Motor Learning Without Doing: Trial-by-Trial Improvement in Motor Performance During Mental Training

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[1]*Université de Bourgogne, Dijon, France;* [2]*Institut National de la Santé et de la Recherche Médicale, Motricité et Plasticité, Dijon, France;* [3]*Cognitive Motor Neuroscience Laboratory, University of Maryland, School of Public Health, Department of Kinesiology, College Park, Maryland;* [4]*Computer Science, and* [5]*Biokinesiology and Physical Therapy, University of Southern California, Los Angeles, California*

Gentili R, Han CE, Schweighofer N, Papaxanthis C. Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *J Neurophysiol* 104: 774–783, 2010. First published June 10, 2010; doi:10.1152/jn.00257.2010. Although there is converging experimental and clinical evidences suggesting that mental training with motor imagery can improve motor performance, it is unclear how humans can learn movements through mental training despite the lack of sensory feedback from the body and the environment. In a first experiment, we measured the trial-by-trial decrease in durations of executed movements (physical training group) and mentally simulated movements (motor-imagery training group), by means of training on a multiple-target arm-pointing task requiring high accuracy and speed. Movement durations were significantly lower in posttest compared with pretest after both physical and motor-imagery training. Although both the posttraining performance and the rate of learning were smaller in motor-imagery training group than in physical training group, the change in movement duration and the asymptotic movement duration after a hypothetical large number of trials were identical. The two control groups (eye-movement training and rest groups) did not show change in movement duration. In the second experiment, additional kinematic analyses revealed that arm movements were straighter and faster both immediately and 24 h after physical and motor-imagery training. No such improvements were observed in the eye-movement training group. Our results suggest that the brain uses state estimation, provided by internal forward model predictions, to improve motor performance during mental training. Furthermore, our results suggest that mental practice can, at least in young healthy subjects and if given after a short bout of physical practice, be successfully substituted to physical practice to improve motor performance.

INTRODUCTION

Motor imagery is a mental process during which a subject internally simulates a movement without any corresponding motor output. Psychophysical experiments have shown that imagined and executed movements have the same spatiotemporal characteristics and obey the same motor rules and biomechanical constraints (Cerritelli et al. 2000; Courtine et al. 2004; Decety et al. 1989; Gentili et al. 2004; Maruff et al. 1999; Papaxanthis et al. 2003). Furthermore, neurophysiological studies have reported that mentally simulated and physically executed movements trigger similar motor representations and share overlapping neural substrates (Ehrsson et al.

2003; Jeannerod 2001; Papaxanthis et al. 2003; Sirigu et al. 1996). Because motor-imagery training has been repeatedly shown to improve motor performance (Debarnot et al. 2009; Gentili et al. 2006; Ranganathan et al. 2004; Yaguez et al. 1998; but see Hall and Erffmeyer 1983; Lamirand and Rainey 1994), mental training is increasingly used in sports and motor rehabilitation (Jackson et al. 2001; Munzert et al. 2009). For instance, mental training improves muscular force (Ranganathan et al. 2004) and arm kinematics (Gentili et al. 2006; Yaguez et al. 1998), reduces movement variability in locomotor tasks (Courtine et al. 2004), and enhances the service performance in volleyball players (Shoenfelt and Griffith 2008). Motor learning by mental training is also associated with changes in brain activation both in healthy (Jackson et al. 2003; Lafleur et al. 2002) and stroke patients (Page et al. 2009).

How can motor-imagery training enhance motor performance despite the lack of sensory feedback from body motion and the environment? The concept of internal models can provide a theoretical basis to this intriguing question. Forward internal models mimic the causal flow of the physical process by predicting the future sensorimotor state (e.g., position, velocity) given the efferent copy of the motor command and the current state. During physically executed movements, noisy and delayed sensory feedback is thought to be combined with forward model output to provide accurate and precise state estimation (Wolpert et al. 1995). During mentally simulated movements, state estimation is only based on forward internal model output (Miall and Wolpert 1996; Wolpert and Flanagan 2001; Wolpert and Ghahramani 2000). Such a forward model scheme provides a parsimonious account of the tight temporal similarity (i.e., isochrony) between imagined and executed movements (Bakker et al. 2007; Decety et al. 1989; Gentili et al. 2004; Munzert et al. 2009; Papaxanthis et al. 2002). During physical training, the estimated state of the motor system can refine future motor commands by generating an internal training signal that modifies plastic neural processes (Desmurget and Grafton 2000; Kawato 1999; Wolpert et al. 1995). During mental training, such plastic mechanism can theoretically occur as well. However, because the state estimation derives from the forward model alone, the training signal is presumably less accurate and less precise than during physical training.

We thus hypothesized that such common plastic learning process during physical training and motor-imagery training should be reflected by qualitative similarities, both in the overall performance improvement curve during training and in the changes in movement kinematics from pre- to posttraining.

However, in motor-imagery training, immediate and delayed motor performance should be inferior, and the trial-by-trial improvement in motor performance should be slower and more variable. To test our hypotheses, we designed an arm pointing task that allow us to measure both the trial-by-trial improvements in motor performance during motor-imagery training, as well as the within trial changes in trajectories between pre- and posttests.

METHODS

Experiment 1

Because of the lack of observable motor activity during motor-imagery training, previous studies compared motor performance before and after training (Allami et al. 2008; Debarnot et al. 2009; Gentili et al. 2006). Here we take advantage of the well-known and robust isochrony between imagined and executed movements (Decety et al. 1989; Gentili et al. 2004; Maruff et al. 1999; Papaxanthis et al. 2002) to compare motor learning during physical and motor-imagery training. To obtain valid and reliable measurements in motor imagery protocols, several movements are necessary because of the short-duration of a single movement and the coarse resolution of mental movement time measurements (Cerritelli et al. 2000; Papaxanthis et al. 2002; Sirigu et al. 1996). We designed a task in which participants physically and mentally performed a multiple-target-arm-pointing task requiring high accuracy and speed. Because the targets were positioned a different eccentric locations on a frontal plane (Fig. 1), participants needed to learn how to carefully control for arm dynamics to achieve the high accuracy and speed in this task. As a result, we were able to record trial-by-trial changes in the duration of the movements during both motor-imagery and physical training.

PARTICIPANTS. Forty healthy participants were randomly assigned into four groups (each group was composed by 5 females and 5 males): a physical-training group [PT, mean age: 22.2 ± 1.5 (SD) yr], a motor-imagery-training group (MIT, mean age: 24.5 ± 2.1 yr), an active-control group (AC, mean age: 22.5 ± 1.7 yr) and a passive-control group (PC, mean age: 21.5 ± 1.9 yr). All participants were right-handed (individual values were >0.88) as determined by the Edinburgh Handedness inventory (Oldfield 1971). They were also good imagers as determined by the Movement Imagery Questionnaire (MIQ) (Hall and Martin 1997), individual scores were >39 (maximum score 56), and by comparing the temporal correspondence between executed and imagined arm movements performed in the horizontal and in the vertical planes (as in (Papaxanthis et al. 2002); the average durations of executed (8.94 ± 0.58 s) and imagined

(9.11 ± 0.63 s) arm movements were almost identical ($t = -1.49$; $P = 0.14$). All participants signed informed consents and the experimental protocol was carried out in agreement with legal requirements and international norms (Declaration of Helsinki 1964).

EXPERIMENTAL DEVICE. Two aluminum dowels (length: 75 cm, diameter: 1 cm) were fixed on a vertical bar (height: 86 cm, width: 10 cm) 44 cm one above the other. On each dowel, we symmetrically placed four targets, i.e., two on the left and two on the right side of the vertical bar (Fig. 1). The horizontal distance that separated the near (3, 4, 5, 6) and farther (1, 2, 7, 8) targets from the vertical bar was 10 and 35 cm, respectively. The eight targets were switches (diameter of 5 mm) and were all linked to an electronic stopwatch (Fig. 1). Another target (target 0) was also linked to the same stopwatch, and was placed on the table 20 cm from the base of the vertical bar.

Participants were sitting in front of the device and had to follow a pointing path with their right index fingertip; the distance between their shoulders and the vertical bar corresponded to ~70% of their arms length. Before movement onset, participants placed their right index fingertip above the target T0. To follow the path, they had to press successively the following switches: 0, 1, 2, 3, 4, 5, 6, 7, 8, 1, 7, 0 (a sequence of 11 arm movements, i.e., 12 pressures). The movement sequence started from–and ended at–the target T0. This movement sequence constituted a trial. Note that participants had previously memorized the order of the targets composing the path (see FAMILIARIZATION SESSION) and that all targets were visible before movement initiation. Therefore our task emphasized improvement in movement speed from target to target, and it was not a serial reaction time task requiring learning of sequence order. A label was placed near each switch to indicate the order of the switches to be pointed. The initial pressure on the switch T0 triggered the chronometer while the last pressure stopped it, recording so the total movement duration. Pressures on the other switches (T1,..., T8) allowed to record the duration elapsed between two successive pressures (i.e., intermediate movement durations).

EXPERIMENTAL PROCEDURES. Participants in the PT, MIT, and AC groups performed a familiarization session, a pretest (4 trials), a 60-trial training session, and a posttest (4 trials). Because mental training requires high levels of concentration, we performed a pilot experiment with three subjects who did not participate to the main experiment to determine the maximum amount of mental training tolerated by subjects. We found that after ~60 trials, subjects started developing fatigue and losing concentration.

FAMILIARIZATION SESSION. Before the experiment, all participants participated in a familiarization session with the setup by pressing the switches with the right index fingertip in random order (twice for each
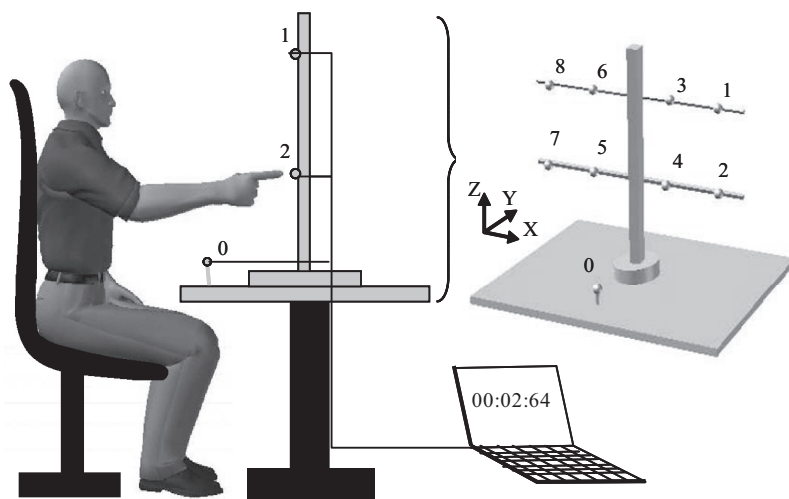

FIG. 1. Experimental device used for the 2 experiments. The device consisted of a vertical bar, 2 parallel aluminum dowels fixed on the bar, and 9 switches (T0 . . . T8) fixed on the dowels and connected to a chronometer integrated into a laptop.

switch). Subsequently, we asked them to memorize the spatial disposition of the switches composing the pointing path. To rule out any potential training effects that could improve the speed of arm movements, we asked participants to move their right arm along the path very slowly and to touch the switches without pressing them. After six to eight practice runs, all participants reported that they had memorized the specific path (i.e., they were able to mentally represent the pointing path with the targets' position with their eyes closed).

PRETEST.   The pretest was the same for all the 40 participants, who were requested to physically point as accurately and as fast as possible toward the 12 switches composing the pointing path. We notified them that all targets had to be reached in the specified order. As a consequence, if they missed a target they had to point again this target and then to continue with the other targets. The four pretest trials were separated by a 15 s intertrial interval, and no information concerning motor performance (i.e., movement duration or velocity) was provided to the participants during or after the pretest trials. The total duration, as well as the intermediate durations (i.e., the duration of each arm movement composing the trial), were measured for each participant, and used as a baseline motor performance.

TRAINING SESSION.   During the training session, participants in the PT group physically followed the pointing path and were encouraged to move as fast as possible at each trial while keeping high accuracy (see preceding). Individual motor performance (i.e., total movement duration, as well as individual movement duration) was recorded for each trial. Participants in the MIT group imagined themselves performing the pointing path (kinesthetic or first person imagery) (as in Bakker et al. 2007; Cerritelli et al. 2000; Courtine et al. 2004; Gentili et al. 2004, 2006; Papaxanthis et al. 2002). They were encouraged at each trial to move mentally their arm along the pointing path as accurately and as fast as possible as they would do if they physically performed the task. The total movement duration during MIT was recorded for each trial by asking the participants to press the T0 target switch with the right index just before starting the imagined movements and to re-press it immediately after they had mentally accomplished the pointing path. By means of this method, we quantified the trial-by trial temporal improvement during MIT and compared it with the temporal improvement during PT. Participants in the AC group were instructed to make accurate and quick gaze shifts to the switches composing the pointing path without moving their arms. We included this control group because we observed during a pilot experiment that the eyes of the participants in the PT and MIT groups shifted from one switch to the other when they respectively executed or imagined the arm pointing movements. As the task required eye-hand coordination, enhancement in arm motor performance (i.e., faster pointing movements) after MIT could be attributed to eye movement training, to an attention effect or to an improvement in memorization of target locations rather than improvement in motor performance per se. Eye position signals are known to influence the cortical reach related network (Andersen and Buneo 2002) and therefore to contribute to the neural commands to the limb. With this control task, we hoped to isolate a direct positive effect of motor-imagery training on motor performance, from indirect effects, not related to our hypothesis regarding the role of state estimation during motor-imagery training in motor learning. Participants in the PC group did not perform the training session, but instead were distracted by discussion or reading during 45 min, i.e., the duration required by the training session in the other groups.

POSTTEST.   The posttest was identical to the pretest and given 3 min after the training session.

STATISTICAL ANALYSIS.   For each participant, we calculated the average total movement durations for the pre- and posttest. Variables showed normal distribution (Shapiro-Wilk and Kolmogorov-Smirnov and Lilliefors tests) and equivalent variance (Hartley, Cochran, and Bartlett tests). Improvement in motor performance was quantified by a repeated-measurements ANOVA with *group* (PT, MIT, AC, and PC) as between subject-factor and *test* (pretest, posttest) as within-subject factor (level of significance, $P < 0.05$). *t*-tests were also used for the analysis of posttest trials (level of significance, $P < 0.05$). For the trial-by-trial temporal analysis, and the model selection, see RESULTS and the Supplemental Materials C and D.[1]

Experiment 2

In this experiment, we tested the changes in arm kinematics before and immediately after physical and motor-imagery training sessions. Furthermore, because efficient motor training leads to the formation of long-term (>24 h) motor memories (see, (Krakauer and Shadmehr 2006), we also examined whether subjects showed savings for the same sequence 24 h later. We used the same experimental device and procedures as in the *experiment 1*. Fifteen participants, none of them took part in the *experiment 1*, were randomly assigned into three groups: PT (mean age: 23.2 ± 1.6 yr), MIT (mean age: 25.2 ± 1.8 yr), and AC (mean age: 24.4 ± 2.1 yr). All had normal or corrected-to-normal vision and exhibited strong right-handedness (individual values were >0.85) (Oldfield 1971). Motor imagery ability was evaluated using the same method as for the first experiment. The average durations of executed (9.10 ± 0.51 s) and imagined (9.31 ± 0.56 s) movements were comparable ($t = -1.07$; $P = 0.30$). Participants in the three groups performed a familiarization session (see *experiment 1*), a pretest, a 60-trial training session and two posttests (posttest_{0h}: immediately after the training session and posttest_{24h}: 24 h after the training session).

Arm movements in the pretest and the two posttests (4 trials per test) were recorded by means of an optoelectronic measuring device (120 Hz, SMART BTS, Milan, Italy). Six infra-red-emitting cameras were placed circularly at a distance of ~4 m from the participants' position. One retro-reflective marker (15 mm diam) was placed at the right index fingertip. The displacements of this marker in the *x, y,* and *z* dimensions were digitally filtered using a dual low-pass Butterworth fifth order filter (cut-off frequency: 6 Hz) (as in Schaal et al. 2004; Singh and Scott 2003). From the filtered data, the three-dimensional (3D) position, velocity, and acceleration were computed. For each pointing movement between two switches, the onset and the end of the movement were, respectively, defined as the time where the tangential velocity was superior and inferior to 5% of its peak value. We computed the following four kinematics parameters: movement duration (MD), peak velocity (V_{peak}), peak acceleration (A_{peak}), and root mean square error (rMSE) between the actual hand trajectory when pointing from target to target from an "ideal" straight line connecting the successive targets. The rMSE was computed according to the following formula

$$\text{rMSE} = \sqrt{\frac{\sum_{i=1}^{N} \left[(x_a - x_i)^2 + (y_a - y_i)^2 + (z_a - z_i)^2 \right]}{N}}$$

where x_a, y_a, z_a and x_i, y_i, z_i are corresponding points of the actual (index a), resample trajectory and the ideal (index i) trajectory, respectively. N is the number of points in the path.

Statistical analysis

For each participant, we calculated the average values for the MD, V_{peak}, A_{peak}, and rMSE in the pretest and the two posttests. Comparisons of kinematics parameters between pre- and posttest were used as an indicator of motor performance improvement. The variables did not show normal distributions (Shapiro-Wilk and Kolmogorov-Smirnov, and Lilliefors tests), and therefore differences were accessed by nonparametric tests (between groups Kruskal-Wallis ANOVA, Wil-

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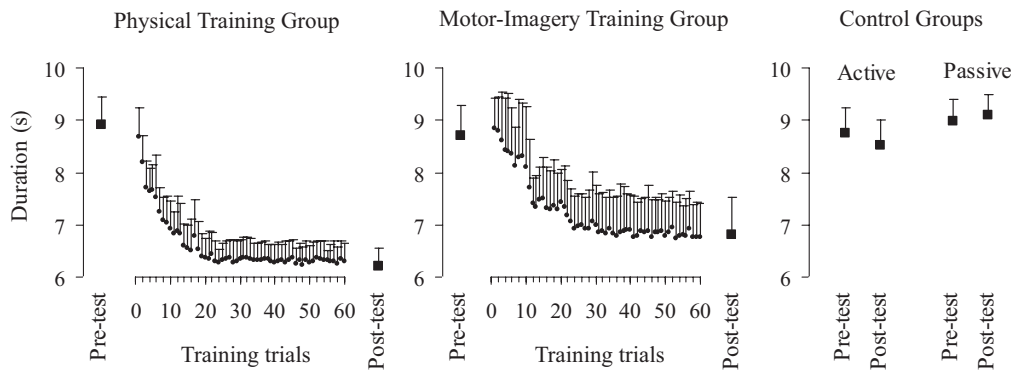[1] The online version of this article contains supplemental data.

FIG. 2. *Experiment 1*. Trial-by-trial improvement in motor performance for the physical and motor-imagery training groups. Spheres show the average values (±SD) trial-by-trial during the training sessions. Average values (±SD) of the total movement duration for the pre- and posttest are shown for the 4 groups (■).

coxon, and Mann-Whitney *U* tests). Results were considered to be significant at $P < 0.05$.

RESULTS

Experiment 1

TEMPORAL PERFORMANCE BETWEEN THE PRE- AND THE POST-TEST. PT and MIT had positive effects on motor performance (see Fig. 2). ANOVA revealed a significant interaction effect of *group* and *test* on total movement duration [$F(3,36) = 129.05$, $P < 0.0001$]. Post hoc comparisons (Newman-Keuls) between the pre- and the posttest showed that temporal performance in the PT ($P < 0.0001$) and MIT ($P < 0.0001$) groups significantly improved, whereas that of the AC ($P = 0.18$) and PC ($P = 0.45$) groups did not. Furthermore, the PT group showed better temporal performance than the MIT group in the posttest ($P = 0.02$). Note, that all four groups had similar temporal performances in the pretest (for all comparisons, $P > 0.5$). In addition, spatial accuracy, defined by the number of targets missed during the pointing sequence, was also comparable between the pretests and posttests for all groups (see Supplemental Material A).

The total decrease in movement duration between the pre- and the posttest was due to decrease in duration of all arm movements composing the pointing sequence as we found that all intermediate movement durations significantly decreased for both the PT and MIT groups (see Fig. 3; uncorrected paired *t*-test; $P < 0.01$ for all arm movement comparisons in both PT

and MIT groups). Furthermore, both groups showed qualitatively similar patterns of temporal performance, that is, similar target-by-target variations in movement durations (see Fig. 3) as shown by high correlation between the intermediate movement durations of the PT group and those of the MIT group in both the pretest ($r = 0.90$; $P < 0.001$) and the posttest ($r = 0.98$; $P < 0.001$).

In the MIT group, there was an excellent correspondence between the duration of executed and imagined movements both at the beginning (mean of pretest physically executed trials and first imagined-training trial) and at the end (last imagined-training trial and mean of posttest physically executed trials) of the training session (see Fig. 2). The pretest accurately predicted the first imagined trial (linear regression model, $R^2 = 0.91$, predictor coefficient: 0.93 ± 0.105 SE) with no bias (constant coefficient: 0.74 ± 0.92 s, not significantly different from 0, $P = 0.45$). At the end of training, the last imagined trial accurately predicted the posttest performance (linear regression model, $R^2 = 0.84$, predictor coefficient 1.05 ± 0.163) with no bias (constant coefficient: -0.25 ± 1.10 s, not significantly different from 0, $P = 0.82$). Note that for the MIT training, we confirmed with surface EMG recording that there was no arm muscle activation, i.e., that the participants performed purely mental training (see Supplemental Material B).

TEMPORAL PERFORMANCE DURING THE POSTTEST. In posttest, temporal performance was overall better in the PT group than in MIT group (see above results). However, this difference decreased from trial to trial because the temporal performance
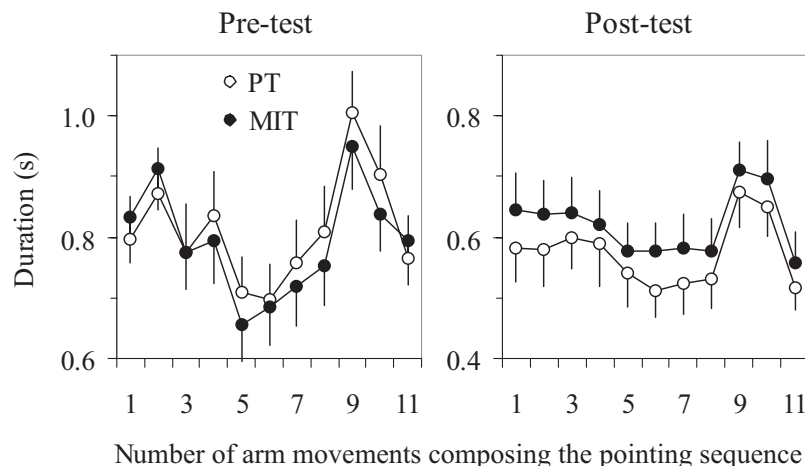

FIG. 3. *Experiment 1*. Average values (±SD) of intermediate arm movement durations. PT, physical training group; MIT, motor-imagery training group.

of the MIT group improved during the posttest (see Fig. 4). The analysis of the four posttest trials after motor-imagery training (MIT group) showed that the duration of the last posttest trial was significantly shorter than the duration of the first posttest trial (paired *t*-test; $t = 6.06$ and $P < 0.001$). After physical training (PT group), the temporal performance remained almost stable; the durations of the first and last posttest trials were not statistically different (paired *t*-test; $t = -0.06$ and $P = 0.95$). Furthermore, while temporal performance of the PT group was significantly better than temporal performance of MIT for the first three posttest trials ($t = -2.95$ and $P < 0.01$; $t = -2.39$ and $P = 0.02$; $t = -2.15$ and $P = 0.04$; for the first, second, and third trial, respectively), it was not significantly different for the fourth posttest trial ($t = -1.97$ and $P = 0.07$).

TEMPORAL PERFORMANCE DURING THE TRAINING SESSIONS. We then quantified the trial-by-trial improvement in the temporal performance during the training session for the PT and MIT groups with simple learning models. Specifically, we tested three possible models, in which the total movement duration monotonically decreases with the number of trials in a negatively accelerated fashion

$$\text{Hyperbolic: Time(Tr)} = a/(1 + b\,\text{Tr}) + c \qquad (1)$$

$$\text{Exponential: Time(Tr)} = a \exp\,(-b\,\text{Tr}) + c \text{ and} \qquad (2)$$

$$\text{Power:Time(Tr)} = a\text{Tr}^{-b} + c \qquad (3)$$

where Time is the total movement time, *a* is the total amount of learning as the number of trials Tr tends to infinity, *b* is the learning rate, *c* is the asymptotic performance as the number of trials Tr tends to infinity.

The exponential model fits the data well in all conditions and for all participants [PT, $R^2 = 0.83 \pm 0.02$, range (0.73; 0.91); MIT, $R^2 = 0.78 \pm 0.02$, range (0.68, 0.87)]. Simple model selection based on fit, however, runs the risk of selecting a model that only fits the particular data set and does not generalize well to new data. We therefore use a Bayesian selection method (see Supplemental Material C), which combines model fit to the data and penalize overfitting (Bishop 1995). Our analysis showed that exponential functions are
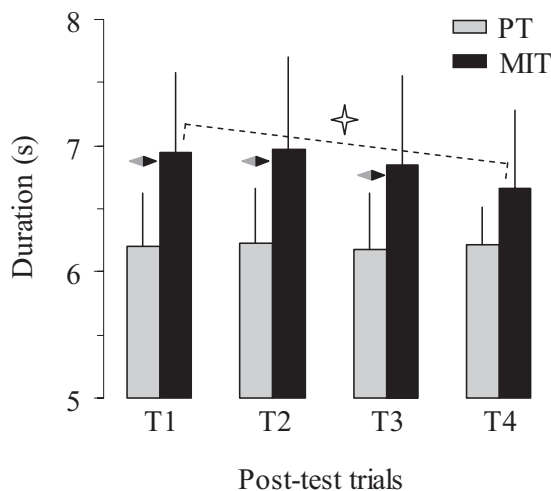
preferred models for all participants except for one participant (*SR3*) in the PT group, for whom the power function was a better model. Next, using a semi-parametric model regression analysis (see Schweighofer et al. 2006 for the details of a similar analysis), we further show that the learning curves of both PT and MIT groups follow exponential functions for all except one participant (see Supplemental Material D).

Because both PT and MIT training produced the same shape of learning curves, we could directly compare the model parameters of the exponential model given by *Eq. 2* (we used the parameters obtained in the direct parametric model fit). We found no significant effect between the two learning conditions on *a*, the parameter that captures the amount of learning (on average, PT: 2.64 ± 0.13 s; MIT: 2.56 ± 0.93 s; Mann-Whitney *U* test, 2-tailed: $P = 0.39$ and $z = -0.907$). Similarly, there was no significant effect on *c*, the parameter that captures asymptotic learning, namely the predicted value of performance after a large number of trials (on average, PT: 6.28 ± 0.11 s; MIT: 6.69 ± 0.24 s; Mann-Whitney *U* test, 2-tailed: $P = 0.22$ and $z = -1.285$). The learning rate *b*, however, was larger in the PT than in the MIT (Mann-Whitney *U* test, $P = 0.023$ and $z = -2.268$). For the PT group, the mean of learning rate *b* was 0.15 ± 0.020 trial^{-1}, and the range of *b* (0.10; 0.30) trial^{-1}. For the MIT group, the mean value of *b* was 0.090 ± 0.014 trial^{-1} and the range (0.04, 0.17) trial^{-1}. We then studied the within-subject trial-by-trial variability by computing the rMSE of the residuals between the exponential model and the data for each subject. After normalization of the data with a natural logarithm transformation (Kolgomorov test before transformation $P < 0.05$, Kolgomorov test after transformation, test $P > 0.05$), a 1-tailed *t*-test showed that the rMSE of the residuals were greater in the MIT than in the PT ($P = 0.04$).

Experiment 2

CHANGES IN KINEMATIC VARIABLES BETWEEN THE PRETEST AND THE POSTTESTS. In both PT and MIT groups, arm movements were faster and straighter immediately after and 1 day after the training session (Wilcoxon's tests, for all kinematics parameters: $z > 2$ and $P < 0.05$). In contrast, the AC group did not show any motor improvement (Wilcoxon's tests, for all kinematics parameters: $z < 0.68$ and $P > 0.05$, see Fig. 5 for average kinematics values from all groups, and Fig. 6 for typical finger paths and velocity profiles). All groups exhibited similar hand kinematics in the pretest (between groups Kruskal-Wallis ANOVA, for all kinematics parameters, $H < 5$ and $P > 0.1$). The PT group had better performances than the MIT group in both posttests at the temporal level (i.e., shorter MD and larger V_{peak} and A_{peak}; Mann-Whitney *U* tests, for all comparisons in posttest$_{0h}$ and posttest$_{24h}$, $P < 0.02$ and $z > -2.20$) but not at the spatial level (i.e., almost equivalent rMSE values, for both posttest$_{0h}$ and posttest$_{24h}$, $P > 0.0.5$ and $z < -0.50$). Note that both groups showed qualitatively similar target-by-target changes in kinematics patterns between the pre- and the two posttests (Fig. 7). We found high correlations between the PT and MIT groups for all the kinematics parameters in the pretest (MD: $r = 0.81$; V_{peak}: $r = 0.94$; A_{peak}: $r = 0.91$; rMSE: $r = 0.95$; for all *r* values, $P < 0.001$), the posttest$_{0h}$ (MD: $r = 0.83$; V_{peak}: $r = 0.93$; A_{peak}: $r = 0.96$; rMSE: $r = 0.96$; for all *r* values, $P < 0.001$) and the posttest$_{24h}$ (MD: $r = 0.88$; V_{peak}: $r = 0.95$; A_{peak}: $r = 0.91$; rMSE: $r =$

FIG. 4. *Experiment 1*. Trial-by-trial improvement in temporal performance during the posttest for PT and MIT. ◄, significant differences between the PT and the MIT group. ☆, significant differences between the 1st and the last posttest trial of the MIT group.
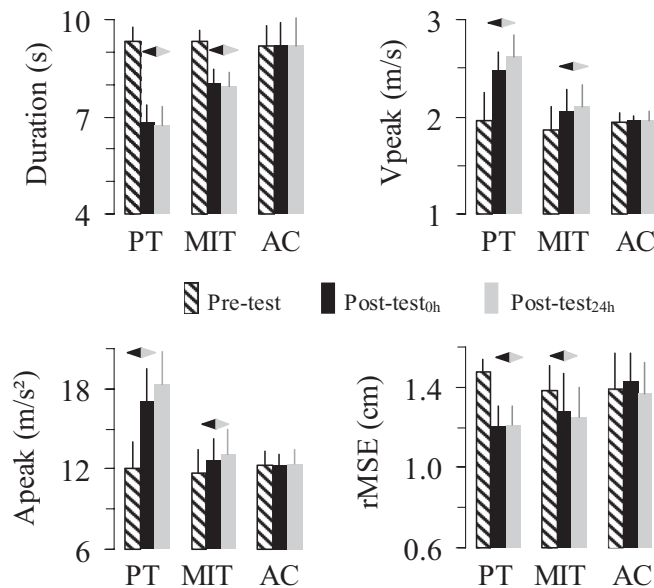
FIG. 5. *Experiment 2.* Improvement in arm kinematics immediately after and 24 h after physical and motor-imagery training. Average (±SD) kinematics parameters are depicted for the PT, MIT, and the active control (AC) groups during the pre- and the posttest. ◄►, significant differences between pre- and posttests.

0.95; for all r values, $P < 0.001$). We verified again that muscle activation during motor imagery training did not differ from that in the rest condition (see Supplemental Materials E) and that movement accuracy was similar between the pre- and posttests for all groups (see Supplemental Materials F).

TEMPORAL PERFORMANCE DURING THE POSTTESTS. The analysis of the four posttest$_{0h}$ trials (Fig. 8) after motor-imagery training (MIT group) showed that the duration of the last posttest$_{0h}$ trial was significantly shorter than the duration of the first posttest$_{0h}$ trial (Wilcoxon's tests, $z = 2.02$ and $P < 0.43$). After physical training (PT group), the temporal performance remained almost stable; the durations of the first and last posttest$_{0h}$ trials were not statistically different (Wilcoxon's tests, $z = 0.13$ and $P = 0.89$). Furthermore, the temporal performance of the PT group was significantly better than temporal performance of MIT for all the posttest$_{0h}$ trials (Mann-Whitney U tests, for all comparisons $P < 0.05$ and $z > -2$). The analysis of the four posttest$_{24h}$ trials (Fig. 8) after both motor-imagery (MIT group) and physical (PT group) training showed that the temporal performance remained almost stable; the durations of the first and last posttest$_{24h}$ trials were not statistically different (Wilcoxon's tests, $z = 0.94$ and $P = 0.34$ for MIT; $z = 0.13$ and

$P = 0.89$ for MIT). Furthermore, the temporal performance of the PT group was significantly better than temporal performance of MIT for all the posttest$_{24h}$ trials (Mann-Whitney u tests, for all comparisons $P < 0.05$ and $z > -2$).

DISCUSSION

In the current study, we investigated the effects of motor-imagery training on motor performance in a multiple-target-arm-pointing task requiring high accuracy and speed. Our aim was twofold: *1*) quantifying the learning process during motor-imagery practice and comparing it with the learning process during physical practice, and *2*) quantifying the changes in arm kinematics after physical and motor-imagery practice and regarding for their long term retention. The first objective was met by recording trial-by-trial the progress in the speed of the movements during both motor-imagery and physical training, and the second by analyzing hand velocity profiles and paths immediately-after and 24 h-after (long term memory formation) physical and motor-imagery training.

Features of motor-imagery training

We found an excellent correspondence between the duration of the pretest trials and the first motor imagery trial but also excellent correspondence between the duration of the last motor imagery trial (60th) and the posttest trials, which is a novel finding. These results are in agreement with, and further extend, previous studies that showed that motor imagery and movement execution follow the same motor laws and share common neural processes (Bakker et al. 2007; Cerritelli et al. 2000; Courtine et al. 2004; Ehrsson et al. 2003; Gentili et al. 2004; Jeannerod 2001; Papaxanthis et al. 2002; Sirigu et al. 1996). Despite this strong evidence, note however that the effects of mental training on motor performance in the sport literature are somewhat controversial. While some studies have provided clear evidences that mental training improves motor performance, for example the service in volley-ball players (Shoenfelt and Griffith 2008), other studies, see for example, the shooting in basketball, have shown that this was only partially true (Hall and Erffmeyer 1983; Lamirand and Rainey 1994).

The temporal similarities between imagined and executed movements observed in our study guarantee that subjects mentally simulated the sequence of arm movements with high precision. Furthermore, the finding that arm muscles, which were activated during actual movements, remained silent during imagined movements, testifies that motor-imagery training was an internal mental process without any motor output. The involvement of internal predictive models in both executed and
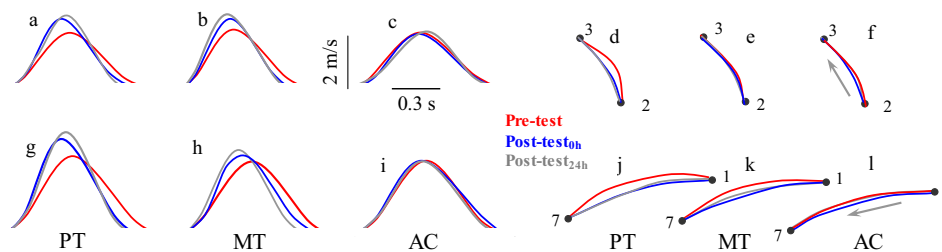

FIG. 6. *Experiment 2.* Arm kinematics for pretest and in the immediate posttest (0$_h$), and 24-h delayed posttest (24$_h$). Typical finger tangential velocity profiles (*a–c*) and paths (*d–f*) obtained from the PT, MIT, and AC groups (1 subject from each group), when performing arm pointing movements from targets 2 to 3. Typical tangential velocity profiles (*g–i*) and finger paths (*j–l*) obtained from the same subjects when performing arm pointing movements from targets 1 to 7. →, movement direction.
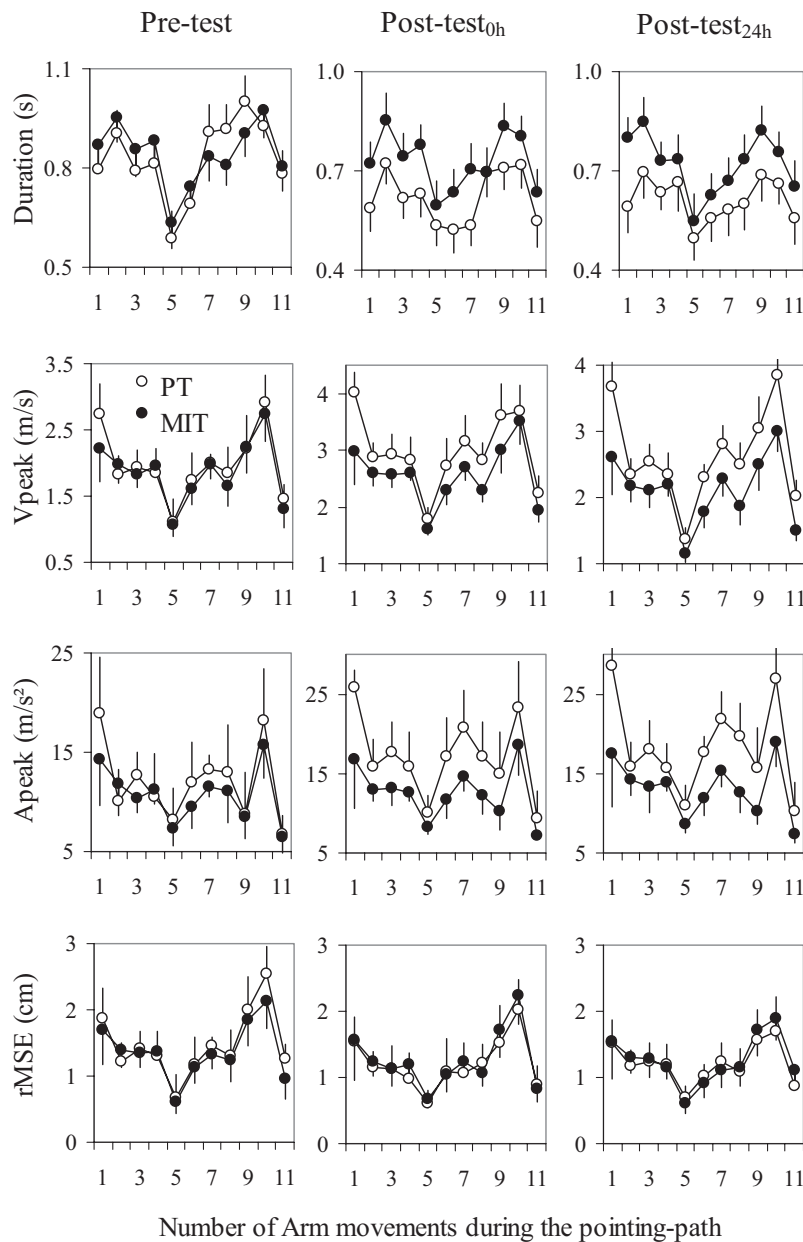
FIG. 7. *Experiment 2.* Average trial-by-trial values of arm kinematics for both PT and MIT groups. From top to down: duration, peak velocity (V_{peak}), peak acceleration (A_{peak}), and root mean squared error (rMSE). From left-to-right: pretest, immediate posttest (posttest$_{0h}$), and 24 h-delayed posttest (posttest$_{24h}$).

imagined movements explains their robust isochrony (Cerritelli et al. 2000; Courtine et al. 2004; Decety et al. 1989; Gentili et al. 2006; Papaxanthis et al. 2002). During an executed movement, the internal forward model relates the sensory signals of the actual state of the arm (e.g., position, time, velocity) to the prepared motor commands and predicts the future states of the arm. During the motor imagery process, motor commands are prepared but are blocked before they reached the muscle level, i.e., no movement occurs. However, a copy of these motor commands is available to the forward model that predicts the future states of the arm and therefore provides temporal information very similar to that of actual movements.

Motor learning during motor imagery

Because of the lack of observable motor activity during motor-imagery training, all previous studies compared motor performance before and after training (Allami et al. 2008;

Debarnot et al. 2009; Gentili et al. 2006) without therefore measuring the performance improvement during the training session. In *experiment 1,* we analyzed the temporal performance trial-by-trial during both motor-imagery and physical training and found qualitative similarities in the learning curves. This is a novel finding and suggests that physical and motor-imagery training share a common plastic learning process. As mentioned in the preceding text, internal forward models are thought to be engaged in both executed and imagined movements (Miall and Wolpert 1996; Wolpert and Flanagan 2001; Wolpert and Ghahramani 2000). Accordingly, we propose that state estimation, based on forward internal model output, is a common process during physical and mental practice that guides motor performance improvement.

Although we found qualitative similarities between the physical training and motor-imagery training learning curves, there were notable quantitative differences. In line with our
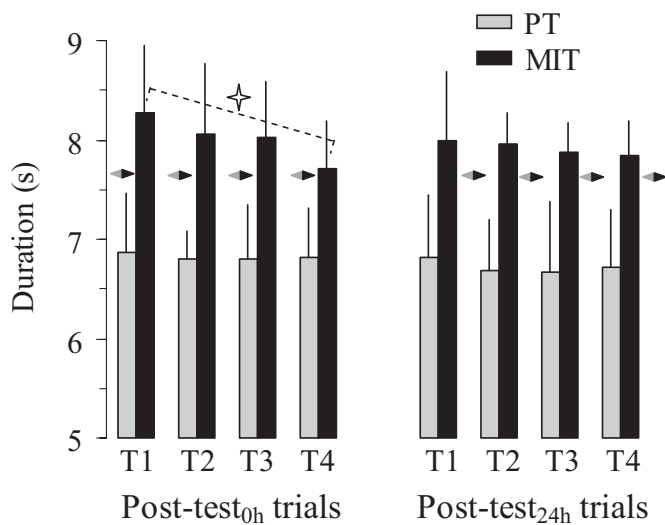
FIG. 8. *Experiment 2*. Trial-by-trial improvement in temporal performance during the posttest$_{0h}$ and the posttest$_{24h}$ for the PT group and the MIT group. ►, significant differences between the PT and the MIT group. ☆, significant differences between the 1st and the last posttest$_{0h}$ trial of the MIT group.

hypothesis, the learning rate in motor-imagery training was smaller than that obtained in physical training. As a result, the amount learned at the end of training was less in motor-imagery training than in physical training. However, and rather unexpectedly, there was no difference in the asymptotic amount learned and in the asymptotic final performance between the two conditions. These results, as well as the increased variability in the trial-by-trial movement duration in motor-imagery training, suggest that state estimation during motor-imagery training is more variable than during physical training but accurate on average. The following mechanisms can account for our results. Because of the trial-by-trial variability in the state estimation, the internal training signal used for learning is itself variable: if this variability of the training signal is large, it will presumably result in a slower update of the motor controller during motor-imagery training compared with physical training. However, because the state estimation in motor imagery is accurate (as suggested by the identical durations of executed and imagined movements both at the beginning and at the end of mental training), the internal training signal overall is itself accurate: this will result in the final performance of the motor controller being as accurate in motor-imagery training as in physical training. Note that this view is in accordance with previous suggestions that the acquisition of a forward model is rapid and precedes learning of the motor controller (Flanagan et al. 2003; Wolpert and Kawato 1998).

Efficiency of motor-imagery training

We observed that arm movements were faster and straighter immediately after and one day after the physical and motor-imagery training sessions. These findings imply that motor imagery is a genuine motor prediction process by which the brain efficiently improves arm motor performance. In addition, although arm dynamics dramatically changed through the pointing path (i.e., arm moving with or against gravity and arm inertia changing with movement direction of pointing), target-

by-target improvement in hand movement trajectories (i.e., faster and straighter hand displacements), both immediately after and one day after, was qualitatively similar after motor-imagery and physical training for all targets. This finding reinforces the idea that motor-imagery training induced a true form of motor learning (Debarnot et al. 2009; Jackson et al. 2003), similar to that of physical training (Walker et al. 2002, 2003) and not a transient change in motor performance. Motor-imagery training may rely on posterior parietal computations (Desmurget et al. 2009). Clinical observations of patients with posterior parietal cortex damage suggest that this brain region is critical for sensorimotor integration and prediction (Sirigu et al. 1996; Wolpert et al. 1998). The cerebellum, which is thought to implement inverse and forward computations (Kawato 1999; Miall et al. 2007; Schweighofer et al. 1998) is another potential neural site engaged in mental training. Allami et al. (2008) have found that a combination of extensive mental practice (75% of the training trials) followed by physical practice (25% of the training trials) is sufficient to give similar result as physical practice alone. In accordance with these results, we observed that arm motor performance during the posttests in *experiments 1* and *2* was improved after motor-imagery training (MIT group). Although our goal was not to mix mental with physical practice, we found that hand speed was enhanced trial-by-trial in posttests for the MIT group but not for the PT group. One day after (posttest$_{24h}$), motor performance was stable for both the MIT and PT groups. These results put forward an interesting question regarding the improvement and consolidation of motor performance after mental practice. Does mental practice have to be combined or to be followed by physical practice to be beneficial for motor learning? Previous investigations have shown that there is an effect of time interval between action observation and motor performance (Bove et al. 2009). The authors studied the effects of a prior observation of finger movements performed at either at 1 or 3 Hz frequency on the execution of self-paced finger movements. They found that observation influenced motor performance when finger movements executed immediately after the observation sequence, while when finger movements executed 45 min after the observation sequence motor performance was not consolidated. All together, these findings indicate that motor performance could be further improved when physical practice follows mental practice or when physical and mental practices are combined. In any case, further investigation is needed to understand how motor performance is consolidated after mental training.

Our control experiment suggests that the improvement in motor performance during mental rehearsal cannot be explained in terms of nonmotor phenomena (namely attention) or to eye movement training, but that it likely involves sensorimotor learning processes. Eye movement is a good indicator of action prediction during action observation and therefore could have a positive influence on motor performance during and after motor-imagery training. Flanagan and Johansson (2003) showed that the coordination between the observer's gaze and the actor's hand is predictive and is highly similar to the gaze–hand coordination when an observer performs the task himself. Because the AC group (eye-movement training) did not show an improvement in motor performance, we can rule out that the faster and straighter arm movements in the MIT group were either due to a better memorization of the pointing path or to an improve-

ment in the planning of eye movements that could also improve arm movement execution (Land and McLeod 2000). Instead our results suggest that the participants in the MIT group progressively learned, to better incorporate the arm's dynamics and the task requirements (moving faster and faster) into the arm motor command to improve their performance.

Sequential order learning versus improvement of the sequence elements

Our motor task involved sequential skilled arm movements. In general, sequential motor tasks include two components: the acquisition of the order of the elements in the sequence, and the ability to perform fast and accurately each element of the sequence. Three experimental paradigms have been proposed to investigate sequential learning: *1*) the serial reaction time task (SRTT), in which the acquisition of the sequence order is inferred from a reduction in response time (Goedert and Willingham 2002), *2*) the measurement of improvement in speed and accuracy (as in our motor task) of a previously learned sequence; this task emphasizes acquisition of the sequence elements rather than acquisition of sequence order (Walker et al. 2003 2002); *3*) the explicit learning of motor sequence, in which the two components of sequence learning can be quantified separately (Ghilardi et al. 2009; Moisello et al. 2009).

Our findings that movement duration decreased while peak velocity and peak acceleration increased after both physical and motor-imagery training, argue in favor of an improvement in sequence elements rather than in the acquisition of the order of the elements. This result, and the finding that motor performance improvement was consolidated (>24 h), corroborate and expend previous studies that found comparable results in similar motor tasks involved physical training of finger movements (Walker et al. 2003). In our study, we can exclude the possibility that subjects learned the order sequence of the targets, or anticipated the targets, for four potential reasons: *1*) targets were fixed and visible to the subjects (i.e., in our task there was not a reaction time requirement); *2*) arm movement velocity dropped to zero at each arm movement (i.e., there was not anticipation from target to target); *3*) our findings show the opposite of what is found in because previous sequence learning studies (Ghilardi et al. 2008; Moisello et al. 2009), which have nicely demonstrated that movements become anticipatory, movement duration increases while peak velocity and acceleration decrease; and *4*) if there was an improvement in the acquisition of the order of the elements in the sequence, subjects of the active control group (i.e., eye movement training) should have improved their performance as well but did not.

Clinical relevance and future work

Our results show that mental practice can be successfully substituted to physical practice to improve motor performance if mental practice is given after a short bout of physical practice, at least in young healthy subjects and in tasks related to ours. Although this finding is novel, further investigation is needed to demonstrate whether mental training practice is effective across motor learning tasks and body parts (i.e., hand movements, whole body movements) and whether it can be extended to other populations such as patients with neurolog-

ical pathologies or injured athletes; if so, mental training could be effectively used as a complementary method to physical training. Finally, our results suggest that under the condition that the patients enrolled in the rehabilitation program have the capability to move voluntary, even partially, therapists should try to combine mental and physical practice because motor performance appears to be better consolidated when mental practice is combined with physical practice.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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