A NEW COUPLING SCHEME OF CEREBELLAR INTERNAL MODELS: ONLINE AND OFFLINE ADAPTATION IN PROCEDURAL TASKS

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ABSTRACT
The cerebellum plays a major role in motor control. It is thought to mediate the acquisition of forward and inverse internal models of the body-environment interaction [1]. In this study, the main processing components of the cerebellar microcomplex are modelled as a network of spiking neural populations. The model cerebellar circuit is shown to be suitable for learning both forward and inverse models. A new coupling scheme is put forth to optimise online adaptation and support offline learning. The proposed model is validated on a procedural task and the simulation results are consistent with data from human experiments on adaptive motor control and sleep-dependent consolidation [2,3]. This work corroborates the hypothesis that both forward and inverse internal models can be learnt and stored by the same cerebellar circuit, and that their coupling favours online and offline learning of procedural memories.

KEY WORDS
Cerebellum, inverse, forward, internal models

1. Introduction

It is largely admitted that the cerebellum plays a major role in motor control (e.g. coordinating movements and making them accurate) by acquiring internal models of the body and the world [1, 4]. In motor control theory, internal models are divided into two groups identified as forward and inverse. The forward model predicts the sensory outcome of an action: it estimates the causal relationship between inputs to the system and its outputs. The inverse model works in the opposite direction, providing a motor command that causes a desired change in state [5]. Both forward and inverse models depend on the dynamics of the motor system and must adapt to new situations and modifications of the motor apparatus [6].

Although Darlot et al. (1996) [7] suggested that a forward model could be first formed in the cerebellar cortex and then converted to an inverse model, most of the existing studies on bioinspired control architectures have compared the advantages of one type of internal model against the other, debating on which of them is most likely to be implemented in the cerebellum [8, 9]. Very few works have investigated the benefits of coupling internal models [10,11], and none has underlied the fact that internal model coupling would endow the system with offline learning capabilities. This is quite surprising, given that sleep is known to contribute to offline consolidation and enhancement of motor adaptation capabilities in humans [12], and that the cerebellum is undoubtedly implied in these adaptation processes [13].

This paper proposes a novel scheme to couple internal cerebellar models. The model is primarily validated on a closed-loop architecture to control the dynamics of a robotic arm. The overall coupling model is depicted in Fig. 1a, whereas the offline functioning of the learning scheme is presented in Fig. 1b, under the assumption that the sequence of actions performed during online training can be replayed offline.

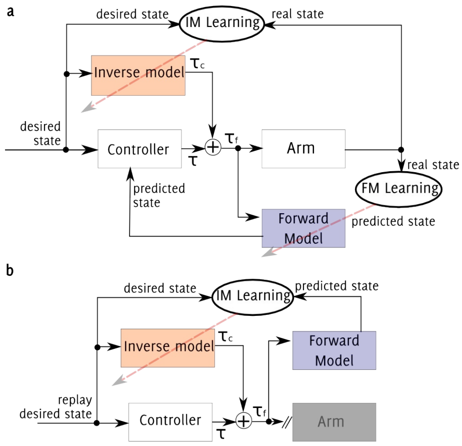

Fig. 1. *Coupling scheme for online and offline motor learning.* (a) Online adaptation. The arm controller receives the desired state and maps it onto a motor command (τ). The desired state is also sent to the inverse model that acts as a feed-forward corrector and calculates the motor correction (τ_c). The resulting command (τ_f) is then sent to the arm actuators. By comparing the desired state against the sensed real state, the inverse model learns to reduce the error between desired and real arm positions. While the motor command τ_f is being sent to the arm, an efference copy of the order is also conveyed to the forward model that learns to predict the consequent future position of the arm. The predicted state is then sent to the arm controller that can recalculate a new trajectory if the expected position in the trajectory differs from the predicted one. Finally, the real state is used to adapt the forward model to mimic the motor apparatus of the arm. (b) Offline adaptation. During offline processing, sensory feedbacks (i.e. the real state signals driving forward and inverse model learning) are not available. Yet, if the forward model is at least partially learnt, the predicted state signals can be used to continue to train the inverse model.

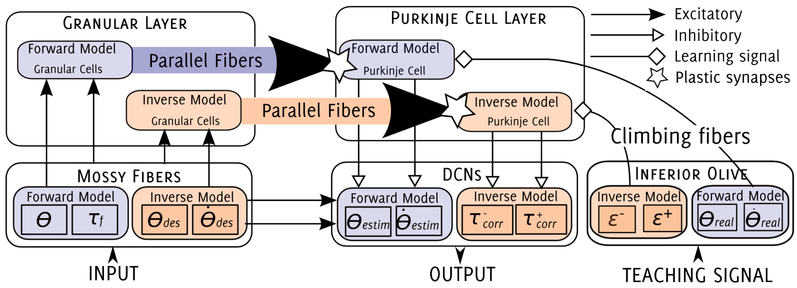

Fig. 2. *The cerebellar microcomplex model.*

The hypothesis of an offline replay relies on earlier animal investigations that have explored the possibility that patterns of brain activity which are elicited during initial task training are replayed during subsequent sleep [14]. The model is assessed on the rotation adaptation task used by Huber et al. (2004) [3] to study motor learning (both online and offline) in humans. Our numerical simulations investigate the benefits of using both internal models to improve online learning capabilities, and they evaluate to what extent the proposed coupling scheme can explain the experimental findings on offline learning occurring during sleep [3].

2. Methods

2.1 Cerebellar microcomplex model

The cerebellar microcomplex circuit is modelled as a network of populations of spiking neurons (Fig. 2) and simulated using an event-driven simulation scheme [15]. Mossy fibres (MFs) are implemented as axons of a population of 1600 leaky integrate-and-fire neurones separated in two regions: Forward and Inverse Model, FM and IM, respectively. Their driving currents are determined by using radial basis functions spanning the input space uniformly. The MFs of the forward model carry sensory information and an efference copy of the motor command. The MFs of the inverse model convey desired joint position and velocity [16]. Each MF region activates a corresponding population of 200 neurones in the deep cerebellar nuclei (DCN). Also, each MF region projects onto a cluster of 10.000 granule cells (GCs), producing a sparse representation of the input space. Each GC subpopulation activates in turn a population of 200 Purkinje cells (PCs), which send inhibitory projections onto DCN neurones. The firing of DCN provides the outputs of the model, i.e. the forward model estimate the future state of each joints and the inverse model correction to be sent to the system. The firing rate of DCN units is mainly determined by the inhibitory action of PCs, which in turn are principally driven by the parallel fibre (PF) activity, axons of the GCs. Therefore, modifying the strength of the synapses between PFs and PCs results in changes of the input-output relation characterising the cerebellar system. Bidirectional long-term plasticity (i.e. potentiation, LTP, and depression, LTD) is modelled at the level of PF-PC synapses (see fig. 2, plastic synapses).

2.2 Procedural adaptation task

The simulated task is inspired from the rotation adaptation task realized by Huber et al. (2004) [3]. In this task human subjects have to move a handheld cursor on a two-dimensional tablet from a central starting point to one of eight targets displayed on a computer screen together with the cursor position. An opaque shield prevent subjects from seeing their arm. Targets are randomly highlighted at regular 1-s intervals. Unbeknown to the subjects, the cursor position is rotated anticlockwise relative to the hand position by a fixed angle (from 15 to 60°, depending on the trial, see details below).

We simulate the rotation adaptation experiment in order to study the possible role of internal model coupling for online learning and offline consolidation. The global architecture of the simulated arm controller is detailed in Fig. 3.

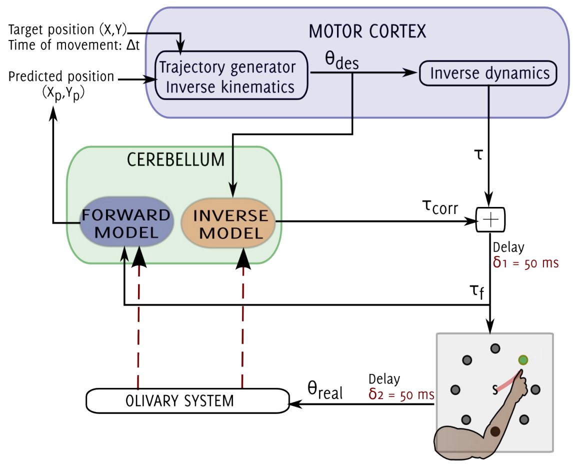

Fig. 3. *Functional diagram of the controller.* A desired trajectory to the highlighted target is computed by the trajectory generator and transformed in the joint-related reference frame via the inverse kinematics model. These desired arm states are used at each time step to compute a crude torque command. The desired state is also sent to the inverse model of the cerebellum, whose output is a corrective command to control arm movements. The cerebellar forward model receives an efference copy of the motor command, and predicts the future state (position and speed) and sends it to the trajectory generator. In the coupling scheme, both internal models drive the system. Trajectory error is sensed at the level of the limb and sent back to the system, which is used to compute the training signal at the olivary system level and conveyed by the climbing fibres to both internal models.

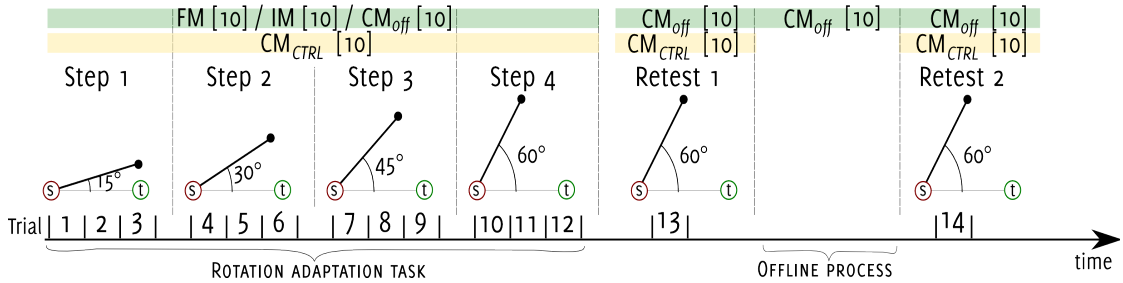

Fig. 4. *The protocol of the rotation adaptation task and the offline learning task.*

The simulated experimental setup consists of a central position S and eight targets evenly distributed on a circle centred at position S (Fig. 5). A trial is defined as the succession of 90 movements. Each movement starts from S and consists in realising a movement of the arm to one of the eight targets, which is randomly changed every second (1s corresponds to the duration of one target-directed movement in our simulation).

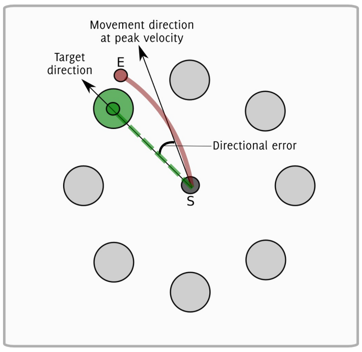

Fig. 5. *Experimental task and calculation of error.* S: Starting point; E: Ending; Green dashed line: Ideal movement towards the target; Red line: actual movement.

Similar to Huber et al. (2004) [3], the experimental protocol involves four incremental steps, for each of which the angular deviation (bias) is increased by 15°, within the range [15°, 60°] (see Fig. 4). Every step is composed of three trials. Three groups (FM, IM, CM_{off}) of ten individuals each are trained on the rotation adaptation task.

The FM group uses a pure forward model to solve the task. The IM group employs a pure inverse model to adapt the response to the unknown angular bias. The CM_{off} group uses the coupling scheme.

Following the four training steps, the extent of rotation adaptation of the CM_{off} group is tested using an imposed bias of 60° (Trial 13 in Retest 1). Then, simulated agents are enabled to undergo an offline consolidation process consisting of a series of 48 trials. Subsequently, subjects are retested on a simple trial (Trial 14, retest 2). To assess the benefit of an offline consolidation process against a pure online learning, performances of the CM_{off} group are compared to a group of control subjects (CM_{CTRL}) which does not perform offline consolidation. Performances are measured by quantifying the directional error (see Fig. 5), which corresponds to the angle between the line from the initial hand position (S) to the central position of the target (T) (dotted green line) and the line to the position of the hand at the peak outward velocity (solid line).

3. Results

3.1 Online adaptation

Figs. 6a,b show the learning performances of the three groups FM, IM, and CM_{off} during the online training sessions (i.e. step 1-4, trial 1-12) of the rotation adaptation task. Fig. 6a displays three examples of arm trajectories towards three different targets.

It shows qualitatively that, at the end of the trial 6, subjects using the coupling scheme (CM_{off} , green solid line) tend to perform better than both subjects using the inverse model only (IM, red dashed line) and subjects using the forward model only (FM, blue dotted line).

Fig. 6b quantifies these results for the entire set of training trials by averaging over all subjects. The mean normalised directional error is plotted as a function of training trials. The three groups of subjects learn to solve the rotation adaptation task and cope with the increasing unknown angular bias (from 15° to 60°) over training steps. Forward model subjects (FM, blue dotted curves) adapt quite rapidly but they reach a plateau after the 2nd trial and do not further reduce the error over training. The passage to a new step (i.e. trials 4,7 and 10) does not have a significant impact on the FM performances and leads to a small increase of the directional error (+8% between trial 3 and 4; +6% between trial 6 and 7; and +2% between trial 9 and 10), which reflects the fast learning capabilities of FM subjects. However, subsequent training trials do not significantly decrease the error, which stabilises around 0.45-0.5 until the end of the training process (trial 12).

On the other hand, inverse model subjects (IM, red dashed curves) are slightly slower to adapt than FMs, but they succeed in minimising the directional error within each training session, going beyond the performances of purely FM subjects. Adaptation of IM subjects is rather characteristic and stereotyped during steps 2, 3, and 4 (i.e. for angular deviation ranging from 30° to 60°). Every time the angular bias is increased (i.e. trials 4,7 and 10), the performances of the inverse model are impaired and directional error increases (between 0.43 and 0.47). This result reflects the slow adaptation capability of the inverse model when facing new contexts. Then, during the 2nd and 3rd trials of each step, the inverse model adapts properly and the directional error decreases significantly (converging to

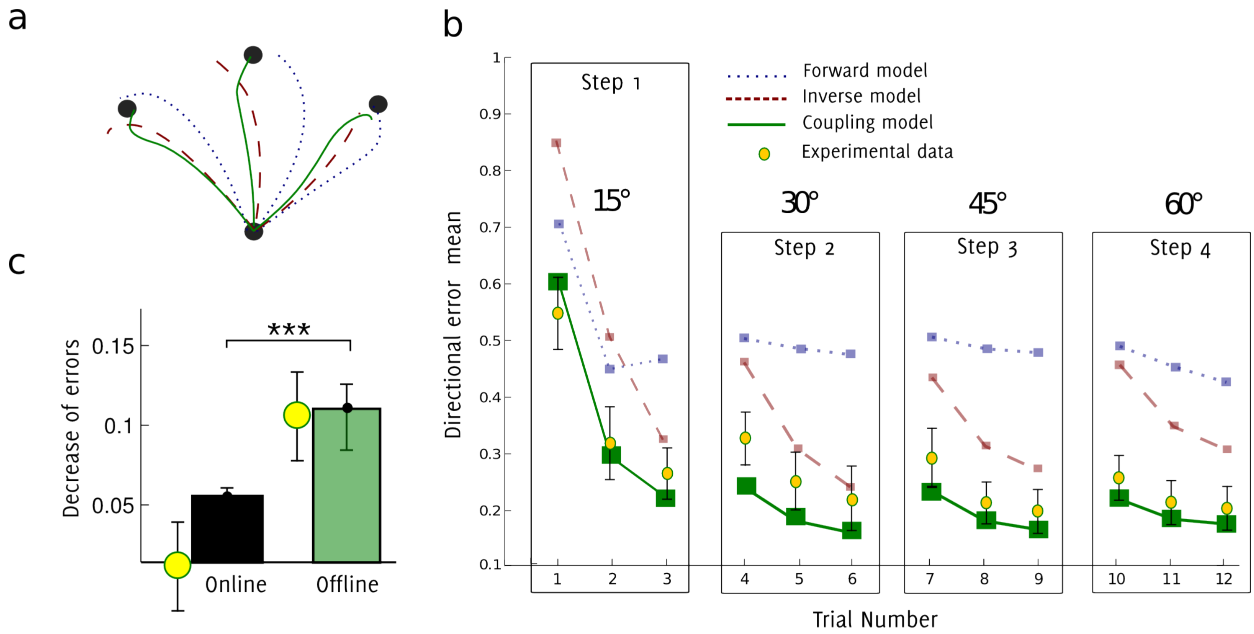

Fig. 6. *Rotation adaptation task. Simulation results for both online and offline learning and comparison with experimental human data.* (a) Example of three target-directed trajectories at the end of trial 6. The system has to adapt its dynamics to compensate for an angular bias of 30°. The blue dotted (resp. red dashed) lines indicate the sample solutions found by purely forward (resp. inverse) model simulated subjects, respectively. The green solid lines denote the trajectories obtained with the coupling scheme model. (b) Results of online learning. The couplingmodel (green solid curves) provides both rapid adaptation and appropriate convergence levels. Also, it reproduces the experimental data obtained with human subjects undertaking the same rotation adaptation task (yellow data, taken from Huber et al. (2004) [3]. (c) Offline learning results. The mean error is significantly reduced in the group of simulated subjects that undergo offline consolidation. The experimental results obtained with real subjects (offline corresponds to sleep-dependent consolidation) are shown in yellow (taken from Huber et al. (2004) [3]). ***Significant values, $p<0.001$.

accuracy values ranging from 0.25 to 0.3). Finally, the subjects using the coupled internal models (CM_{off}, green solid curves) perform better than both IM and FM subjects along the entire training period, showing both fast adaptability and error reduction over time. The mean error rises slightly when the angular bias changes (i.e. trials 4,7 and 10) but then it decreases significantly and converges to values ranging from 0.15 to 0.2. Fig. 6b also displays the learning performances of human subjects (yellow data points) as reported by Huber et al. (2004) [3].

It is shown that the simulated CM_{off} subjects (green data) have online learning performances comparable to those of real subjects over the entire training process. These results suggest that the proposed coupling scheme, which favours the cooperation between internal predictor and corrector models, offers a plausible solution to optimise procedural motor learning.

3.2 Offline learning and consolidation

As aforementioned, another potential advantage of the coupling scheme is that it supports offline learning assuming that the sequence of actions executed during online training can be replayed offline [14]. In order to assess whether an offline consolidation process can further increase the system performances reached at the end of the online adaptation protocol, 2 groups of 10 simulated subjects are considered. Both groups consist of subjects adopting the coupling scheme (CM). However, one group (CM_{off}) is allowed to undergo offline learning, whereas the other (CM_{CTRL}) is not. The Fig. 4 shows the protocol. Both groups (CM_{off} and CM_{CTRL}) undertake the 12 training trials. A first probe test (trial 13) is executed to evaluate the extent of the online rotation adaptation in both groups. Then, subjects from group CM_{off} undergo a simulated offline learning process consisting of a set of 48 trials (4320 trajectories randomly replayed) during which no sensory feedback is provided to the system. Therefore, the learning signal can only be computed based on the prediction provided by the forward model, and the inverse model can adapt its dynamics only when this teaching information is available. Finally, both groups CM_{off} and CM_{CTRL} undertake a second probe test (trial 14) and their performances are compared.

Fig. 6c shows the results of this comparison both from our simulations and from experimental data obtained on human subjects [3]. A repeated measure analysis of variance and post-hoc tests show that the two groups have similar performances during the first probe test (i.e. when tested immediately after online training, trial 13). On the other hand, the second probe test (trial 14) shows that the mean directional error of CM_{off} subjects is significantly reduced compared to control subjects. Compared to the first probe test (trial 13), a performance enhancement of $12.7 \pm 2.1\%$ is reached by CM_{off} subjects. By contrast, control subjects exhibit a lower performance improvement of $5.2 \pm 1\%$. The increase of performance of simulated CM_{off} subjects is consistent to that observed experimentally on human subjects after a night of sleep (yellow data, +11 ± 3 % [3]). Since all parameters were controlled in our simulation, the improvement we report could only be explained by the offline consolidation process, and not by other factors such as circadian cycle. However, simulated control subjects appear to have better performances during the probe test (trial 14) compared to human subjects tested again after 8 hours of wakefulness, who do not show any significant improvement.

4. Conclusion

This work addresses the issue of coupling internal models (i.e. forward and inverse) in the cerebellum in order to enhance both online and offline learning capabilities. The proposed connectionist architecture takes inspiration from the cerebellar microcomplex circuit and it employs spiking neural populations to process information. Long-term synaptic plasticity (both LTP and LTD) is implemented to achieve adaptive motor control. It is shown that the system can acquire representations of closed-loop sensorimotor interactions, suitable to adapt the behavioural response to changing sensory contexts. The coupling model reproduces the experimental findings on human procedural learning during the rotation adaptation task proposed by Huber et al. (2004) [3]. The sleep-dependent consolidation observed experimentally is mimicked here by an offline learning phase during which a replay of the contextual information elicited during online training occurs. This hypothesis is corroborated by several experimental studies: for example, it has been shown that patterns of activity recorded during online practice of a motor skill task reappear during episodes of REM sleep, while such activity is not seen in control subjects [14].

In both cases, the model cerebellar microcomplex is used to adapt the dynamics of a fairly simple controller (e.g. two degrees of freedom arm). The model would probably need more neuronal resources to deal with more complex motor control tasks. One possible solution may be to use a modular approach as previously proposed by Wolpert and Kawato (1998) [10]. The coupling model would then be taken as a functional unit, and various behaviours could be generated by combining the output of several units. Because one unit could be used in different contexts, a large repertoire of behaviours could be generated, even with a limited number of modules.

References

[1] Ito, M., The Cerebellum and Neural Control. *Raven Press, New York,* 1984

[2] Walker, M.P., Stickgold, R., Sleep-dependent learning and memory consolidation. *Neuron*, *44*(1), 121–133

[3] Huber, R., Ghilardi, M.F., Massimini, M., Tononi, G.: Local sleep and learning. *Nature, 430*(6995), 78–81

[4] Kawato, M., Furukawa, K., Suzuki, R., A hierarchical neural-network model for control and learning of voluntary movement. *Biol Cybern, 57,* 169–185

[5] Kawato, M., Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol., 9,* 718–727

[6] Lalazar, H., Vaadia, E., Neural basis of sensorimotor learning: modifying internal models. *Curr. Opin. Neurobiol., 18*(6), 573–581

[7] Darlot, C., Zupan, L., Etard, O., Denise, P., Maruani, A., Computation of inverse dynamics for the control of movements. *Biological Cybernetics, 75*(2), 173–186

[8] Pasalar, S., Roitman, A.V., Durfee, W.K., Ebner, T.J., Force field effects on cerebellar purkinje cell discharge with implications for internal models. *Nature Neuroscience, 9*(11), 1404–1411

[9] Dean, P., Porrill, J., Ekerot, C., Jorntell, H., The cerebellar microcircuit as an adaptive filter: experimental and computational evidence. *Nat Rev Neurosci., 11*(1), 2010, 30–43

[10] Wolpert, D.M., Kawato, M., Multiple paired forward and inverse models for motor control. *Neural Networks, 11*(7-8), 1317–1329

[11] Kawato, M., Kuroda, T., Imamizu, H., Nakano, E., Miyauchi, S., Yoshioka, T., Internal forward models in the cerebellum: fMRI study on grip force and load force coupling. *Prog. Brain Res., 142,* 2003, 171–188

[12] Stickgold, R., Sleep-dependent memory consolidation. *Nature, 437*(7063), 1272–1278

[13] Ito, M., Historical review of the significance of the cerebellum and the role of purkinje cells in motor learning. *Ann. N. Y. Acad. Sci., 978,* 273–288

[14] Maquet, P., Schwartz, S., Passingham, R., Frith, C., Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *The Journal of Neuroscience, 23*(4), 1432–1440

[15] Ros, E., Carrillo, R., Ortigosa, E.M., Barbour, B., Agis, R., Event-driven simulation scheme for spiking neural networks using lookup tables to characterize neuronal dynamics. *Neural Computation, 18*(12), 2959–2993

[16] Ito, M., Cerebellar circuitry as a neuronal machine. *Prog. Neurobiol., 78,* 2006, 272–303