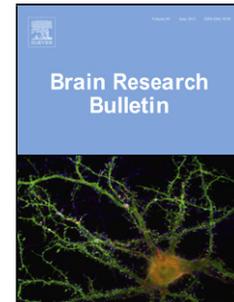


## Accepted Manuscript

Title: Consolidation of human somatosensory memory during motor learning

Authors: Anna Vera Cuppone, Marianna Semprini, Jürgen Konczak



PII: S0166-4328(17)31840-5  
DOI: <https://doi.org/10.1016/j.bbr.2018.03.013>  
Reference: BBR 11335

To appear in: *Behavioural Brain Research*

Received date: 13-11-2017  
Revised date: 9-2-2018  
Accepted date: 7-3-2018

Please cite this article as: Cuppone AV, Semprini M, Konczak J, Consolidation of human somatosensory memory during motor learning, *Behavioural Brain Research* (2018), <https://doi.org/10.1016/j.bbr.2018.03.013>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

**Title:**

Consolidation of human somatosensory memory during motor learning

**Authors:**

Anna Vera Cuppone<sup>1</sup>, Marianna Semprini<sup>2</sup>, Jürgen Konczak<sup>3</sup>

<sup>1</sup>Motor Learning and Robotic Rehabilitation Laboratory, Department of Robotics, Brain and Cognitive Sciences, Istituto Italiano di Tecnologia, Genova, Italy

<sup>2</sup>Neural Computation Laboratory, Center for Neuroscience and Cognitive Systems, Istituto Italiano di Tecnologia, Rovereto, Italy

<sup>3</sup>Human Sensorimotor Control Laboratory, School of Kinesiology and Center for Clinical Movement Science, University of Minnesota, USA

**Corresponding authors**

Marianna Semprini, via Morego 30 16163 Genova (Italy) , +39 010 71781212.

**Competing interests statement:**

The authors have no competing interests to declare.

## 1. ABSTRACT

Sensorimotor learning is a bidirectional process associated with concurrent neuroplastic changes in the motor and somatosensory system. While motor memory consolidation and retention have been extensively studied during skill acquisition, little is known about the formation and consolidation of somatosensory memory associated with motor learning. Using a robotic exoskeleton, we tracked markers of somatosensory and motor learning while healthy participants trained to make goal-directed wrist reaching movements over five days and evaluated retention for up to 10 days after practice. Markers of somatosensory learning were changes in wrist position sense bias (systematic error) and precision (random error). The main results are as follows: First, somatosensory (proprioceptive) memory consolidation shows signs of cost savings with repeated sensorimotor training – the same feature is known for motor memory formation. Moreover, somatosensory learning generalized to untrained workspace. Second, somatosensory learning over days can be characterized as an early improvement in sensory precision and a later improvement in sensory bias. Third, the time course of learning gains in position sense acuity coincided with improvements in spatial movement accuracy. Finally, the gains of somatosensory learning were retained for several days. Improvements in position sense bias were still visible up to 3 days after the end of practice for the trained workspace positions, but decayed faster in the untrained workspace. Improvements in position sense precision were retained for up to 10 days and were workspace independent. The findings are consistent with the view that an internal model of somatosensory joint space is formed during motor learning.

### **Keywords:**

Consolidation, Learning, Memory, Motor Control, Retention, Somatosensory.

## 2. INTRODUCTION

Many motor skills acquired in childhood such as bicycle riding are well retained into adulthood. This long-term retention of motor skills is based on the ability of the human nervous system to form motor memories that may last for years. They can be so well preserved that patients with Alzheimer's disease may continue to play piano compositions while being unable to recall the composer or title of the work, indicating that motor or procedural memories may persist when many declarative memories are lost (Crystal et al., 1989).

It is well known that the learning of a new motor skill relies on a sensory error signal that in itself is commonly based on the processing of visual, auditory or somatosensory cues. Yet, motor learning is not a one-directional process with sensory signals informing the motor system. Instead, sensorimotor learning is bidirectional and is associated with concurrent neuroplastic changes in the motor and somatosensory system (Nasir et al., 2013; Ostry and Gribble, 2016). For example, a recent study documented that activity in the orofacial somatosensory cortex changed during orofacial motor learning (Arce-McShane et al., 2014). In this study, two monkeys learnt a tongue-protrusion task over 8-12 days. Chronically implanted microelectrode arrays tracked learning-induced cortical changes. Increases in the proportion of task-modulated neurons and increases in trial-by-trial cross-covariance between the tongue-protrusion force and the spiking activity of task-modulated orofacial M1 and S1 neurons were observed - evidence for a process of parallel neuroplasticity in motor and somatosensory cortex that links the sensation of movement to the movement itself.

The formation and consolidation of motor memories has been extensively studied. We know from motor adaptation studies, in which people learnt velocity-dependent force fields, that the motor memory of the consolidated skill may last for at least 5 months (Shadmehr and Brashers-Krug, 1997). In addition, prism adaptation studies reported visuo-motor aftereffects lasting for 40 days (Hay and Pick, 1966) or up to 27 months from the initial training (Martin et al., 1996). In contrast, we know very little about the formation and consolidation of somatosensory memory associated with motor learning. We do know from previous studies that training regimens as short as 45 min or less than 400 repetitions induce measurable changes in proprioceptive acuity (Wong et al., 2011; Elangovan et al., 2017). However, we have an incomplete understanding for how long and to what extent somatosensory learning can be retained, and how it decays over time.

In addition, we do not know, to what extent motor and somatosensory memories share common characteristics. We do know that the formation of memory is characterized by so-called ‘savings’ in motor performance that occur during the process of skill acquisition. Here, ‘saving’ refers to a more rapid rate of relearning after the initial learning phase (Krakauer and Shadmehr, 2006). Evidence for such learning cost ‘savings’ comes again from studies of adaptive motor learning (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1997; Smith et al., 2006). They show that relearning is more rapid and complete than original learning. That is, a learner who retained motor memory after initial learning did not have to start at the original performance level and subsequently learnt faster. In other words, repeated learning reduced the learning costs over time. If somatosensory and motor learning are indeed intricately linked and share the same basic mechanism, the effect of repeated sensorimotor training should be visible in proprioceptive as well as motor function and somatosensory (proprioceptive) learning should result in similar learning cost ‘savings’.

To map the changes in proprioceptive function associated with repeated sensorimotor learning and to verify the hypothesis that proprioceptive learning shows similar cost savings to motor learning, we measured wrist joint position sense acuity before, during and after an intensive 5-day sensorimotor training. Retention of training-induced proprioceptive changes was evaluated up to 10 days after training. In addition, we examined sensorimotor transfer to understand how sensory changes in proprioceptive acuity relate to improvements in untrained motor function by evaluating wrist pointing to unexplored and untrained parts of the wrist joint workspace. Finally, in order to minimize the effect of vision on motor learning, visual feedback was restricted during the wrist pointing movement. Instead, learners received vibro-tactile joint position feedback to their forearm.

### **3. MATERIALS AND METHODS**

#### **3.1. Subjects**

Ten young adults (5 right-handed and 5 left-handed, 5 males and 5 females, age  $26.4 \pm 3.3$  years [mean  $\pm$  SD]) with no known neuromuscular disorders gave informed consent and participated in the study. The dominant hand was tested, and all subjects were naïve to the task. The study conformed to the ethical standards of the 1964 Declaration of Helsinki and was approved by the ethics committee of the ASL3 of the Università degli studi di Genova (Italy).

### 3.2. Apparatus and experimental setup

The experimental device was a back drivable wrist exoskeleton with 3 degrees of freedom (DoF) described in detail previously (Masia et al., 2009; Cuppone et al., 2015). The robot allowed the movement of wrist flexion/extension ( $\pm 70^\circ$ ), abduction/adduction ( $\pm 40^\circ$ ) and forearm pronation/supination ( $\pm 57^\circ$ ). The robot was powered by 4 brushless motors that provided an accurate haptic rendering and compensated for the weight and inertia of the device. Vibro-tactile feedback was generated by 4 vibration motors (307-100 Precision Microdrives). A real-time workstation controlled both the robotic device and the vibration motors by means of an analog-digital I/O PCI card (Sensoray, model 626) with four counters reading the wrist positions from the optical encoders embedded in the DC motors. The software environment was based on Real-Time Windows Target™. The system was integrated with a visual virtual reality environment running at 60 Hz that presented visual feedback to the participant on a computer screen, positioned in front of the subject about 1 m away.

### 3.3. Experimental design

Participants trained and their performance was assessed over a period of 15 days. Figure 1A outlines the number of assessment and training sessions performed each day. Each training session lasted about 40 minutes. In the first two days, subjects trained once per day (Tr1 and Tr2). Sensory and motor performance was evaluated before training (Baseline), and 5 minutes immediately after the end of each training session (Tr1+5', Tr2+5'). Short-term retention was assessed after 2 hours (Tr2+2h). We called this block the *first learning phase*. On Day 3 participants did not train, but were evaluated (Tr2+1d) to obtain a second retention measure of the initial learning. On Day 4 and 5 training and assessment was repeated in the same fashion as on Day 1 and 2. We called this block the *second learning phase*. To evaluate the retention of learning after training, participants performed the assessment test on Day 6, 7, 8, and 15 (see Figure 1A).

*Figure 1 About Here*

### 3.4. Assessment of proprioceptive acuity

In order to assess proprioceptive acuity of the wrist joint position sense, we asked participants to perform an ipsilateral joint position matching (JPM) task (Goble, 2010). With vision occluded, the subject's hand was passively moved by the robot along a minimum jerk trajectory from the central start position to a predetermined position (target), held for 3 s, and then repositioned to the start position.

After a subsequent acoustic cue, the participant attempted to match the previous joint position by actively moving the wrist to the perceived target position. Participants held the position and verbally indicated to the experimenter that their matched joint position was reached. The experimenter confirmed and the robot moved the hand back to the starting position. The targets were spaced on an ellipse with semi-major and semi-minor axis corresponding to 35° of flexion/extension and 10° of abduction/adduction accounting for the biomechanical anisotropy of the wrist between the two DoFs. The 8 targets had the following joint coordinates (Fle/Ext, Abd/Add): Target 1 (+35°, 0°); Target 2 (+9.6°, +9.6°); Target 3 (0°, +10°); Target 4 (-9.6°, +9.6°); Target 5 (-35°, 0°); Target 6 (-9.6°, -9.6°); Target 7 (0°, -10°); Target 8 (+9.6°, -9.6°). The first 5 targets were practiced during training, while the remaining 3 targets were not trained. The 8 targets were repeated 5 times, for a total of 40 trials. In order to avoid that participants began to memorize targets, the presentation of targets was randomized.

### 3.5. Sensorimotor training: Wrist reaching task

Subjects performed discrete center-out reaching movements to five targets. Participants only saw the final target position on the screen, while vision of the wrist/hand was occluded by a panel. When a target was reached, an auditory stimulus and visual feedback of hand's position were given and the robot passively moved the subject's wrist back to the center of the workspace, before initiation of the next trial. The five targets were equally spaced on a semi-ellipse with the major and minor axes corresponding to 35° of flexion/extension and 10° of abduction (i.e. half the workspace of the JPM assessment task). Each training session consisted of a total of 240 movements that were administered in four blocks of 60 movements with 12 repetitions of each of the five targets. Between blocks participants rested for 5 minutes. The order of the target presentation within a block was randomized. Each block had a different level of task difficulty. With increasing task difficulty, participants were required to execute the task with higher spatial accuracy as the target size decreased. During execution, the maximum Euclidian distance (ED) between wrist and target position was evaluated at runtime in joint coordinates:

$$ED = \sqrt{(x_W - x_{TG})^2 + (y_W - y_{TG})^2} \quad (1)$$

, where TG and W are the target and the wrist position, while x and y are the coordinates in the joint space of flexion/extension and abduction/adduction respectively. The difficulty level increased from 1 to 4 as the ED decreased (level 1: ED = 3°; level 2: ED = 2°; level 3: ED = 1.5°; level 4: ED = 1°; see Figure 1C).

While performing a center-out movement, participants received vibro-tactile feedback. We applied VTF for several reasons. First, we intentionally restricted visual feedback, in order to “challenge” learner to rely on proprioception and to control for the contribution of vision to learning outcomes. Second, we knew from our previous work (Cuppone et al., 2016) that VTF augments proprioceptive feedback and enhances somatosensory and motor performance. Four vibro-tactile actuators (307-100 Precision Microdrive) were positioned on the forearm (Figure 1B). Each vibromotor provided feedback for movement in a specific direction for the 2 DoFs of the wrist. The lateral vibrator turned on during wrist flexion, the medial during extension, while the anterior vibrator was active during adduction and the posterior during abduction. While performing the center-out task, the real-time system checked whether the participant deviated from the ideal straight line path towards the target by evaluating the lateral deviation (defined as the vector connecting the wrist current position to its orthogonal projection on the ideal trajectory). The feedback was available when the lateral deviation was higher than the given threshold. The threshold corresponded to the ED set in each difficulty level, as shown in Figure 1C. Therefore, the higher the difficulty level, the lower was the necessary minimal lateral deviation that triggered VTF.

Furthermore, movement feedback about the extent of the deviation from the ideal path was encoded by vibration amplitude and frequency in three frequency bands (70, 80, 90 Hz). Both amplitude and frequency increased as the deviation from the ideal path increased (see Table 1).

*Table 1 About Here*

### **3.6. Measurements**

#### *3.6.1. Proprioceptive assessment outcome measures*

The ipsilateral joint position matching task yielded two measures of sensory acuity: Position error and position error variability. Position error (PE) represents a measure of trueness or its inverse, bias. It is defined as the Euclidean distance between the target and the barycenter of the final joint positions of the five trials per target:

$$PE = \sqrt{(x_B - x_{TG})^2 + (y_B - y_{TG})^2} \quad (2)$$

, where B is the barycenter, TG the target and x and y are the coordinates in the joint space of flexion/extension and abduction/adduction respectively. The barycenter coordinates are:

$$x_B = \frac{1}{R} \sum_i^R x_i; y_B = \frac{1}{R} \sum_i^R y_i \quad (3)$$

, where  $x_i$  and  $y_i$  are the joint coordinates of final joint position and R is the total number of trials repetitions per target (= 5).

Position error variability (SDPE) represents a measure of precision or reliability and is defined as the standard deviation of the final joint positions over the 5 trials repetitions:

$$SDPE = \sqrt{var_x^2 + var_y^2} \quad (4)$$

, where  $var_x^2$  and  $var_y^2$  are  $\sqrt{\frac{1}{R-1} \sum_{i=1}^R |x_i - x_B|^2}$  and  $\sqrt{\frac{1}{R-1} \sum_{i=1}^R |y_i - y_B|^2}$  respectively, with  $x_B$ ,  $y_B$ ,  $x_i$  and  $y_i$  defined as in Equation 3.

### 3.6.2. Motor outcome measures

In order to evaluate the changes in motor performance due to training, we considered two variables: Movement time and maximum angular displacement. *Movement Time (MT)* represents the time between movement onset and end. Movement onset is identified as the first time when the wrist angular velocity exceeded 5% of the peak velocity. Movement end is detected when, for the first time, the Euclidian distance between joint position and target is smaller than the target size, i.e. the participant reaches the target zone. *Maximum Displacement (Dmax)*, is the highest measured lateral deviation of the wrist joint trajectory from the ideal path (i.e. the straight line connecting the starting point with the target).

### 3.7. Statistical data analysis

To determine the effect of sensorimotor training on somatosensory learning, we performed two-way (5 TIME by 2 WORKSPACE) repeated measure Analysis of Variance (RM ANOVA) procedures for PE

and SDPE with the factors TIME (Baseline, Tr2+5', Tr2+2h, Tr4+5' and Tr4+2h) and WORKSPACE (trained vs. untrained). To determine the effect of sensorimotor training on somatosensory learning over the complete training (1<sup>st</sup> + 2<sup>nd</sup> learning phase), we executed a three-way (4 LEARNING TIME by 2 PHASE by 2 WORKSPACE) RM ANOVA for PE and SDPE with the factors LEARNING TIME (4 assessment sessions within each learning phase: Baseline, Tr1+5', Tr2+5' and Tr2+2h for the 1<sup>st</sup> learning phase; Tr2+2d, Tr3+5', Tr4+5', Tr4+2h for the 2<sup>st</sup> learning phase), PHASE (1<sup>st</sup> or 2<sup>nd</sup> learning) and WORKSPACE (trained vs. untrained). For the analysis of retention a two-way (5 RETENTION TIME by 2 WORKSPACE) RM ANOVA for PE and SDPE with the factors RETENTION TIME (Baseline, Tr4+1d vs Tr4+2d vs Tr4+3d vs Tr4+4d) and WORKSPACE (trained vs. untrained) was performed. For subsequent post-hoc analysis we applied repeated t-tests with Bonferroni corrections.

For both variables (PE and SDPE) in each analysis we checked the violation of sphericity with the Mauchly's Test, and we found  $p > 0.05$ , which states that there is no difference in variances for all pairwise group comparisons.

## 4. RESULTS

### 4.1. Training effects on wrist position sense

To evaluate somatosensory learning, we analyzed position error (PE) as a measure of bias and position error variability (SDPE) as a measure of precision. Figure 2 provides an overview of the various training and assessments sessions that took place over a 15-day period. To determine training effects across the four days of training, we performed repeated measures ANOVA for PE and SDPE with the factors TIME (9 assessments from baseline to training day 4+2h) and WORKSPACE (trained vs. untrained). We found that participants significantly reduced PE over the 4-day training (main effect for TIME;  $F(4, 36) = 6.64, p < 0.001$  RM ANOVA; see Figure 2, middle panel). Subsequent post-hoc analysis revealed that mean PE decreased from  $3.07^\circ \pm 0.16^\circ$  at baseline to  $2.30^\circ \pm 0.13^\circ$  immediately after training end (Tr4+5';  $t(9) = 3.49, p = 0.007$ , paired t-test) - a relative improvement of 23%. Two hours after the end of training (Tr4+2h), mean PE had dropped further to  $1.98^\circ \pm 0.20^\circ$  ( $t(9) = 3.59, p = 0.006$ , paired t-test), a 32% decrease with respect to baseline. Analysis of the *first learning phase* showed that mean PE after two days of training was reduced in the first two hours after the cessation of training

from  $2.92^\circ \pm 0.20$  (Tr2+5') to  $2.66^\circ \pm 0.17^\circ$  (Tr2+2h). Neither the main effect for WORKSPACE nor the TIME x WORKSPACE interaction were significant.

The corresponding analysis for SDPE showed that participants also increased position sense precision with training. Mean SDPE decreased from  $3.22^\circ \pm 0.20^\circ$  at baseline to  $2.21^\circ \pm 0.11^\circ$  at the end of practice (Tr4+5') - an improvement in response reliability of 29% ( $t(9) = 4$   $p = 0.003$ , paired t-test; Figure 2, bottom panel). The respective main effects for TIME and WORKSPACE were significant (TIME:  $F(4, 36) = 12.5$   $p < 0.001$  ; WORKSPACE:  $F(1, 9) = 11.5$   $p < 0.001$ ) as well as the WORKSPACE x TIME interaction ( $F(4, 36) = 2.8$   $p = 0.042$ , RM ANOVA). Two hours after the last training session (Tr4+2h), SDPE had further decreased to 34% of the baseline value ( $t(9) = 5.54$   $p < 0.001$ , paired t-test). It is noteworthy, that at the end of *first learning phase*, mean SDPE had decreased from baseline by 22% after 2 hours after training (Tr2+2h: ( $t(9) = 3.87$   $p = 0.003$ , paired t-test) only for trained positions. That is, the early change in SDPE was workspace dependent. In summary, the finding of a decrease in position sense bias and an increase in position sense precision indicate that somatosensory learning occurred over the 4-day training period.

*Figure 2 About Here*

#### 4.2. Effect of repeated training on wrist position sense

To understand how repeated sensorimotor learning influences position sense acuity and to examine, if repeated learning after initial consolidation was indeed associated with reduced learning costs, we compared the *first learning* with the *second learning phase*. Figure 3 shows the comparisons between the first and the last assessment in each of the two learning phases. A three-way repeated measures with the factors PHASE (first vs. second), LEARNING TIME (4 assessment sessions in each phase), and WORKSPACE (trained vs. untrained) for PE yielded significant main effects for LEARNING TIME ( $F(3, 27) = 4.55$   $p = 0.01$ , RM ANOVA) and PHASE ( $F(1, 9) = 9.01$   $p = 0.015$ , RM ANOVA), but no significant effect for WORKSPACE ( $p > 0.05$ ). During the *first learning phase* no significant change in PE was observed. However, between the beginning and the end of the *second learning phase* (days 2-4), mean PE decreased significantly (Tr2+2d:  $2.95^\circ \pm 0.33^\circ$ ; Tr4+2h:  $1.91^\circ \pm 0.2^\circ$ ;  $t(9) = 6.06$   $p = 0.009$ , paired t-test). The mean relative reduction in PE in the *first learning phase* was  $11.2\% \pm 7.5\%$ , and  $30.7\% \pm 4.9\%$  in the *second learning phase* (see Table 2 for details and all statistical comparisons).

Subsequent analysis of SDPE revealed significant main effects for PHASE ( $F(1, 9) = 34.5$   $p < 0.001$ , RM ANOVA), LEARNING TIME ( $F(3, 27) = 4.3$   $p = 0.013$ , RM ANOVA), and WORKSPACE ( $F(1, 9) = 15.7$   $p = 0.003$ , RM ANOVA) as well as a significant PHASE x WORKSPACE interaction ( $F(1, 9) = 6.7$   $p = 0.029$ , RM ANOVA). For the trained positions, SDPE decreased significantly only in the *first learning phase* ( $3.47^\circ \pm 0.27^\circ$  to  $2.62^\circ \pm 0.14^\circ$ ;  $t(9) = 3.4$   $p = 0.004$  paired t-test; mean relative change:  $-22.5\% \pm 4.9\%$ ; see Figure 3, right panel). For the untrained positions, reduction in response precision was significant only in the *second learning phase*; SDPE was effectively reduced by  $16.3\% \pm 6\%$  from Tr2+2d to Tr4+2h ( $t(9) = 2.97$   $p = 0.016$ , paired t-test; see Figure 3, right panel). Table 3 reports all comparisons performed for the trained/untrained positions.

In summary, the results indicate that significant reductions in PE occurred in the *second learning phase*, regardless of the workspace (trained/ untrained). SDPE, a measure of position sense precision, decreased significantly during the *first learning phase* for trained positions. This effect was delayed for the untrained positions, which showed a significant decrease in SDPE only at the end of the *second learning phase*.

Table 2 About Here

Table 3 About Here

Figure 3 About Here

### 4.3. Retention of somatosensory learning

To evaluate retention of somatosensory learning, we compared PE and SDPE at the baseline with the corresponding values for the next three days following the cessation of training (Tr4+1d, Tr4+2d, Tr4+3d) and after 10 days (Tr4+10d). On the first day after completion of all training (Day 6), mean position error for both the trained and untrained workspace had increased with respect to previous day (see Figure 2, retention phase), but was still significantly different with respect to baseline at the beginning of training (Baseline:  $3.07^\circ \pm 0.16^\circ$ ; Tr4+1d:  $2.32^\circ \pm 0.22^\circ$ ;  $t(9) = 2.56$   $p = 0.03$ , paired t-test).

Two days after the end of training, mean PE for the trained positions remained significantly lower than baseline (Baseline:  $3.13^\circ \pm 0.41^\circ$ ; Tr4 +2d:  $1.90^\circ \pm 0.19^\circ$ ;  $t(9) = 2.51$   $p = 0.03$ , paired t-test), while it had increased for untrained positions and was no longer significantly different from the pre-training state ( $p > 0.05$ ). Ten days after training, the effects of learning were no longer detectable. Mean PE at Tr4+10d for neither the trained nor the untrained positions was significantly different from the

corresponding baseline value. The polar plots in Figure 4 graphically highlight how limb position sense bias and precision changed during the 10-day retention phase for the different target positions. In contrast to bias that increased over time, precision did not show signs of significant decay: mean SDPE for both trained and untrained target workspace was significantly different from baseline throughout the retention phase (RETENTION TIME:  $F(4, 36) = 28.4$   $p < 0.001$ , WORKSPACE:  $F(1, 9) = 27.2$   $p < 0.001$ ; see Figure 4, bottom panel).

*Figure 4 About Here*

#### **4.4. Measures of motor learning**

During training we monitored maximum angular displacement (Dmax) and movement time (MT) as measures of motor learning. For each of the four training sessions, we compared a subject's performance at the beginning (EarlyTr1) with the performance at end of each session (LateTr<sub>i</sub>, with  $i = 1, 2, 3, 4$ ). Performance at session begin was expressed as the mean value of the second and third target sequence. The first target sequence was considered a familiarization phase and therefore excluded from further analysis. The late training effects were based on the mean of the 11<sup>th</sup> and 12<sup>th</sup> target sequence in each session (each session consisted of 12 target sequences of 5 trials each). Figure 5 shows the training-related change of MT and Dmax for each level of difficulty. The level of difficulty was based on the type of vibrotactile feedback the learner received (see Table 1 for details). Respective repeated measures ANOVA procedures with the factors TIME (early vs. late training) and LEVEL (level 1 to 4) for both variables yielded a significant main effects for TIME (Max Displacement:  $F(3, 27) = 14.5$   $p < 0.001$ ; Movement Time:  $F(3, 27) = 26.8$   $p < 0.001$ , RM ANOVA) and LEVEL (Max Displacement:  $F(3, 27) = 3.9$   $p = 0.02$ ; Movement Time:  $F(3, 27) = 67.8$   $p < 0.001$ , RM ANOVA). The TIME x LEVEL interaction was not significant ( $p > 0.05$ ). Movement time significantly decreased at the end of the first training session (EarlyTr1:  $4.73s \pm 0.38s$  vs. LateTr1:  $3.58s \pm 0.26s$ ,  $t(9) = 3.7$   $p = 0.005$ , paired t-test) - the relative mean reduction in MT was  $22.8\% \pm 5.3\%$ . MT did not significantly change from LateTr1 to LateTr2, but decreased later, from LateTr2:  $2.94s \pm 0.15s$  to LateTr3:  $2.19s \pm 0.20s$  ( $t(9) = 2.3$   $p = 0.044$ , paired t-test). MT did not change significantly at the last training session (LateTr3 vs. LateTr4,  $p > 0.05$ ; see Figure 5, top panel). By the end of the third training session Dmax was significantly different from early training (EarlyTr1:  $2.83^\circ \pm 0.16^\circ$  vs LateTr3:  $1.96^\circ \pm 0.12^\circ$ ,  $t(9) = 4$   $p = 0.003$ , paired t-test), indicating the

magnitude of lateral deviations of the wrist joint trajectory from the ideal path had decreased with practice.

Figure 6 shows the relative change of motor outcomes (MT and Dmax) and the position sense measures (PE and SDPE), in order to illustrate the extent of somatosensory and motor learning. Each motor and sensory measurement was normalized with respect to its own baseline. We applied linear regression procedures to fit the respective mean data. The coefficient of determination for MT ( $m: -13.27 \pm 1.76$ ,  $R^2 = 0.73$ ) was significantly different from that of PE ( $m: -4.84 \pm 2.21$ ,  $R^2 = 0.34$ ,  $t(9) = 3.5$   $p = 0.006$ , paired t-test) and of SDPE ( $m: -7.86 \pm 1.28$ ,  $R^2 = 0.6$ ,  $t(9) = 2.3$   $p = 0.043$ , paired t-test), indicating that temporal changes in motor learning were fast. In contrast, the slope of Dmax indicating the pace of spatial motor learning was not different from both sensory measures (PE and SDPE;  $p$ 's > 0.05).

*Figure 5 About Here*

*Figure 6 About Here*

## 5. DISCUSSION

The goal of the present study was threefold: First, to map the effect of repeated sensorimotor training on position sense acuity as a marker of proprioceptive function. Second, to establish if repeated somatosensory learning builds upon previously acquired somatosensory memory and shows 'costs savings' similar to those observed for motor memory consolidation during motor learning. Third, to investigate the retention of somatosensory learning for a period of up to 10 days after the end of training.

The main results of the study are summarized as follows: First, somatosensory (proprioceptive) learning shows signs of cost savings with repeated sensorimotor training. Consolidation of learning was observed after 2 hours at the end of each learning phase. Moreover, somatosensory learning generalized to untrained workspace. Second, somatosensory learning over days can be characterized as an early improvement in sensory precision and a later improvement in sensory bias. Third, the time course of learning gains in position sense acuity coincided with improvements in spatial movement accuracy. Finally, the gains of somatosensory learning were retained for several days. Improvements in position sense bias were still visible up to 3 days after the end of practice for trained workspace positions, but decayed faster in the untrained workspace. Improvements in position sense precision

were retained for up to 10 days and were workspace independent. In the following, we will discuss our main findings and their implications in more detail.

### **5.1. Somatosensory learning, cost savings and memory consolidation**

Consolidation of motor skill memory has been widely studied. Twenty years ago, a set of seminal studies showed that adaptation to a viscous force field in reaching movements is more rapid and complete when participants are trained a second time after an interval of hours or days (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1997). In addition, this adaptive motor learning is not local, but generalizes to neighboring regions of the workspace (Shadmehr and Mussa-Ivaldi, 1994; Gandolfo et al., 1996), which implies that the formation of internal motor models underlies motor skill acquisition (Krakauer and Shadmehr, 2006). We here saw that the formation of somatosensory memory associated with motor practice shares some of the same features. Learning gains in proprioceptive acuity were consolidated within hours after practice. Repeated practice over days showed ‘savings’, meaning that acuity had not dropped to pre-training levels. And, finally, the improvements in proprioceptive acuity generalized to untrained workspace. Computationally, these features are consistent with the acquisition of an internal somatosensory model of joint space. They are inconsistent with a view that somatosensory learning results in a neural map of visited somatosensory states expected by an associative learning process. Somatosensory learning closely corresponds to motor learning with the distinction that the degree of generalization to untrained portions of the sensory space is more extensive than the generalization to untrained motor workspace observed during adaptive motor learning (Shadmehr and Mussa-Ivaldi, 1994; Wolpert et al., 1998; Shadmehr and Holcomb, 2009).

The analysis of how both markers of position sense acuity, bias and precision, changed over the 4-day training period, provided additional insight into the learning process. Based on this analysis, early somatosensory learning was characterized by rapid improvements in somatosensory precision, that is, response variability decreased and responses became more consistent. With continued practice (days 3-4 in our experiment) somatosensory bias showed solid gains - reductions in positions sense bias were 11% in the first and 31% the second learning phase (see Figures 2, 3). Importantly, learning generalized as reductions in position sense bias were observed in the whole joint workspace. Yet, improvements in precision during early practice were localized to the workspace experienced during training, and only subsequently generalized to the untrained portion of the workspace.

As a caveat, one may argue that our results are not directly comparable to the findings obtained in force adaptation studies (e.g. (Shadmehr and Mussa-Ivaldi, 1994)). It is true that our motor task did not include a perturbing force field, but represented a skill learning task with the goal to improve motor performance by producing straight joint trajectories “as quickly as possible”. Nevertheless, the task provided a strong incentive to reduce lateral deviations of the generated trajectory – a feature also seen during force adaptation learning. That is, while the tasks represented different forms of implicit learning (Squire and Zola, 1996), they both required proprioceptive sensing.

Moreover, while our study showed clear evidence for a transfer of sensory learning to untrained workspace, another study reported that proprioceptive acuity improved only in the region of the arm’s workspace explored during learning (Wong et al., 2011). Two factors likely contributed to the observed differences. In the study by Wong and coworkers, learners only trained once and proprioception was only assessed immediately after practice. In contrast, our participants trained over a period of 5 days and retention was monitored for another 10 days. Thus, it is plausible that observable changes of proprioceptive acuity in the untrained workspace require a more intensive training volume than a single training session can provide.

## **5.2. Retention of somatosensory learning**

One aim of the study was to examine to what extent somatosensory memory is retained after learning. Numerous studies documented that somatosensory learning coincides with force-field learning (Haith et al., 2008; Ostry et al., 2010; Vahdat et al., 2011; Mattar et al., 2013), visuomotor adaptation (Malfait et al., 2008; Cressman and Henriques, 2009; Volcic et al., 2013) and prism adaptation (Harris, 1963; Welch, 1974; Melamed et al., 1979). However, these studies did not systematically investigate retention over days. Yet, gaining a more complete understanding, of how somatosensory memory consolidates or decays over time is informative for understanding processes of motor skill acquisition, because they rely of proprioceptive information.

The analysis of position sense bias and precision in our study revealed two times courses of retention. Proprioceptive precision was essentially retained for up to 10 days after practice for both trained and untrained workspaces. That is, the gains in response variability to the same proprioceptive stimuli were preserved after practice. In contrast, position sense bias remained approximately stable for the first two days after practice (and different from baseline; see Figure 2), but then showed signs of decay. Ten days after practice, the learning gains had nearly vanished and the respective mean

position error was no longer different from the baseline mean. It is noteworthy that rates of memory decay were different for the trained and untrained workspace. Position sense bias for the trained workspace remained stable for up to three days after practice (Day 8 or Tr4+3d; see Figure 2), while it began to increase for the untrained target position already after two days. This indicates that although sensory learning extended to untrained joint space positions with practice, the effect of generalization in the untrained joint space was more transient.

### **5.3. Comparing the time course of motor and somatosensory learning**

This study concurrently monitored measures of motor and proprioceptive function, which allowed us to compare the time-course of learning-related changes in the sensory as well as in the motor domain. In general, the sensorimotor training program of the first five days required learners to make increasingly accurate wrist joint movements. In order to be successful in the task, learners had to improve their spatial movement accuracy. This demand on motor learning required the availability of joint position information with sufficient spatial resolution. Comparing the time course of improvements in proprioceptive with those in motor function shows, indeed, that gains in position sense precision closely matched the gains in movement accuracy (i.e., reduced  $D_{max}$ , see Fig. 6). Substantial improvements in proprioceptive bias were not seen before the second day to training, indicating that shifts in bias occur in the time scale of days, not hours. Because this study lacks data on the neural correlates of sensorimotor learning, one can only speculate about the underlying neural mechanisms. However, studies of experience-dependent somatosensory learning in rodents have identified a fast process of synaptic plasticity in somatosensory cortex that is driven by long-term potentiation (Hardingham et al., 2003) and may lead to changes in excitatory post-synaptic potentials within minutes and hours. Another process of structural plasticity that requires days, involves cellular elements in the cortex including changes in dendritic spines, presynaptic terminals and axons (Fox, 2009).

A set of other studies investigating the time course of proprioceptive learning used an approach in which proprioceptive information was misaligned with available visual information during motor execution and then mapped the process of adaptive sensorimotor learning. The underlying process referred to as proprioceptive recalibration shows that shifts in the perception of limb position can be slower than the changes in motor performance (Zbib et al., 2016), which is not what we have observed here. While it is quite plausible that the process of proprioceptive recalibration may occur

independently of motor learning (Mostafa et al., 2015), the current study shows that the motor learning and somatosensory learning are temporally closely linked when visual and proprioceptive information is congruent and no sensory recalibration is required.

#### **5.4. The role of vibro-tactile feedback in somatosensory learning**

During learning, participants saw the target, but did not receive visual feedback about their movement trajectories. This allowed us to control for and minimize the contribution of vision to goal-directed motor learning. Instead we applied VTF as wrist trajectory guidance feedback. We opted for VTF as it constitutes another form of somatosensory information in conjunction to proprioception. Its effectiveness as a sensory substitute or augmentation to vision was demonstrated earlier (Cuppone et al., 2016), and can be based on two scenarios: Firstly, VTF stimulates overlapping neuronal networks involved in the processing of somatosensory afferents in the somatosensory cortices. Such co-stimulation could serve to amplify neural activity in those regions that are central for forming proprioceptive percepts. Secondly, it is the movement related error feedback provided through VTF that is essential for inducing the observed changes in limb position sense. In other words, the sensory modality providing the relevant error cues is not important, but it is the saliency of the error information. We would contend that both factors plausibly play a role in enhancing proprioceptive function.

#### **5.5. Summary and conclusion**

Gibson (Gibson, 1966) defined perceptual visual learning as an increase in the organism's ability to extract information from the environment, as a result of experience and practice. Here we studied the process of visuo-somatosensory-motor learning and mapped the increase of the human ability to "extract" somatosensory-based information and consolidate it to memory. We found that somatosensory learning is temporally closely linked to motor learning and reveals similar features of memory formation. Motor and somatosensory memory consolidation show both signs of cost savings with repeated sensorimotor training. The link between motor and somatosensory learning becomes evident as the time course of learning gains in position sense acuity coincided with improvements in spatial movement accuracy. Moreover, somatosensory learning generalized to untrained workspace - a finding consistent with the view that an internal model of somatosensory joint space is formed during motor learning. Finally, the gains of proprioceptive acuity as measured by position sense bias were

retained for several days, but decayed faster in the untrained workspace. Improvements in position sense precision were retained for up to 10 days and were workspace independent.

## 6. ACKNOWLEDGEMENTS

The authors gratefully acknowledge Dr. Valentina Squeri for offering insightful comments on the experimental work and on earlier versions of the manuscript. The authors declare no competing financial interests.

ACCEPTED MANUSCRIPT

## 7. REFERENCES

- Arce-McShane FI, Hatsopoulos NG, Lee J-C, Ross CF, Sessle BJ (2014) Modulation dynamics in the orofacial sensorimotor cortex during motor skill acquisition. *J Neurosci* 34:5985–5997.
- Brashers-Krug T, Shadmehr R, Bizzi E (1996) Consolidation in human motor memory. *Nature* 382:252–255.
- Cressman EK, Henriques DYP (2009) Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102:3505–3518.
- Crystal HA, Grober E, Masur D (1989) Preservation of musical memory in Alzheimer's disease. *J Neurol Neurosurg Psychiatry* 52:1415–1416.
- Cuppone A, Squeri V, Semprini M, Konczak J (2015) Robot - assisted training to improve proprioception does benefit from added vibro - tactile feedback. In: 37th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC), pp 258–261. Milan.
- Cuppone AV, Squeri V, Semprini M, Masia L, Konczak J (2016) Robot-assisted proprioceptive training with added vibro-tactile feedback enhances somatosensory and motor performance. *PLoS One* 11:1–18.
- Elangovan N, Cappello L, Masia L, Aman J, Konczak J (2017) A robot-aided visuo-motor training that improves proprioception and spatial accuracy of untrained movement. *Sci Rep* 7:1–10.
- Fox K (2009) Experience-dependent plasticity mechanisms for neural rehabilitation in somatosensory cortex. *Philos Trans R Soc Lond B Biol Sci* 364:369–381.
- Gandolfo F, Mussa-Ivaldi FA, Bizzi E, Sciences C (1996) Motor learning by field approximation. *Proc Natl Acad Sci U S A* 93:3843–3846.
- Gibson JJ (1966) The senses considered as perceptual systems. In. Boston: Houghton Mifflin.
- Goble DJ (2010) Proprioceptive acuity assessment via joint position matching: from basic science to general practice. *Phys Ther* 90:1176–1184.
- Haith A, Jackson C, Miall C, Vijayakumar S (2008) Unifying the sensory and motor components of sensorimotor adaptation. Available at: <http://books.nips.cc/nips21.html>.
- Hardingham N, Glazewski S, Pakhotin P, Mizuno K, Chapman PF, Giese KP, Fox K (2003) Neocortical long-term potentiation and experience-dependent synaptic plasticity require alpha-calcium/calmodulin-dependent protein kinase II autophosphorylation. *J Neurosci* 23:4428–4436.
- Harris CS (1963) Adaptation to displaced vision: visual, motor, or proprioceptive change? *Science*

140:812–813.

- Hay JC, Pick HL (1966) Visual and proprioceptive adaptation to optical displacement of the visual stimulus. *J Exp Psychol* 71:150–158.
- Krakauer JW, Shadmehr R (2006) Consolidation of motor memory. *Trends Neurosci* 29:58–64.
- Malfait N, Henriques DY, Gribble PL (2008) Shape distortion produced by isolated mismatch between vision and proprioception. *J Neurophysiol* 99:231–243.
- Martin T a, Keating JG, Goodkin HP, Bastian a J, Thach WT (1996) Throwing while looking through prisms: I. Focal olivocerebellar lesions impair adaptation. *Brain* 119:1183–1198.
- Masia L, Casadio M, Sandini G, Morasso P (2009) Eye-hand coordination during dynamic visuomotor rotations. *PLoS One* 4:e7004.
- Mattar A a G, Darainy M, Ostry DJ (2013) Motor learning and its sensory effects: time course of perceptual change and its presence with gradual introduction of load. *J Neurophysiol* 109:782–791.
- Melamed LE, Beckett PA, Halay M (1979) Individual Differences in the Visual Component of Prism Adaptation. *Perception* 8:699–706 Available at: <http://dx.doi.org/10.1068/p080699>.
- Mostafa AA, Kamran-Disfani R, Bahari-Kashani G, Cressman EK, Henriques DYP (2015) Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace. *Exp Brain Res* 233:817–827 Available at: <http://dx.doi.org/10.1007/s00221-014-4157-9>.
- Nasir SM, Darainy M, Ostry DJ (2013) Sensorimotor adaptation changes the neural coding of somatosensory stimuli. *J Neurophysiol* 109:2077–2085 Available at: <http://jn.physiology.org/cgi/doi/10.1152/jn.00719.2012>.
- Ostry DJ, Darainy M, Mattar AAG, Wong J, Gribble L (2010) Somatosensory Plasticity and Motor Learning. *J Neurosci* 30:5384–5393.
- Ostry DJ, Gribble PL (2016) Sensory Plasticity in Human Motor Learning. *Trends Neurosci* 39:114–123 Available at: <http://dx.doi.org/10.1016/j.tins.2015.12.006>.
- Shadmehr R, Brashers-Krug T (1997) Functional stages in the formation of human long-term motor memory. *J Neurosci* 17:409–419.
- Shadmehr R, Holcomb HH (2009) Neural Correlates of Motor Memory Consolidation. *Science* (80- ) 327:821–825 Available at: <http://www.sciencemag.org/cgi/doi/10.1126/science.277.5327.821>.
- Shadmehr R, Mussa-Ivaldi F a (1994) Adaptive representation of dynamics during learning of a motor

task. *J Neurosci* 14:3208–3224.

Smith MA, Ghazizadeh A, Shadmehr R (2006) Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol* 4:1035–1043.

Squire LR, Zola SM (1996) Structure and function of declarative and nondeclarative memory systems. *Proc Natl Acad Sci U S A* 93:13515–13522.

Vahdat S, Darainy M, Milner TE, Ostry DJ (2011) Functionally Specific Changes in Resting-State Sensorimotor Networks after Motor Learning. *J Neurosci* 31:16907–16915.

Volcic R, Fantoni C, Caudek C, Assad JA, Domini F (2013) Visuomotor Adaptation Changes Stereoscopic Depth Perception and Tactile Discrimination. *J Neurosci* 33:17081–17088 Available at: <http://www.jneurosci.org/cgi/doi/10.1523/JNEUROSCI.2936-13.2013>.

Welch RB (1974) Research on Adaptation to Rearranged Vision: 1966–1974. *Perception* 3:367–392 Available at: <http://dx.doi.org/10.1068/p030367>.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. *Trends Cogn Sci* 2:338–347.

Wong JD, Wilson ET, Gribble PL (2011) Spatially selective enhancement of proprioceptive acuity following motor learning. *J Neurophysiol* 105:2512–2521 Available at: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3094168&tool=pmcentrez&rendertype=abstract> [Accessed December 10, 2014].

Zbib B, Henriques DYP, Cressman EK (2016) Proprioceptive recalibration arises slowly compared to reach adaptation. *Exp Brain Res* 234:2201–2213.

## 8. FIGURE LEGENDS

**Figure 1. Experimental protocol.** **A)** Participants trained in four separate sessions spread over 5 days. Each training consisted of 240 goal-directed movements. Proprioceptive and motor assessments (white blocks) were performed before, after training (5 minutes and 2 hours) and during retention. **B)** Top view of the WristBot and of the vibro-tactile actuators positioned on the forearm. **C)** The four levels of difficulty for the wrist reaching training task shown for one target. Green circle represents the visual target. The pink circle indicates the current wrist position, which was not visible for the participant. The dashed line is the ideal path. Vibro-tactile feedback was available only in the gray regions of the workspace with vibration frequency proportional to the lateral distance. Waves with high, medium and low frequency represent the vibration frequencies of 90Hz, 80Hz and 70Hz, respectively.

**Figure 2. Training-related change of proprioceptive bias and precision.** The top panel indicates the time line of the entire protocol. Middle and bottom panels show the means for bias (PE) and precision (SDPE) of trained (green line) and untrained (orange line) positions. Whiskers indicate 1 SE. Dashed lines indicate the actual training sessions.

**Figure 3. Comparing proprioceptive bias and precision in the two learning phases.** Mean PE (left panel, bottom part) and SDPE (right panel, bottom part) for the *first learning phase* and *second learning phase* for trained and untrained positions. Whiskers indicate 1 SE.

**Figure 4. Retention for somatosensory learning.** The polar plot shows mean values across subjects of PE and SDPE for each target position. The variable's value related to a target position corresponds to a single direction of the polar plot. Targets from 1 to 8 correspond to 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315° angular values of polar coordinates. The positive angle is measured counterclockwise from the right horizontal axis. The gray area indicates the untrained joint positions. Baseline performance is in pink while in bordeaux PE and SDPE values of different retention days.

**Figure 5 Training outcome measures.** Mean values across subjects of Maximum Angular Displacement (top panel) and Movement Time (bottom panel) for each level of difficulty at the beginning of the first training and at the end each training session. Whiskers indicate 1 SE.

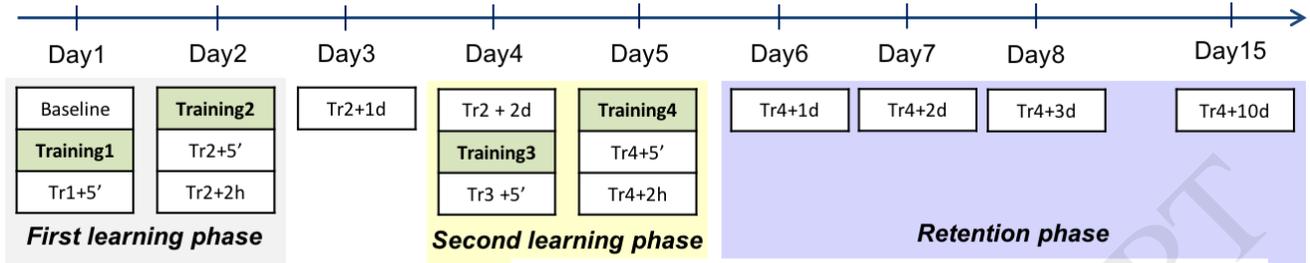
**Figure 6. Comparison of somatosensory and motor learning outcome measure.** The top panel indicates the time line of the protocol. The assessment sessions considered for the measure of

somatosensory learning are highlighted. The bottom panel indicates the relative change of MT, Dmax, PE and SDPE Ratio evaluated as  $1 - \text{Normalized values}$ . In the case of motor outcomes (MT and Dmax), normalization was performed dividing each training phase (EarlyTr1, LateTr1, LateTr2, LateTr3 and LateTr4) by EarlyTr1. For somatosensory outcomes (PE and SDPE) normalization was applied dividing assessment measurements (Baseline, Tr1+5', Tr2+5', Tr3+5' and Tr4+5') by the Baseline. Top x-axis refers to time for somatosensory variables; bottom x-axis refers to time for motor variables.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

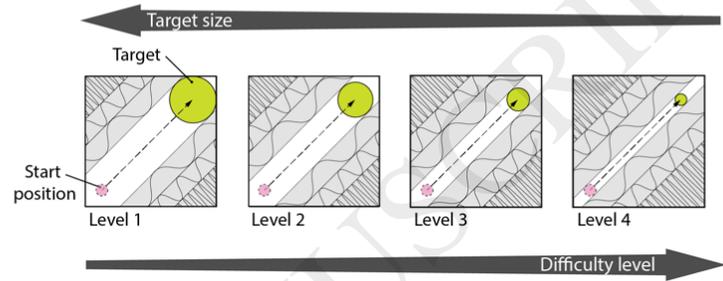
A)

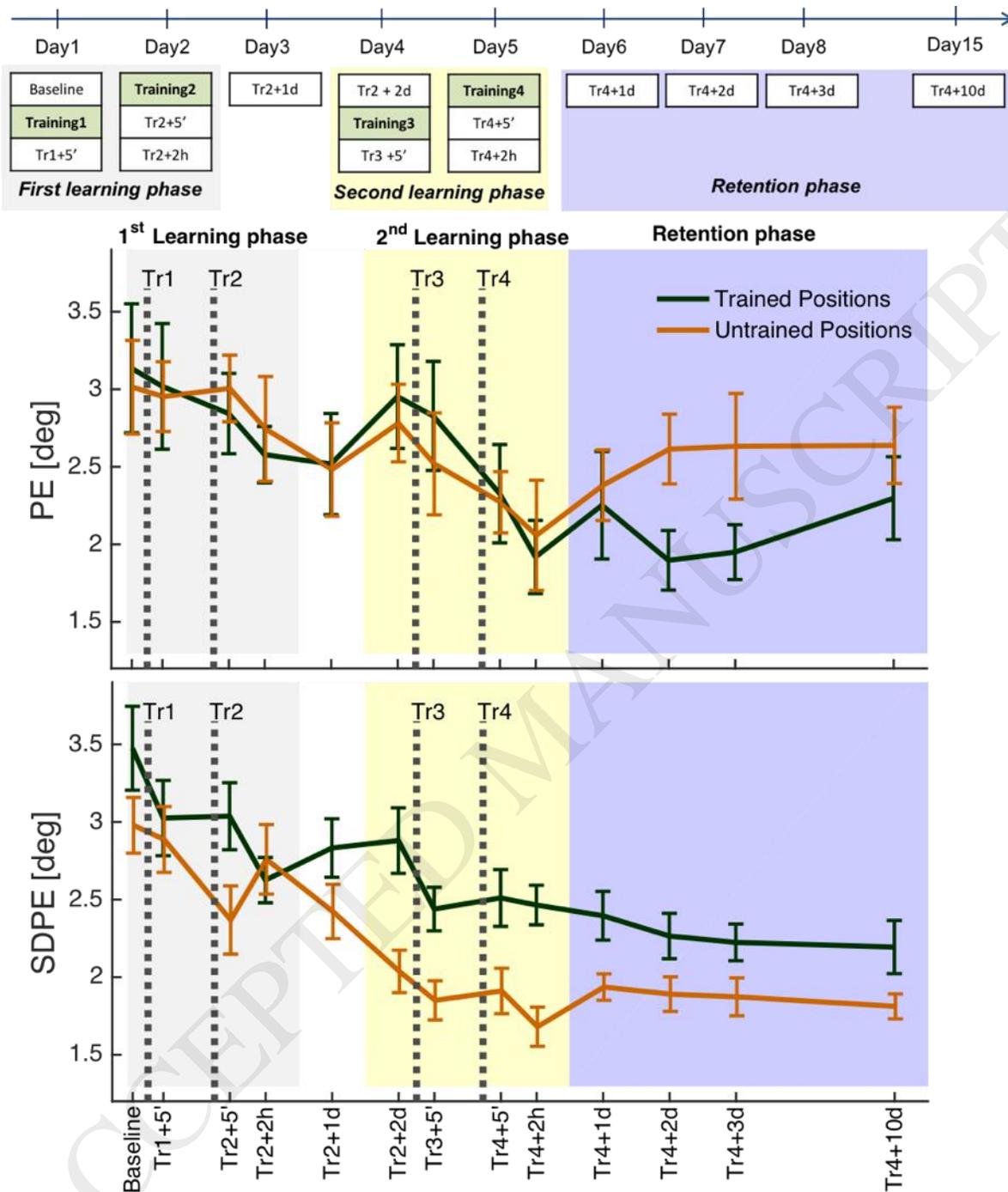


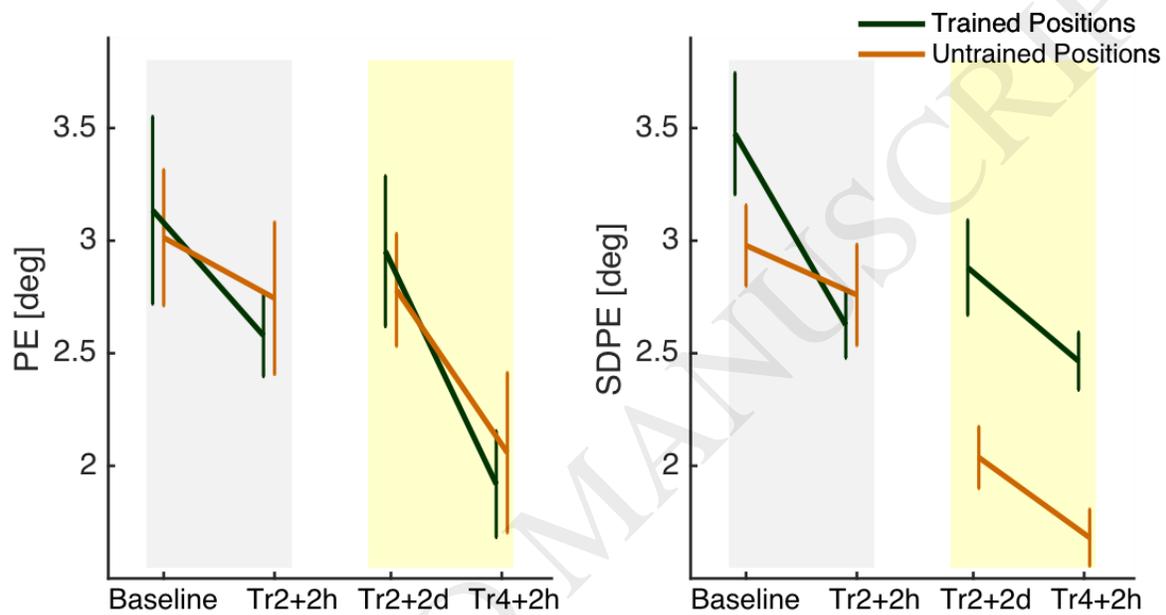
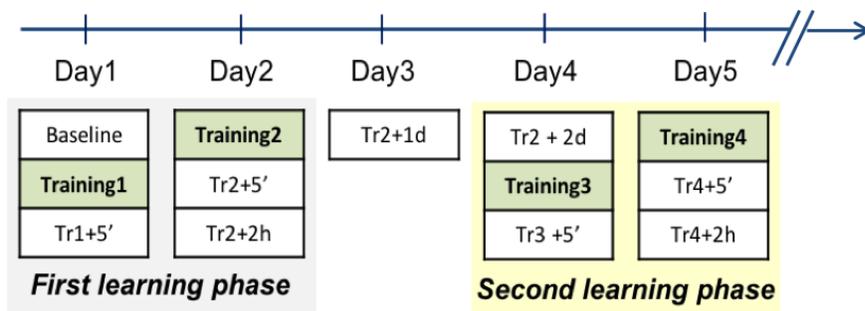
B)

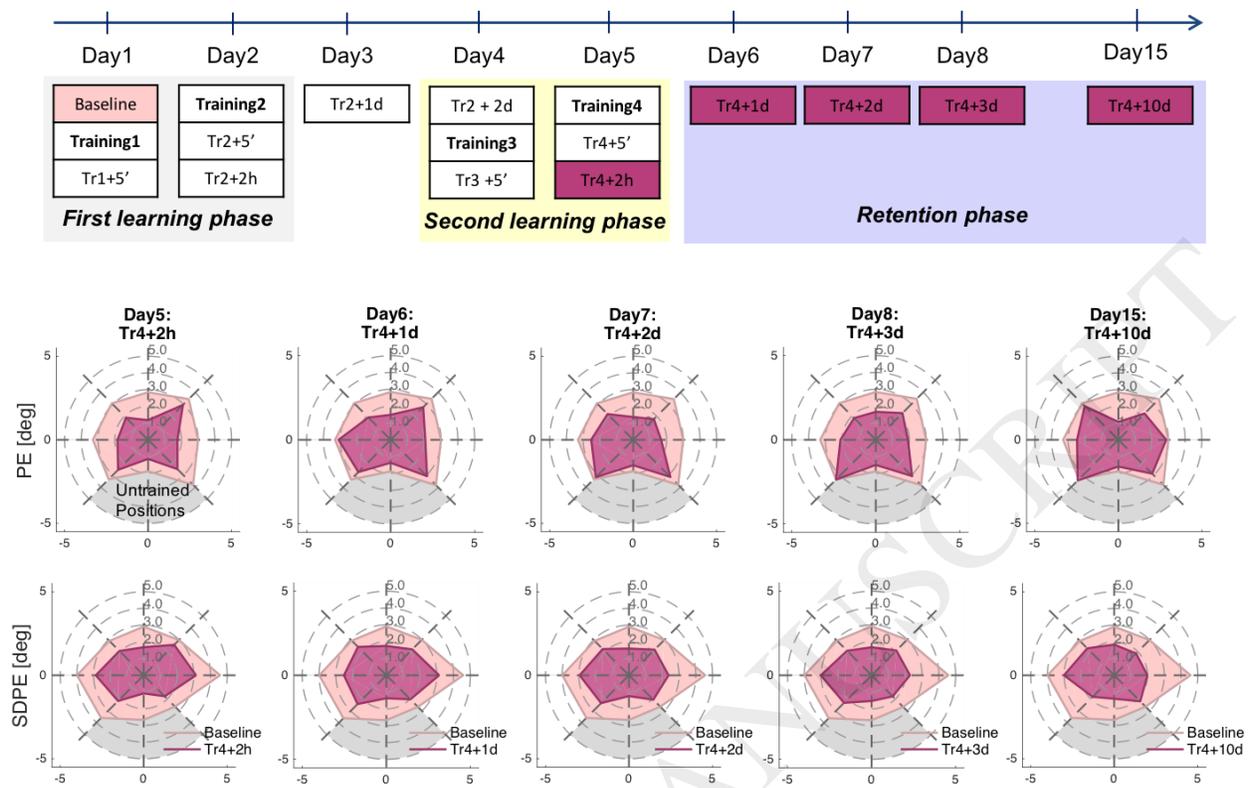


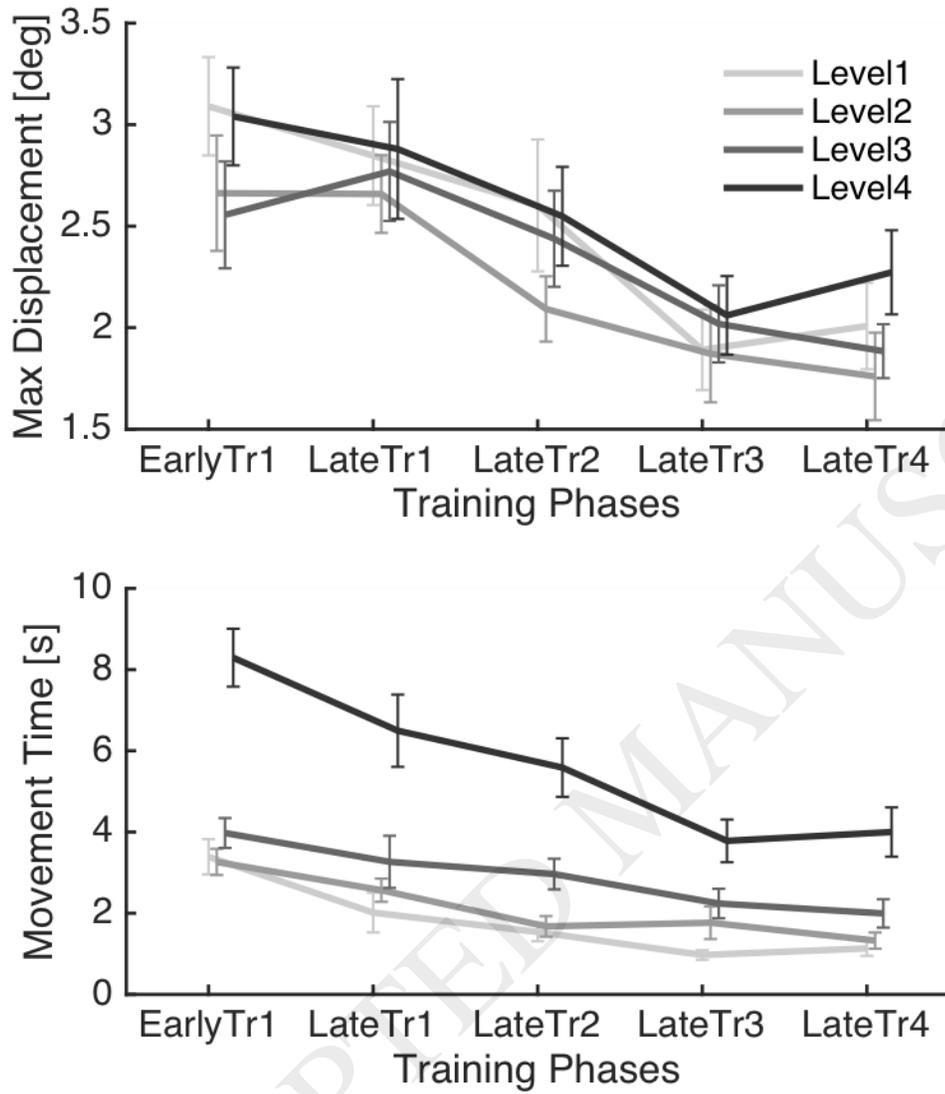
C)

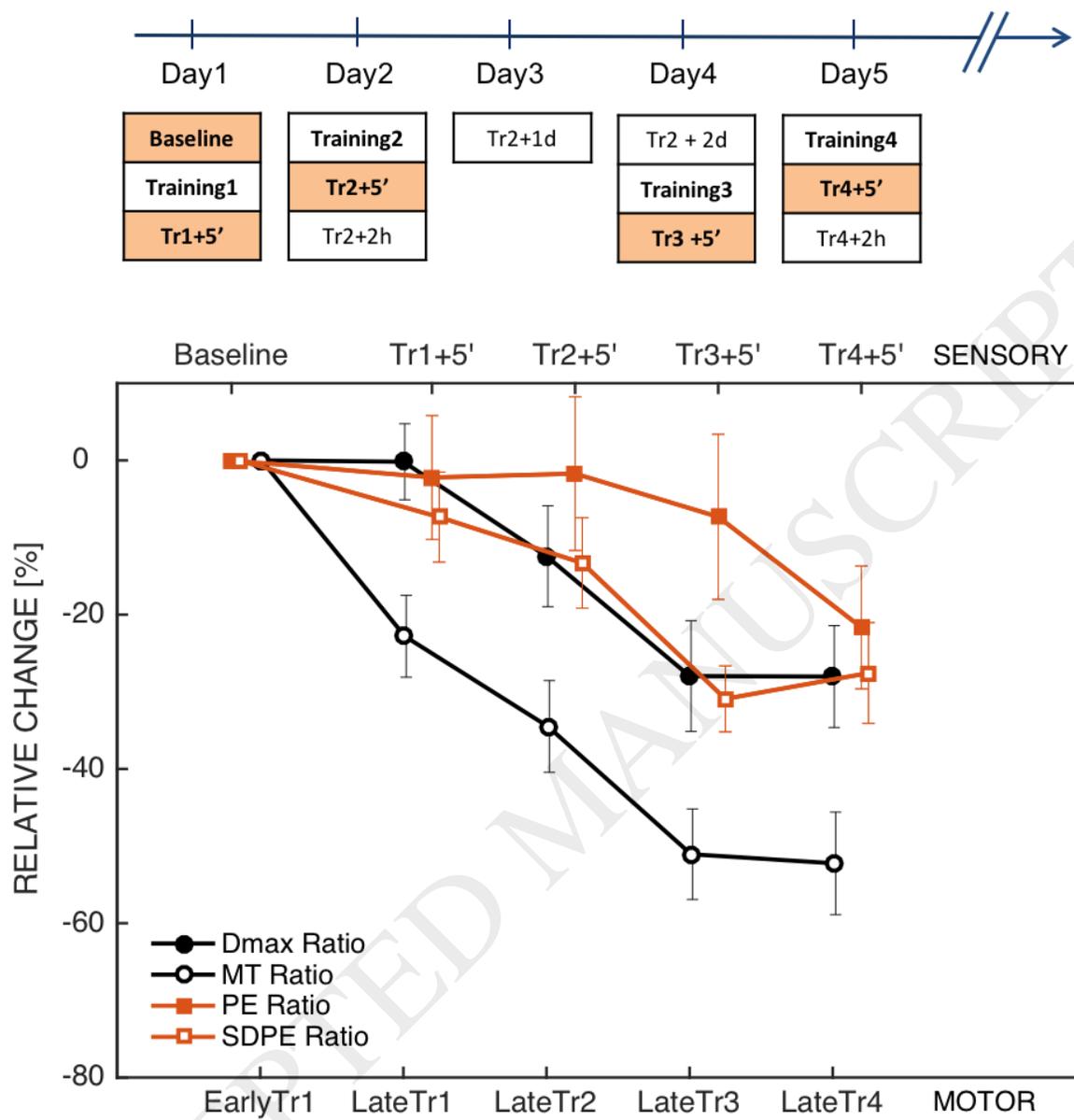












**Table 1.** Settings for the vibration frequency coding of the applied vibro-tactile feedback

Difficulty level	Vibration Frequency [Hz]	Amplitude [g]	Range [deg]
<b>Level 1</b>	70	0.9	3 - 6
	80	1	6 - 9
	90	1.1	> 9
<b>Level 2</b>	70	0.9	2 - 5
	80	1	5 - 8
	90	1.1	> 8
<b>Level 3</b>	70	0.9	1.5 – 4.5
	80	1	4.5 – 7.5
	90	1.1	> 7.5
<b>Level 4</b>	70	0.9	1 - 4
	80	1	4 - 7
	90	1.1	> 7

**Table 2.** Position error (Mean  $\pm$  Standard Error) for trained and untrained positions of the two learning phases. Post-hoc p-values are reported for the intra-phase (initial vs. final assessment) and inter-phase comparisons (1st learning vs. 2nd learning phase). Initial assessment = baseline or Tr2+2d; final assessment = Tr2+2d or Tr4+2h; n.s. = not significant.

PE [deg]	1 <sup>st</sup> learning phase	2 <sup>nd</sup> learning phase	
<b>Trained positions</b>			
Initial assessment	3.13 $\pm$ 0.41	2.95 $\pm$ 0.33	n.s.
Final assessment	2.57 $\pm$ 0.18	1.91 $\pm$ 0.23	t(9) = 3; p = 0.014
	n.s.	t(9) = 3.3; p = 0.009	
<b>Untrained positions</b>			
Initial assessment	3.01 $\pm$ 0.3	2.78 $\pm$ 0.25	n.s.
Final assessment	2.74 $\pm$ 0.33	2.06 $\pm$ 0.35	t(9) = 2.4; p = 0.04
	n.s.	t(9) = 3.3; p = 0.009	

**Table 3.** Position error variability (Mean  $\pm$  Standard Error) for trained and untrained positions of the two learning phases. Post-hoc p-values are reported for the intra-phase (initial vs. final assessment) and inter-phase comparisons (1st learning vs. 2nd learning phase). Initial assessment = baseline or Tr2+2d; final assessment = Tr2+2d or Tr4+2h; n.s. = not significant.

SDPE [deg]	1 <sup>st</sup> learning phase	2 <sup>nd</sup> learning phase	
<b>Trained positions</b>			
Initial value	3.47 $\pm$ 0.27	2.88 $\pm$ 0.21	t(9) = 2.79; p = 0.021
Final value	2.62 $\pm$ 0.14	2.46 $\pm$ 0.12	n.s.
	t(9) = 3.87; p = 0.004	n.s.	
<b>Untrained positions</b>			
Initial value	2.97 $\pm$ 0.17	2.04 $\pm$ 0.13	t(9) = 4.28; p = 0.002
Final value	2.75 $\pm$ 0.22	1.68 $\pm$ 0.12	t(9) = 4.6; p = 0.001
	n.s.	t(9) = 2.97; p = 0.016	