Internal models in the cerebellum: a coupling scheme for online and offline learning 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 two procedural tasks 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.

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].

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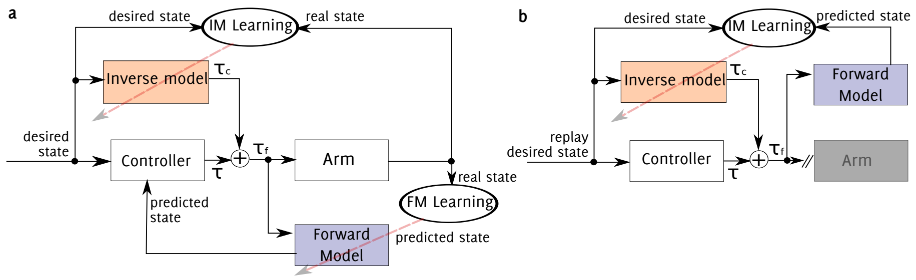

Fig. 1. *Coupling scheme for online and offline motor learning*. (a) Online adaptation. The arm controller receives the desired state and maps it onto a motor command (τ). The desired state is also sent to the inverse model that acts as a feed-forward corrector and calculates the motor correction (τ_c). 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.

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. This hypothesis 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 prominently 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]. Second, the model is also validated on a significantly different motor adaptation task, proposed by Walker and Stickfold 2004, in which subjects have to type simple numerical sequences on a computer keyboard [2]. Again, both the online and offline learning capabilities of the model are compared to experimental data.

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

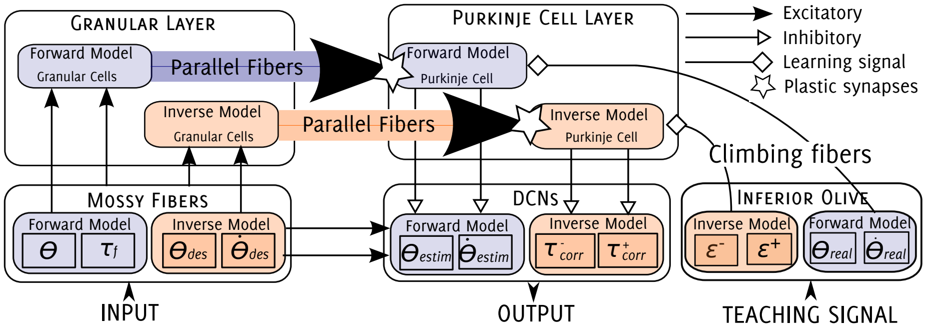

Fig. 2. *The cerebellar microcomplex model.*

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 (θ) and an efference copy of the motor command τ_f. The MFs of the inverse model convey desired joint position θ_{des} and velocity $\dot{\theta}_{des}$ [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 (position θ_{estim} and velocity $\dot{\theta}_{estim}$) and the inverse model correction to be sent to the system (following an agonist-antagonist muscle representation, one population called agonist coding for the positive correction torque τ^{+}_{corr} and one population called antagonist coding for the negative correction torque τ^{-}_{corr}).

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).

The LTP is implemented as a non-associative weight increase triggered by each GC spike, simulating the homosynaptic potentiation rule described by Lev-Ram [17]. As shown in equation 1, the weight of a GC_i -PC_j connection is increased by α every time GC i discharges ($\delta_{GC_i} = 1$):

$$w_{GC_i - PC_j}(t) = w_{GC_i - PC_j} + \alpha \delta_{GC_i}(t) \qquad (1)$$

On the other hand, LTD is implemented as an associative weight decrease triggered by a spike from the inferior olive. This is the heterosynaptic rule described in 1982 by Ito [18]. This learning rule is presented in the equation 2 and uses a temporal kernel K

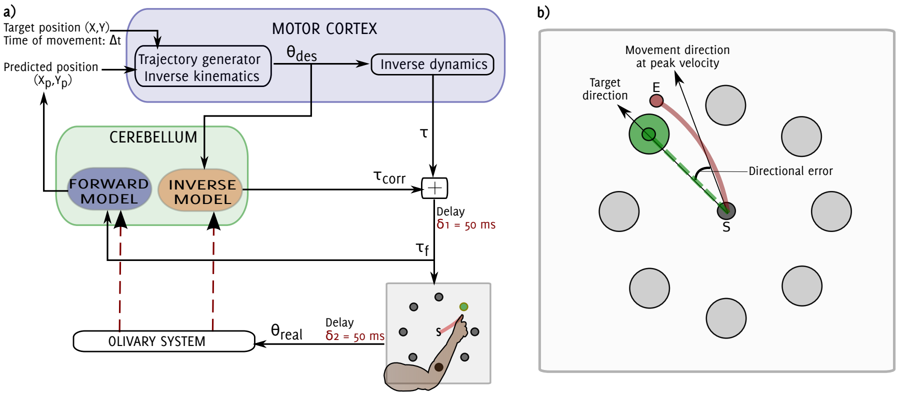

Fig. 3. *Overview of the biomimetic control architecture used to learn the rotation adaption task.* (a) Functional diagram of the controller. A desired trajectory to the highlighted target is computed by the trajectory generator and transformed in the joint-related reference frame via the inverse kinematics 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. (b) Experimental task and calculation of error. S: Starting point; E: Ending; Green dashed line: Ideal movement towards the target; Red line: actual movement.

which correlates each spike from the inferior olive with the past activity of connected GCs (see [20] for more information).

$$w_{GC_i-PC_j}(t_{IO}) = w_{GC_i-PC_j} - \beta \int_{-\infty}^{t_{IO}} K(t-t_{IO})\delta_{GC_i}(t)dt \qquad (2)$$

In my simulations, α and β parameters are set to 0.1 and 0.025, respectively.

The teaching signal is conveyed by a population of 400 inferior olive (IO) neurones, simulated to produce the climbing fibre projections targeting PCs. In the inverse model, the teaching signal relies on the estimated motor errors ε^- and ε^+, which are extracted from the discrepancy between the desired state of each joints and their real state (position θ_{real} and velocity $\dot{\theta}_{real}$). The latter variables are also used to drive the learning of the forward model. Normally, the real state of the joints is calculated in the central nervous system using congruent information from proprioceptive and visual sources. However, in our simulation, the positions and velocities of each joint are known variables, and corrective signals are directly derived algorithmically.

All the neuronal units of the microcomplex (i.e. GCs, PCs and DCNs) are modelled as conductance based, leaky integrate-and-fire units [19]. The irregular discharge of the IO is simulated by means of a Poisson spike-train generation model.

2.2 Global architecture of the system

The global architecture of the generation of arm movement is illustrated in figure 3. We use the architecture described recently by Carrillo et al. in [20] to control a 2 joints simulated arm in real time. First, a minimum jerk model computes the desired smooth movement of the arm end-point toward the target positioned in (X, Y). The desired trajectory is expressed in Cartesian coordinates for the defined time of movement $\varDelta t$. This desired movement is then transformed into arm-related coordinates: $\theta_{des}(t) = (\theta_{s,des}, \theta_{e,des})$ are the desired angular position of the shoulder and elbow. Since we use an arm with only two degrees of freedom, there are no redundancy or inversion problems. As there is a small chance that cerebellum could play a major role in dealing with these inconveniences, the model should still be valid for more complex arm devices.

These coordinates are the input of a crude inverse dynamic controller, which extracts a set of torque commands $\tau = (\tau_s, \tau_e)$, then sent to the articulations with a time delay $\delta 1 = 50ms$. All mathematical solutions of minimum jerk, inverse kinematics and dynamics model have been taken from [20]. An error is added to the minimum jerk model, through an added rotation of α degrees at each time step.

Two adaptive internal models encoded by our simulated cerebellum were included to the system, an inverse and a forward model. In the inverse model scheme, the desired angular position for both joints are sent to the cerebellum. The model then calculates a corrective torque signal $\tau_c = (\tau_{s,c}, \tau_{e,c})$ that compensates the rotation error during the realisation of the movement. The torque command applied to each articulation i is the sum of the torque τ_i computed by a basic inverse dynamics model according to the desired kinematic trajectory, and of the cerebellar correction ($\tau_{i,c}$): $\tau_f = \tau + \tau_c$. These two commands are then sent to the limbs with a delay $\delta 1$ = 50 ms. The error in the execution of movement is computed at the level of the arm, and sent back to the system with a delay $\delta 2 = 50$ ms. This error is mainly used to determine the learning signal conveyed by the inferior olive in order to produce anticipative motor corrections.

In the forward model scheme, the simulated cerebellum receives information about the current state of each articulation (the angular position of the elbow and the shoulder $\theta(t) = (\theta_s, \theta_e)$) and an efference copy of the torque command $\tau_f = \tau_{s,f} + \tau_{e,f}$. The model then predicts the future position and velocity of the articulations ($\theta(t) = (\theta_{s,est}, \theta_{e,est})$ and $\dot{\theta}(t) = (\dot{\theta}_{s,est}, \dot{\theta}_{e,est})$). The coordinates are transformed into Cartesian coordinates and sent to the trajectory generator (X_p, Y_p). This prediction is compared to the expected position of the arm. If there is a discrepancy between the two positions, the entire movement from the current estimated place is recomputed by the minimum jerk model. Because this process is supposed to require important neuronal resources, we limited its use at once every 100ms.

We fixed the duration of the motor execution to 0.7s for each movement, followed by a pause period of 0.3s during which joints are reset to their central position, and the activity of the models is allowed to fall back to normal. Because of this short execution time and taking into consideration the delay of the sensory feedback , we assume that high level motor correction (recalculation of the entire trajectory) could not be performed in the absence of a prediction of the sensory feedback signal.

2.3 Main procedural adaptation task

The first 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. 3a. The ideal trajectory of the arm is computed according to the minimum jerk model ([21]). In order to learn the rotation adaptation task (i.e. to compensate for the unknown anticlockwise bias), two internal models encoded by the modelled cerebellar microcomplex of Fig. 2 form the core of the adaptive closed-loop controller.

The simulated experimental setup consists of a central position S and eight targets evenly distributed on a circle centred at position S (Fig. 3b). 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).

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 do not perform offline consolidation.

Performances are measured by quantifying the directional error (see Fig. 3b), 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 Rotation adaptation task: online learning

Figs. 5a,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

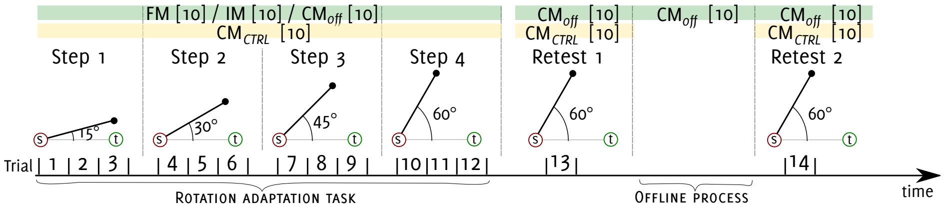

Fig. 4. *The protocol of the rotation adaptation task and the offline learning task.*

task. Fig. 5a 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. 5b 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 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. 5b 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 be-

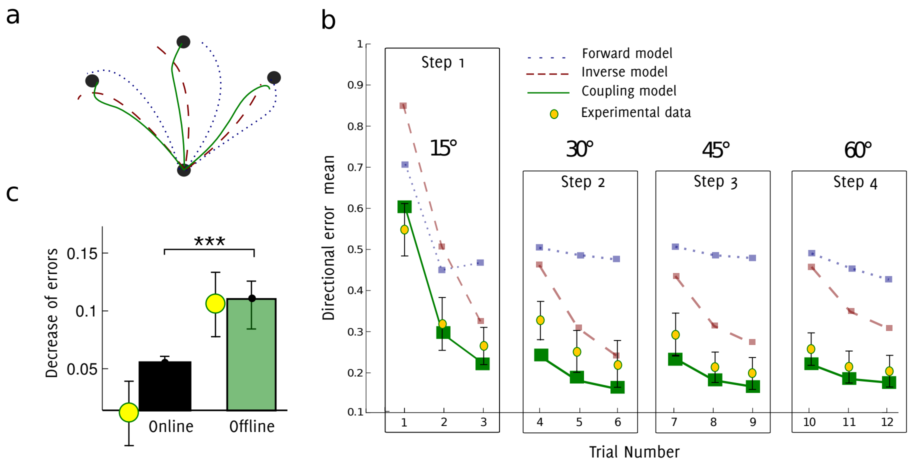

Fig. 5. *Rotation adaptation task. Simulation results for both online and offline learning and comparison with experimental human data.* (a) Example of three target-directed trajectories at the end of trial 6. The system has to adapt its dynamics to compensate for an angular bias of 30°. The blue dotted (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 coupling model (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.

tween internal predictor and corrector models, offers a plausible solution to optimise procedural motor learning.

3.2 Rotation adaptation task: 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

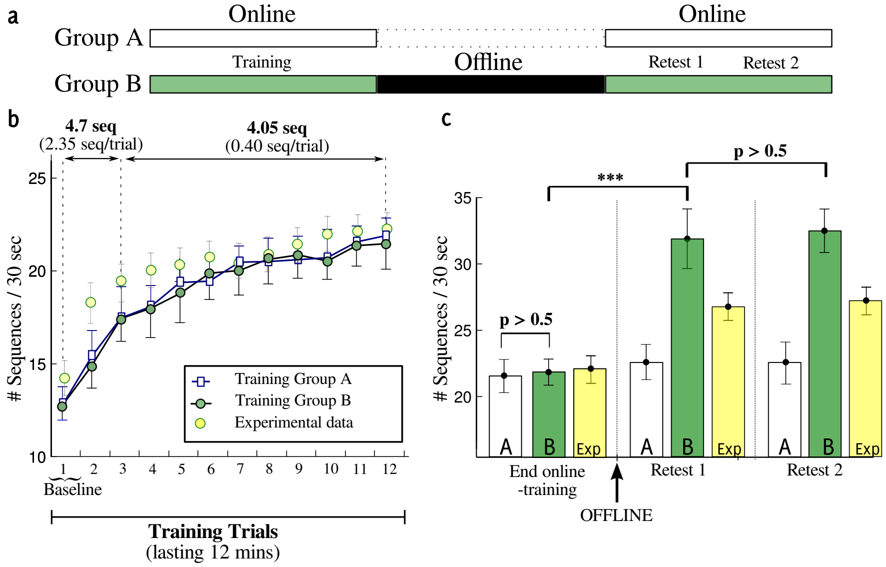

Fig. 6. *Sequential finger tapping task.* (a) Experimental protocol. (b,c) Simulation and experimental results (from Walker and and Stickfold 2004, [2]).

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. 5c 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 $\pm$ 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.

3.3 Cross-task validation. Results on a ‘sequential finger tapping task’

In order to further validate the coupling scheme model, a second (totally different) procedural task was simulated: the sequential finger tapping task proposed by Walker and Stickfold (2004) [2].

This task requires subjects to press four numeric keys on a standard computer keyboard with the fingers of their non-dominant hand. A five elements sequence, 4-1-3-2-4, must be repetead as quickly and accurately as possible for a period of 30 s. Each 30 s trial is then scored according to the number of complete sequences achieved. The entire training consists of 12 trials (with 30 s rest periods between trials). The score from the first training trial is taken as a baseline, while the score from the final trial is taken as the post-training performance. 30 simulated subjects are allocated into 2 groups (A and B). Group A undergoes online adaptation only, whereas group B undergoes both online and offline learning.

The protocol and results are presented in Figs. 6a, and b,c, respectively. Subjects from groups A and B show similar performance improvement across the 12 training trials, with a non significant difference of 4.8% observed at the end of training (Figs. 6b). Overall performances improved by about 64% across the 12 training trials, with 40% occurring across the first three trials, and the remaining 24% occurring at a slower but relatively constant rate across the final ten trials. Figs. 6c illustrates the effect of offline learning and consolidation. It is shown that subjects from group B, after offline training, exhibit a significant improvement compared to control group A (probe test 1). They display no further significant improvement with additional online training (probe test 2).

Figs. 6b,c also show the correspondance between simulation results and experimental data obtained on human subjects [2].

4 Discussion

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].

The same architecture is also validated on a second procedural task (i.e. the sequential finger tapping task proposed by Walker and and Stickfold 2004 [2]), which strengthens the idea that the proposed coupling scheme may offer a plausible model to *(i)* combine the advantages from fast online adaptation properties of forward models and accurate but slower convergence of inverse models, and *(ii)* achieve offline consolidation of procedural memories to enhance motor control capabilities.

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.

Other questions related to the offline consolidation process can be further investigated using our model. As we observed, a sufficiently long offine consolidation leads to an improvement of overall performances. This observation raises a fundamental question concerning how the potential improvement varies as a function of the duration of the offline process. Finally, in our simulations to solve the rotation adaptation task, for instance, random sequences of entire trajectories were replayed when performing offline consolidation. It remains to be elucidated how the benefits of offline learning would vary if contextual information were only partially replayed. This question is currently under investigation using the presented coupling model.

To conclude, we voluntary omitted the role of the parietal lobe in this study, although this region is known to be implicated in target reaching tasks, and more generally in motor prediction processes (for a good review see [22]). The differential roles in prediction of the cerebellum and the parietal lobe are still under debate, and it is highly possible that these two structures work as a functional loop for predicting the sensory consequences of movement and making adequate corrections. It has been previously suggested that one of the distinctions may be that, contrary to the predictions made by the cerebellum, those of the parietal cortex would be made available to awareness [22]. However, to the best of our knowledge, this is still highly speculative, and has not been validated yet. A complementary view stresses the fact that the parietal cortex could be more involved in the comparison between sensory and motor information by maintaining the anticipated sensory consequence of the movement, this prediction being made by forward models located inside the cerebellum [23]. If this hypothesis were to prove true, then it would give insights on (1) how the teaching signal sent to drive learning of internal inverse models could be computed, and (2) why a strong correlation between the increase of slow wave activity in parietal cortex areas during sleep and the performance improvement after sleep are reported in procedural tasks [3]. An extended version of the coupling scheme could therefore integrate a simplified model of the parietal lobe, which could help to dissociate the role of both structures during online and offline motor adaptation.

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