optimize their adaptive response in the presence of either step or ramp perturbation. On the other hand, it was observed that in spite of disruption of the motor cortex using TMS, subjects were able to find the optimal trajectory to the target [32].
- Based on their definition, outputs of the forward and inverse models are in the sensory state space and the muscle commands space, respectively [29]. Considering the evidence proposed by a neurophysiological study, Purkinje cells in the cerebellar cortex of over trained monkeys code for kinematic (i.e., sensory state) and not dynamic (i.e., muscle commands causing muscle tensions) information [75]. However, cells in the motor cortex and other frontal motor areas show strong sensitivity to task dynamics [17,76]. These are in accordance with the idea of computing forward model in the cerebellum and inverse model in the motor cortex.
- In [77] it was suggested that neural computation of inverse model (mapping from desired sensory states of the arm to the required force) was implemented using a set of bases. Based on the patterns of generalization, they extracted some properties of these bases. These properties were consistent with the activity fields of cells in the motor cortex and the cerebellum [77].
- It has been observed that there are task related cells (so-called “dynamic” or “muscle-like”) in M1 region of monkey’s brain which are sensitive to changes in force properties of the task [77]. These findings suggest that M1 is involved in motor learning [76] and perhaps computing internal models.
- Based on optimal feedback control theory, having the belief about the state of human body and the world, we need to find the optimal gains of the sensorimotor feedback loops in a way that some measure of performance is maximized. It has been suggested that the primary motor cortex is responsible for regulating these “feedback gains” in order to have a proper sensorimotor map for transforming the internal belief about proprioceptive states into motor commands [70]. This is similar to the definition of inverse model.

Some other characteristics of internal models

Up to now adaptation rates and neural bases of internal models have been discussed. Before explaining our hypothesis, here some other related characteristics of internal models are reviewed:

- Interesting findings have been proposed about conscious performance of voluntary movements during learning a new motor skill. In the initial stages of this learning, a forward model may be developed in the cerebellum. Behavioral predictions generated by this model are related to rapid skilled movements at a conscious level [78,79]. By continuing practice, the inverse

model is established and the behavior becomes automatic. The more someone practices, the more the behavior falls under automatic control. In this condition behavior can be performed without conscious thought. In contrast, less-skilled subjects likely use less well-developed inverse model and must rely more upon forward models [80].

- In 2012 Williams and Gribble [81] performed a study to test whether motor learning by observation was effector dependent or not. In their experiments, subjects observed reaching movements made by right or left arm in a force field. Their performance improved after watching either of these two movements. The results suggest that information about novel forces acquired via observation was represented in an effector-independent coordinate framework.

The motor performance improvement via action observation or imagination can be explained using a theoretical framework based on internal models. When someone imagines executing a motor task, FM can be used as the plant (controlled object) in a closed loop control structure. The internal feedback from FM improves inverse model formation and consequently the performance [20,82]. Some investigators [37,49,83] suggested that learning a FM of a nonlinear plant and then using it in inverse model adaptation, might facilitate controller tuning.

An explanation about how action observation can lead to improvement in motor performance is as follows: when someone watches another person's movement, he/she predicts next state using his/her internal forward model and the current observed state. This prediction is compared with the actual observed state at the next time step and results in an error signal that can be used to modify the forward model. Results in [84] are in accordance with this idea. It has been observed in some studies that training in a visuomotor rotation paradigm causes a shift in the perceived state of the arm [84–86]. Cressman and Henriques [84] also demonstrated that even by passively viewing hand movements in a visuomotor rotation paradigm, perceived location of the arm will change. Two different reasons have been proposed for these observations: (1) changes in a forward model [85] and (2) proprioception recalibration [84]. Therefore, our idea about FM modification as a result of action observation seems to be logical and the finding in [84] might be explained as a result of forward model adaptation:

- As mentioned above, effector-independency (dependency) of adaptation suggests that subjects learn something about the manipulated tool (arm) [19,34]. It has been also observed that at the beginning of learning, motor skills are non-effector-specific, but when the learning is improved, they become increasingly effector-specific [2]. A possible explanation based on internal models for these observations is that in the initial phase of learning, a forward model of the manipulated tool (e.g., the robot imposing the force field) is learned. This model can be used during performing movements with the same tool by other effectors. Later in training, an inverse model (controller) is formed which is effector specific and therefore cannot be used in other situations. This might explain effector dependency with continued training. It could also be a reason for the finding in [81]; i.e., there might be a relationship between modifying forward model by action observation – explained earlier – and effector-independency of learning by action observation [81].
- It has been proposed that during reach adaptation, motor output is changed by two components [24,87]: one is caused by repetition, and the other depends on the sensory prediction errors. First component reminds FM characteristics, e.g. similar to the output of FM, sensory prediction errors are also in

the sensory states space and therefore are appropriate as teaching signals for adaptation of forward models [29]. Motor learning using prediction errors is dependent on the integrity of the cerebellum [10,66,88,89]. The idea that sensory prediction errors drive cerebellar adaptation is supported by theoretical, neurophysiological, and behavioral studies [54,89,90]. Thus, cerebellum and forward models might have a key role in the component driven by sensory prediction errors. On the other hand, regarding the second component recent motor learning studies have presented evidences in accordance with the possibility of learning a specialized inverse model through repetition [87,91,92]. It was also hypothesized that use-dependent learning may only depend on the local changes in cortical motor areas such as primary motor cortex [87], which is also a candidate neural structure for temporary formation of IMs [68].

The reviewed characteristics and findings about internal forward and inverse models are summarized in Table 1.

Consequences of the hypothesis

This article reviewed some properties of adaptive fast and slow processes contributing in motor output and then some related observations and ideas about internal forward and inverse models. To the best of our knowledge, the relation between internal models in brain and fast and slow adaptive processes has not been investigated so far. For more clarity, similarities between these two research lines were summarized in Table 1. Our hypothesis is that there might be a tight relationship between forward (inverse) model and fast (slow) process. More investigations and experiments are required for further validation of this hypothesis.

The proposed hypothesis can be helpful to achieve a better understanding of motor adaptation mechanism in brain. This knowledge can have possible applications in diagnosis and treatment of movement disorders induced by brain lesions, designing therapeutic programs for patient rehabilitation, and also in medical research.

For example there is no effective drug or rehabilitation process which can help cerebellar patients. Considering the concept of FM/IM and fast/slow process, rehabilitation programs might be designed more effective and specific.

Current strategies to enhance motor function after brain and spinal cord injury are not quite satisfactory for example motor recovery of more than 30% of stroke patients was not perfect after the rehabilitation process [93,94]. Performance improvement can be augmented using proper motor training, and also targeting the mechanisms underlying brain plasticity using noninvasive brain stimulation methods such as TMS and tDCS. However, without more understanding of mechanisms involved in learning and control of voluntary movements, motor adaptation and motor recovery, this improvement is hardly achievable. This knowledge can be helpful in refinement of existing rehabilitation strategies and designing new methods.

Another potential application can be in medical researches such as investigating the effects of pharmacologic intervention in the brain. One possible method to investigate how/which specific regions of brain are influenced by the medication, is through designing special motor experiments based on the proposed concepts and analyzing performance of subjects.

Conflict of interest statement

None.

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