

**PROTECTION AND EXTINCTION OF MOTOR MEMORIES: INTERFERENCE  
FROM THE DECLARATIVE MEMORY SYSTEM IN CONTEXT SWITCHING**

by  
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## Abstract

Procedural memories (skills) and declarative memories (facts, events) were believed to be independent processes, relying on different parts of the brain, namely the medial temporal lobe for the latter and, depending on the task, the cerebellum, striatum or other parts of the brain for the former. However, recent evidence shows that, those two memory systems can interfere. Here, we performed three experiments to explore the relationship between these two memory systems. In all experiments, the motor task was reaching in a force field and the declarative memory task was learning and recall of a list of words (word task). We also employed a non-declarative memory task as control (count vowels in words: vowel task). In Exp. 1, volunteers adapted to field A and then received brief exposure to field B. Subsequently, they experienced either the word or vowel task. The word group was impaired in the ability to recall the memory of A in the subsequent trials. This suggested that in the context of two competing motor memories (A and B), the declarative memory task interfered with selection and recall of a previously acquired motor memory. To determine whether this effect was specific to the problem of selection between two motor memories, or was simply due to anterograde or retrograde interference on a single memory, we performed two experiments. In Exp. 2, volunteers trained in the word or vowel task immediately before adapting to a force field. We found no difference in performances of the two groups, suggesting that activation of declarative memory does not engage resources that are necessary for acquisition of motor memory. In Exp. 3, we trained in a force field for a short block followed by word learning or vowel counting. We found that with increased training, the motor memory gains stability, but word memorization had no discernible effects on the acquisition or stabilization of the motor memory. Therefore, we find that the interaction between declarative and motor memories is present only in the context of selection between multiple competing motor memories, and not during acquisition.

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## Introduction

### I) Motor adaptation

#### 1) Motor adaptation and motor learning

Motor adaptation is the trial-and-error process of gradually improving movement performance in altered conditions (Bastian, 2008; Krakauer, 2009). Unlike motor (or skill) learning, it does not require the acquisition of a new skill, as in a new set or sequence of muscle activation, but rather the learning of a new map between a well-known movement and the sensory feedback goal. For instance, when you first learn how to serve when playing tennis, you have never learned how to make those movements within that specific sequence, and therefore this is a new skill you need to learn. On the other hand, when you go from using a touchscreen on a cellular phone to using a touchscreen on a computer, you already know how to make the movement to scroll down, but you have to adjust to the fact that to scroll down you now need to move your finger down on the computer screen instead of moving it up on your phone to get the same result. When you get back to using your phone though, you get used to moving your finger up again very quickly. This is adaptation, as it is driven by the process of correcting for your sensory feedback errors. It happens in a variety of movements: arm reaching (Shadmehr & Mussa-Ivaldi, 1994), walking (Reisman et al, 2005), eye movements (Wallman and Fuchs, 1998). The timescale of adaptation is that of minutes to hours, whereas de-adaptation is usually a little faster than that of adaptation (Davidson & Wolpert, 2004). The number of movements, rather than the actual time it takes to make them, is thought to be the main factor as to the rate of learning.



## 2) Motor commands

To generate a movement, the brain sends a motor command to the muscles of the arm. If that movement is perturbed, sensory feedback is different from what was predicted. That is, the sensory feedback that the brain gets is different than expected for producing those specific motor commands. This difference is called a sensory prediction error. Indeed, arm movements last long enough that the sensory feedback is essential to learning. In response to a prediction error, the brain needs to learn a new map between the motor commands and the actual output in terms of sensory consequences. This map is called a forward model, and is thought to rely on the cerebellum (Maschke et al, 2004). While encountering errors, the forward model gets updated to improve performance: this is called error-dependent learning. Another process that comes into play to improve performance during adaptation is called reward-seeking exploration, which consists of changing motor commands to increase the reward obtained by making the correct movement. This is thought to rely more on the basal ganglia (Shadmehr & Krakauer, 2008). Those two processes help produce a rewarding motor command, which through repetition builds a feedback controller, which links sensory feedback and the motor commands. This repetition happens only when the applied perturbation is abrupt, because when the perturbation is gradual there is no repetition, the motor commands and the feedback are constantly changing. This updating of the forward model during adaptation is called model-based learning, which differs from the model-free reinforcement learning that can occur through simple repetition (Krakauer & Mazzoni, 2011).

## 3) Force-field adaptation

One task that has been well studied for arm movements is called force-field adaptation (Shadmehr & Mussa-Ivaldi, 1994). In this paradigm, a volunteer manipulates a robot handle to go

from a starting position to a target some distance away, and gets perturbed during the movement by a field pushing his arm perpendicular to the direction of movement. That field is velocity-dependent, with a constant matrix linking the hand velocity to the force applied to it by the robotic arm. The volunteer therefore has to learn a new way to move their hand to go to the target in time despite being pushed away from the path they were planning on using.

## II) The two-state model

### 1) Spontaneous recovery and savings

Two phenomena are of particular interest in motor adaptation: spontaneous recovery and savings. Savings is the observation that after being exposed to a task once, the second exposition to that same perturbation will yield a faster rate of learning (Krakauer et al., 2005). Spontaneous recovery has been shown in numerous tasks: saccades (Ethier et al., 2008), force-field adaptation (Criscimagna-Hemminger & Shadmehr, 2008)...The idea is to look at competing memories. When training in a certain field A, and then being probed for the forces that were applied, there is a certain outcome. When doing the same paradigm but, between field A and the probe, training for a very short time in field B (opposite of field A) until output goes back to baseline (a phenomenon called extinction), it can be seen that the outcome will rise from baseline to reach the level of the outcome of the people who only trained in A. That rise is called spontaneous recovery (Shadmehr et al., 2010).

## 2) The model

To explain those two phenomena, Smith et al. (2006) proposed a multi-state model of motor memory. It assumes different timescales in the formation of memories, which has been shown in learning and forgetting curves (Rubin & Wenzel, 1996; Scheidt et al., 2000). Although this model has been shown not to explain all aspects of savings (Zarahn et al., 2008), it has proven to explain spontaneous recovery for force-field adaptation (Smith et al., 2006) and eye movements (Ethier et al., 2008).

The model states that there are two different processes at play when forming a motor memory: a fast process, that is very sensitive to error but has poor retention, and a slow process, that retains well but adapts slowly. The total output is the sum of those two. The equations for the model are as follows (Shadmehr & Mussa-Ivaldi, 2012):

$$x_f^{(n+1)} = a_f x_f^{(n)} + b_f (y^{(n)} - \hat{y}^{(n)})$$

$$x_s^{(n+1)} = a_s x_s^{(n)} + b_s (y^{(n)} - \hat{y}^{(n)})$$

$$0 < a_f < a_s < 1$$

$$0 < b_s < b_f < 1$$

where  $y^{(n)}$  is the output at time n,  $\hat{y}^{(n)}$  is the estimate of the state at time n:

$$\hat{y}^{(n)} = x_f^{(n)} + x_s^{(n)},$$

$y^{(n)} - \hat{y}^{(n)}$  is the error in the estimation that the model learns from, a is the forgetting parameter (one for each state), and b specifies the sensitivity to error for each state. The assumptions for the slow and fast states, i.e. the differential sensitivities to error and retentions, are accounted for in the last two equations.

Figure 1 gives an example of the estimation for a specific paradigm. The parameters used were:  $a_f = 0.92$ ,  $a_s = 0.996$ ,  $b_f = 0.03$ ,  $b_s = 0.004$ . The paradigm consists of training in a null field for 192 trials, then training in an A (clockwise) field for 384 trials, then in a B (counterclockwise, opposite of A) field for 20 trials, and then being probed in error-clamp trials, where error is clamped to zero (see Materials and Methods). For the first part in the null field, the error is estimated to stay at zero. Then when the training starts on the A field, the fast process rises fast, but stops increasing rapidly and starts decaying, whereas the slow process rises much more slowly, and keeps increasing. When the opposite perturbation is applied, the fast process decreases toward that value very quickly, whereas the slow process almost does not change given the short amount of time. During the error-clamp trials, the fast process reaches zero rapidly, and the slow process decreases slowly and steadily toward zero. As shown in Smith et al. (2006), the simulations are very close to the actual behavioral data. In particular, at the beginning of the error-clamp block, that fast decay toward zero from the fast process produces a rebound, which is showing spontaneous recovery, as the actual data shows.

Another asset of this model is that it assumes a way of learning that seems natural (Shadmehr & Mussa-Ivaldi, 2012): indeed, perturbations from the environment that are deemed transient do not need to be remembered (fast process), whereas it seems useful to retain the effects of a long-term disturbance (slow process).

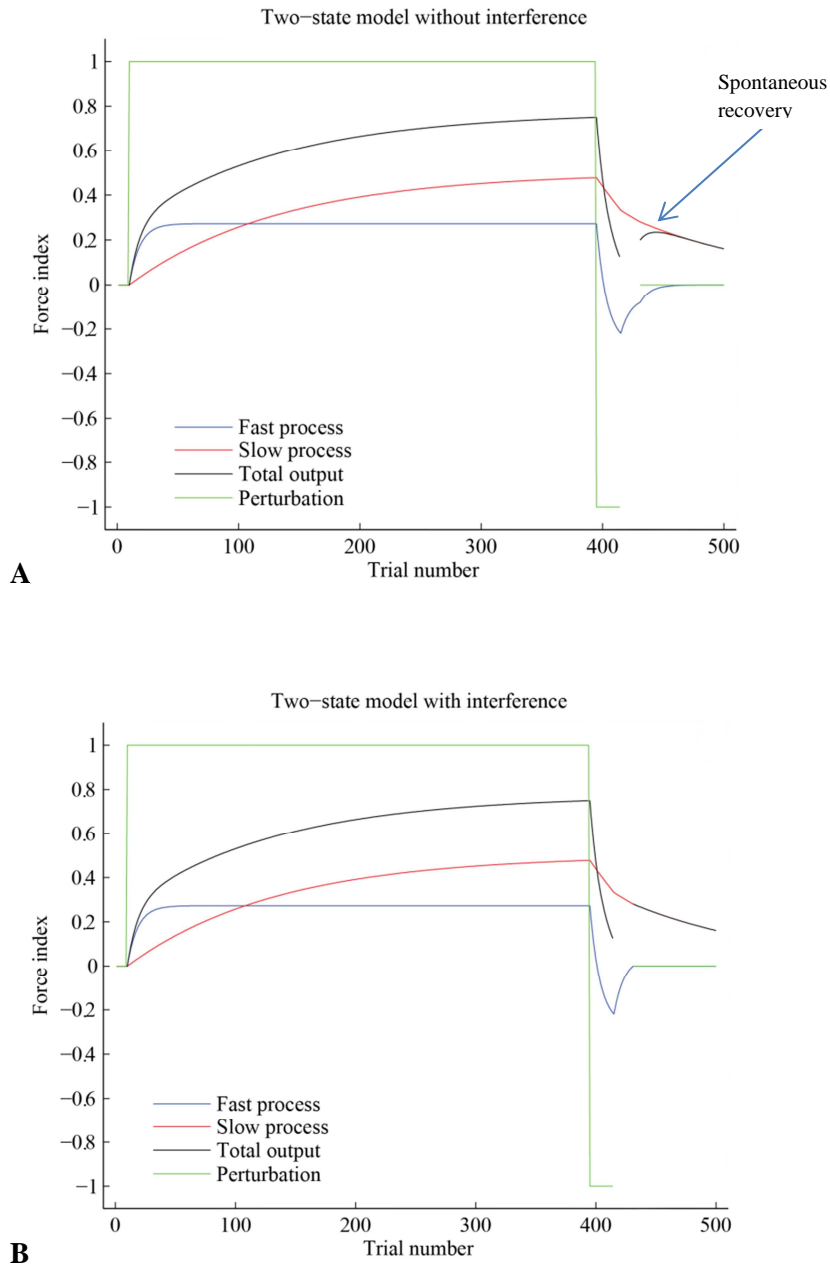


Figure 1: 2 state model: Model of fast and slow process for motor memory formation during motor adaptation. A Participants train on a null field, then are perturbed in a clockwise (A) field for 384 trials, then learn the opposite field (B) for 20 trials, followed by a 3 minute interval during which no task is given, before being probed for motor memory in a channel block. If there is no interference, spontaneous recovery appears in the total output. B An interfering task is performed. If there is interference, spontaneous recovery does not happen.

### III) Interference

#### 1) Procedural and declarative memory

Procedural memory refers to skill and habit learning, including motor memories. This type of memory, depending on the task, is thought to rely on the cerebellum, striatum, and other parts of the brain (Robertson, 2012). There are two main types of interference: anterograde and retrograde. To understand this, suppose there are two tasks: task 1 and task2. Anterograde interference occurs when task 1 interferes with the subsequent learning of task 2, making the performance on task 2 less than that of somebody engaging in that task without prior exposure to the interfering task, or when task 2 interferes with relearning of task 1. Different parameters show interference, for instance an increase in the initial error or a decrease in the learning rate, as compared to someone learning the task without any prior exposure to either task 1 or task 2. The two-state model presented in the previous section has been shown to account for anterograde interference (Sing & Smith, 2010). Retrograde interference marks the effect of one task on a previously learned task, when task 1 is learned, followed by training in the interfering task (task 2), then comparing the performance on the recall of task 1 to the performance from people not training in the interfering task.

In force-field adaptation, interference has been studied in various ways. Shadmehr and Brashers-Krug (Brashers-Krug et al., 1996; Shadmehr & Brashers-Krug, 1997) showed that learning one field and then the opposite field prevented savings. However, that interference did not manifest after waiting for some amount of time, approximately 6 hours, since relearning was then faster.

The declarative memory is the memory of facts and events, and is thought to rely on the medial temporal lobe. Declarative memories show interference as well: when learning one word

list and then another one right after, the second one interferes with the memory of the first one (Lechner et al., 1999).

## 2) Interference between procedural and declarative memories

Given that those two memory systems depend on different parts of the brain, it was thought that the two were independent. Additionally, in Alzheimer's disease, the declarative system is impaired but the learning of new skills was still somewhat functioning (Gabrieli et al., 1993), whereas in Huntington's disease it is the opposite (Gabrieli et al., 1997).

However, Poldrack et al. (2001) showed through functional brain imaging that the medial temporal lobe activation could be correlated with the activation of the striatum, which are linked respectively to declarative and procedural memory.

In effect, studies (Brown & Robertson, 2007 a, b; Keisler & Shadmehr, 2010) have shown that those two systems, in some specific tasks, could interfere, suggesting a competition or a coupling between overlapping resources between those two memory systems.

## Materials and methods

Ninety-four healthy volunteers participated in three experiments (23 +/- 4.11 years, mean +/- STD, 44 males). All participants were naïve to the paradigm and the purpose of the experiment, and reported being right-handed. Experimental procedures were approved by the Johns Hopkins University School of Medicine Institutional Review Board, and each participant signed a consent form. One volunteer's data was discarded from the analysis because they were found to be an outlier in experiment 1 (see below), another participant's because they did not follow the requirements of the task in experiment 2, and another one because of lack of sufficient knowledge of vowels during experiment 3.

The experiments included two different tasks: a motor task, and a cognitive task. The motor task consisted of a point-to-point reaching arm movement to a single target, using a robot handle. The handle, as well as the participant's hand, were covered by a screen, and a projected white cursor represented the position of the handle. Participants were instructed to go from a starting position, a yellow cross, to a green 1 cm<sup>2</sup> target 10 cm away from the body midline, with a certain speed. Different colors were showing whether the movement was too slow or too fast, and if the movement time was within 500 +/- 70 ms, and the tangential velocity between 0.20 and 0.55 m/s, the target exploded, indicating a successful trial. After each trial the robot handle brought the hand back to the starting point. There were three types of trials: null trials, where no constraint was implemented. Field trials, where the hand of the subject was perturbed through a velocity-dependent curl force field, counterclockwise, using the following equation for force:  $\mathbf{f} = \mathbf{B} \dot{\mathbf{x}}$ , where  $\dot{\mathbf{x}}$  is the hand velocity, and  $\mathbf{B} = [0 \ -13; 13 \ 0]$  N.s/m. Error-clamp trials (channel trials), where the subject's hand was constrained to go in a straight line, surrounded by "walls" through a stiff one-dimensional spring (spring coefficient = 2000 N/m; damping coefficient = 45 N.s/m). In



error-clamp trials, the lower time limit for the movement was removed, effectively removing the possibility of an unsuccessful trial because of a too fast movement. Force at the handle, position and velocity were recorded at a rate of 100 Hz. During error-clamp trials, learning was measured with a force index, corresponding to the ratio of the force produced by the participant at peak velocity (with respect to baseline) over the ideal force (i.e. the force the robot would produce at that specific velocity). In other trials, the maximum perpendicular displacement was taken as a measure. The cognitive task could be one of two: memorizing word pairs (called the memory task), or counting vowels in meaningless strings of letters (called the non-memory task), and were modeled after work by Keisler & Shadmehr (2010). The memory task is thought to involve the declarative memory system, whereas the non-memory task (as well as the absence of task) is thought not to involve that system. In one block of the memory task, participants were shown 12 pairs of words, one at a time, for three seconds each, all in a row, and they were told to memorize the pairs. After this study phase, participants were given a three-second break followed by a test phase, consisting of showing the participants one word from each pair, one at a time for three seconds each, in a different order than the pairs, and the participants were asked to give their answer out loud as to what the other word from the pair was, during those three seconds. After that, the same pairs were shown again, in the same way, but in a different order, and a second test phase followed. Overall the task lasted around three minutes. The words for the first block were taken from Keisler & Shadmehr (2010), the ones for the other nine blocks were randomly drawn from the “Oxford 3000” word list (Wilson 1988). All participants for the word task were native English speakers. For the non-memory task, strings of letters with no meaning were shown. They were between 3 and 12 letters, containing between 1 and 5 vowels. 48 strings per block were shown, each for three seconds, with a three-second break every twelve strings. After each block participants were given their score. Each experiment lasted about an hour and a half.

The experiments had two purposes: looking at the interference of the declarative memory system through the memory task on motor adaptation, which had been studied by Keisler & Shadmehr (2010), and looking at the retention of that interference.

Experiment 1: twenty-eight volunteers participated in this experiment (22.2 +/- 4.59 years, mean +/- STD, 9 males). We searched for outliers using the median deviation of the medians on the force index calculated as the regression ((Rousseeuw & Croux, 1993; see appendix for more details), and discarded one participant's data. In experiment 1, we studied the retrograde interference from the declarative memory system onto the motor memory system, after learning two opposite fields. This experiment had been performed in Keisler & Shadmehr (2010). After a first block of 192 trials in a null field containing 26 pseudorandomly distributed channel trials, a long learning period of a clockwise field (A) was given: 384 trials, including 52 channel trials, followed by a short period of learning the opposite counterclockwise field (B) for 20 trials without any channel trial. Following that motor training the cognitive task was performed: either the memory task (14 participants) or the non-memory task (13 participants). Out of 13, 11 were native English speakers, the other two were Chinese people that had been in the US for more than 5 years. To probe for motor performance the last part was a block of 192 channel trials (Figure 2A). Assuming interference using the two-state model from Smith et al., 2006, which assumes on the one hand a fast process, that is very sensitive to error but has poor retention, and a slow process, which has good retention but is little influenced by error, we expect interference on the fast process, as reported in Keisler & Shadmehr (2010). This would imply an output in the force index for the non-memory task group showing spontaneous recovery in the channel block, but this would not be the case for the memory task group, and both groups would merge eventually.

Experiment 2: twenty-one volunteers participated in this experiment (23.3 +/- 2.01 years, mean +/- STD, 13 males). One volunteer did not follow the requirements of the task, therefore their data was discarded. In experiment 2, we wanted to determine whether there was anterograde

interference from the declarative memory system onto the motor memory system. Participants performed a block of 192 trials in a null field to record baseline training, with 26 channel trials pseudorandomly interspersed. Then they did the cognitive task, followed by a block a 192 counterclockwise (B) field trials (Figure 7A). 20 people were separated in two groups, one where the cognitive task was the memory task (11 participants), and another one where they were doing the non-memory task (9 participants); 7 of those 9 participants were native English speakers, the other 2 were Chinese people that had been in the US for more than 5 years.. Assuming interference, according to the two-state model from Smith et al., 2006, we again expect interference on the fast process, as reported in Keisler & Shadmehr (2010). We would thus expect the output of the memory task group to be lower than the non-memory task group, or to be the same for both groups in the absence of interference.

Experiment 3: forty-five volunteers participated in this experiment (23.2 +/- 4.53 years, mean +/- STD, 22 males). One participant did not know what vowels were, therefore the data was discarded. In experiment 3, our goal was to look at the retrograde interference of the declarative memory onto the motor memory, looking first at spontaneous recovery. We were also interested in retention during the ten consecutive blocks. For this, we used a paradigm consisting of a training session of 192 null trials, followed by a learning block of 20 counterclockwise (B) field trials. 26 channel trials were pseudorandomly interspersed in the null block, 5 in the learning block, the fifth one being the very last trial of the block. After that, participants either did the memory task, the non-memory task, or just rested for three minutes. This was followed by a block of 15 channel trials, and another learning block of 20 B field trials containing 5 channel trials, the last trial being a channel trial. This sequence of a 3-minute cognitive task or rest followed by 35 trials was repeated ten times (Figure 11). 34 people took part in this experiment, randomly assigned to the three different groups: 13 people were in the memory group, 11 in the non-memory group, and 10 in the no task group. Out of the 11 people in the non-memory task group,

9 were native English speakers, 2 were Chinese people that had been in the US for more than 5 years. Supposing that there is interference, we would then expect the output of the memory task group to start lower (when looking at the force index) than the other two, and then the outputs of the three groups to merge to reach the same values, as reported previously. If there is no interference, the three groups will behave the same way regardless of the cognitive task that was applied.

After analyzing those data, we wanted to look at a potential correlation between the performance on the cognitive task and the motor task. The hypothesis was that the better you perform on the cognitive task (i.e. the more words you remember), the worse you will perform on the motor task, as expected from interference. 10 volunteers were therefore added to the memory group, so we would be able to look at data gathered from 23 subjects for those correlations. Declarative memory performance was measured by counting the number of words correctly remembered, and motor learning was assessed in various ways: the average of the force index of the first two trials of a channel block, the mean of the force index during a channel block, the decay taken as the difference in the force index between the last two trials and the first two trials of a channel block; the same parameters taken from a learning block; the difference in motor performance across the cognitive task to look specifically at the effect of that cognitive task on motor performance on a trial-to-trial or block-to-block basis, by taking the difference in force index either between the first trial of the channel block immediately following the cognitive task and the last trial (which is a channel trial) in the learning block immediately preceding the cognitive task, or the average of that channel block and the average of that learning block.

Data analysis: Another question we had was whether previously reported results (Keisler & Shadmehr, 2010) might have been a sampling bias, due to a small sample (6 people in each group instead of more than 10 here). In order to look at the likelihood of getting significant results, we looked at 6,000 times three groups of six people each, all randomly drawn from the

13, 11 and 10 people recruited for this experiment, since 6 people were in each group in the previous results. We then ran a statistical analysis on those groups, a one-way ANOVA and a Kruskal-Wallis test on the average of the first two trials of the first channel block following the first cognitive task, since significance was reached that way in those results. We looked at the distribution of the p values for those two tests, finding that it was not unlikely to find significant results in subsets of the data collected in this study. All analyses were conducted with Matlab 2011b, and all statistical tests: one-way ANOVAs, Kruskal-Wallis tests and repeated-measures ANOVAs were performed with IBM SPSS Statistics 21.

## Results

### Experiment 1

Our aim here was to study retrograde interference from the declarative memory system onto the motor memory system, after learning opposite fields for different periods of time. 27 participants were distributed in two groups: 14 in the memory task (word) group, 13 in the non-memory task (vowel) group.

First of all, subjects did indeed follow the cognitive task: performance for the memory task was 9 words remembered on average (for the sum of both lists, out of 24; STD = 5.79), and the non-memory task had a mean of 37.8 correct answers (out of 48; STD = 6.72). For motor performance, for most figures we divided the long block of learning the A field in two parts, equal in duration (192 trials including - 26 channel trials - in each), for early and late training. Looking at trajectories first (Figure 2B), there is little difference in the way both groups learn the motor task prior to any cognitive task. There does seem to be a difference during learning, but when looking at maximum displacement there turned out to be no statistical significance (see *infra*). As far as kinematics are concerned, parallel velocity (both for channel trials (Figure 3B) and null and field trials (Figure 3A)) and perpendicular velocity profiles (Figure 3C) look very similar for both groups. The traces for the maximum perpendicular displacement, taken as the maximum absolute horizontal distance from the straight line joining the starting position and the target, (Figure 4B) appear on top of one another during the learning period, as expected. The perpendicular force profiles (Figure 4A) look very similar during the learning period, but during the channel block following the cognitive task the traces get separated. A one-way ANOVA on the average of the first 30 trials of the peak perpendicular force during the channel block shows

significance:  $F_{(1,25)} = 4.839$ ,  $p = 0.037$ . Finally two methods to estimate adaptation were used: the first one was a force index taking force at maximum velocity, and dividing by the ideal force, that is to say the maximum velocity times the viscosity of the field. That gives a ratio of force at maximum velocity over the ideal force, that we call the force index (or adaptation index). Another way to calculate the force index is to take the regression of the force profile onto the velocity profile. For both of these, the traces are on top of each other for both groups during the baseline block, and a difference appears during the channel block (Figure 5). A one-way ANOVA on the mean of the channel block gives: for force at maximum velocity,  $F_{(1,25)} = 9.446$ ,  $p = 0.005$ ; for the regression:  $F_{(1,25)} = 9.439$ ,  $p = 0.005$ . There also seems to be a difference between groups in the learning block, which is unexpected: for the regression,  $F_{(1,25)} = 5.121$ ,  $p = 0.033$ ; for the force at maximum velocity,  $F_{(1,25)} = 5.329$ ,  $p = 0.03$ . To account for that difference in groups and see whether the effect we see in the channel block still holds, we took the average of the force index for the last five channel trials of the learning block for each participant and normalized the channel block with respect to that value, to ensure both groups' performances were comparable in the learning block. Figure 6 shows the performance in the channel block, expressed as the percentage of the end of learning. The performance for both indices during the channel block still gives a significant difference between groups. A one-way ANOVA on the mean of the force index in the channel block showed: for the force at maximum velocity,  $F_{(1,25)} = 8.522$ ,  $p = 0.007$ ; for the regression,  $F_{(1,25)} = 8.150$ ,  $p = 0.009$ . Finally, there was no significant difference in the learning of the B field when looking at maximum displacement:  $F_{(1,25)} = 2.753$ ,  $p = 0.11$ . Overall, these results suggest interference between the declarative memory system and the motor memory system as the output of both groups appear quite different.

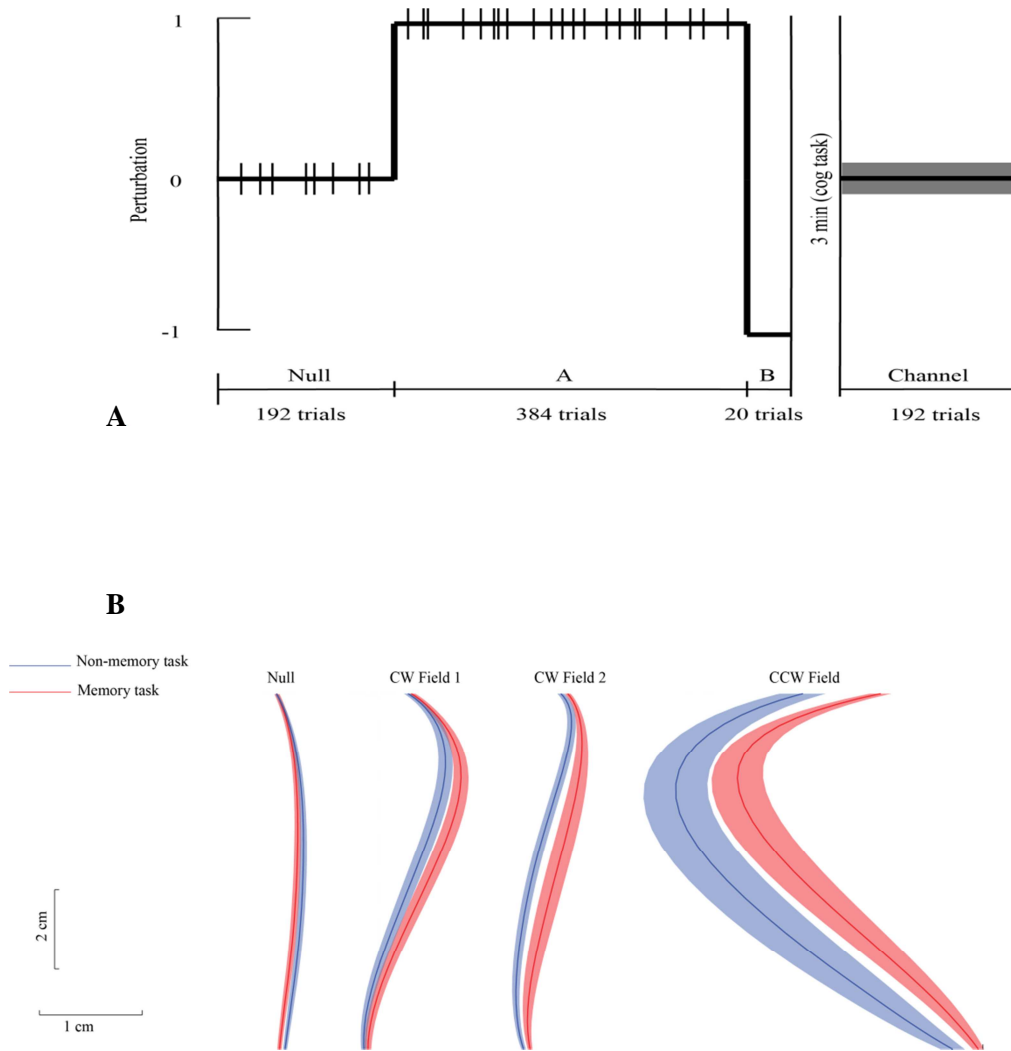
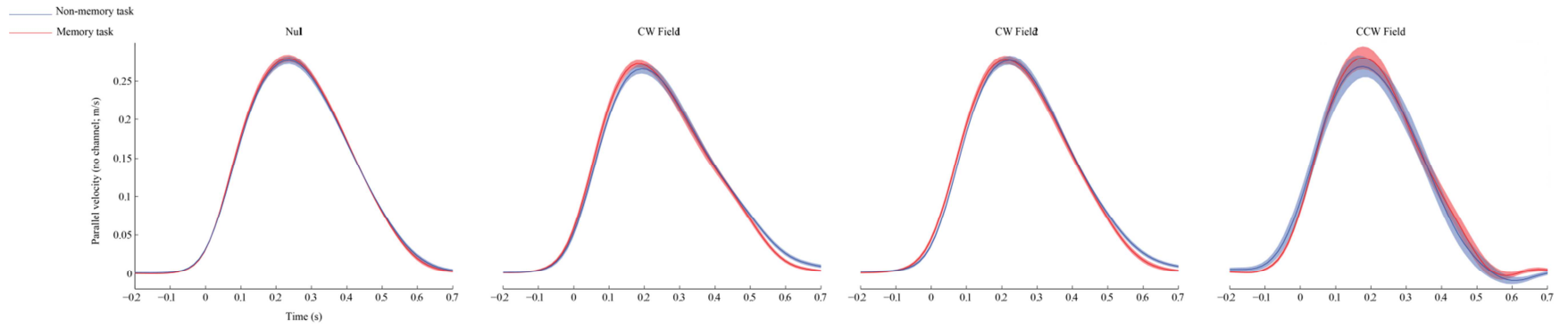
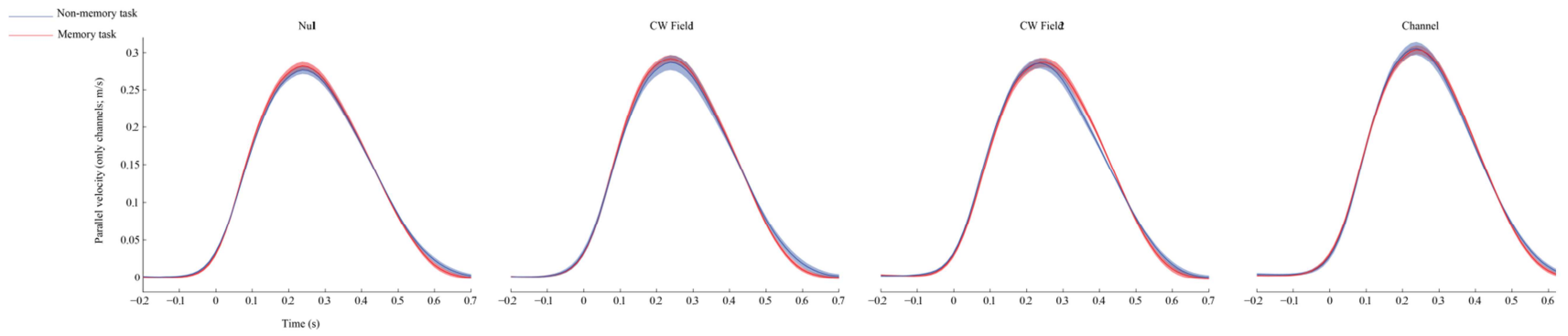


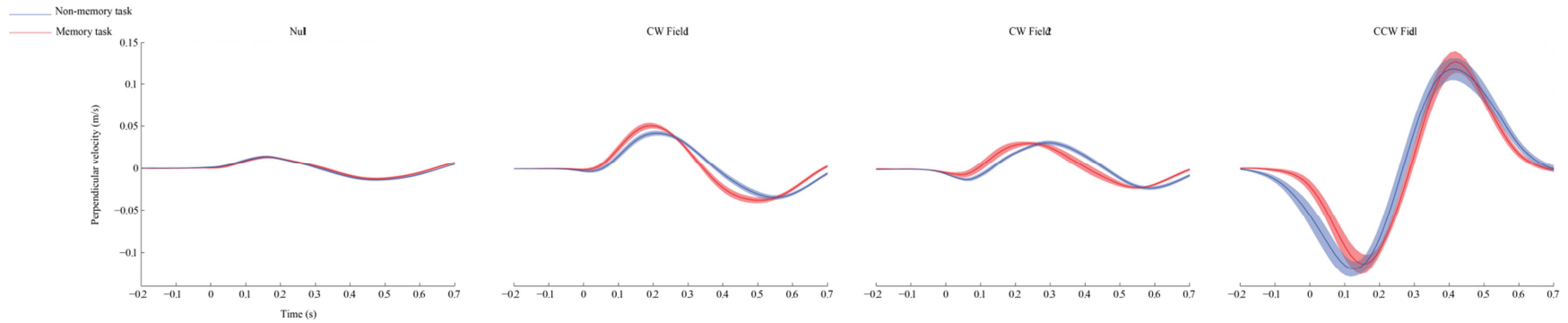
Figure 2: **A**: Experiment design: participants trained in a null field (no perturbation, 192 trials including 26 interspersed error-clamp trials), then in a clockwise (A) field for 384 trials (including 26 interspersed error-clamp trials), followed by a counterclockwise (B) field of 20 trials and, after a 3 minute cognitive task (either memory task (word) or non-memory task (vowel)), a probing block of 192 error-clamp trials. Vertical ticks indicate error-clamp trials during baseline training and learning.

**B**: Trajectories from starting to end point. Both groups show the same behavior. The main line is the average value across subjects, the shaded areas around it are standard errors (SEM). The first learning block for the A field is divided into two equal parts (CW1 and CW2).



**A****B**

C



19

Figure 3: Parallel velocity profiles throughout the movement for field trials, averaged over each block. The first learning block for the A field is divided into two equal parts (CW1 and CW2). Both groups show the same behavior. **A:** in null and field trials. **B:** in channel trials.

**C:** Perpendicular velocity profiles throughout the movement for field trials, averaged over each block. The first learning block for the A field is divided into two equal parts (CW1 and CW2). Both groups show the same behavior.

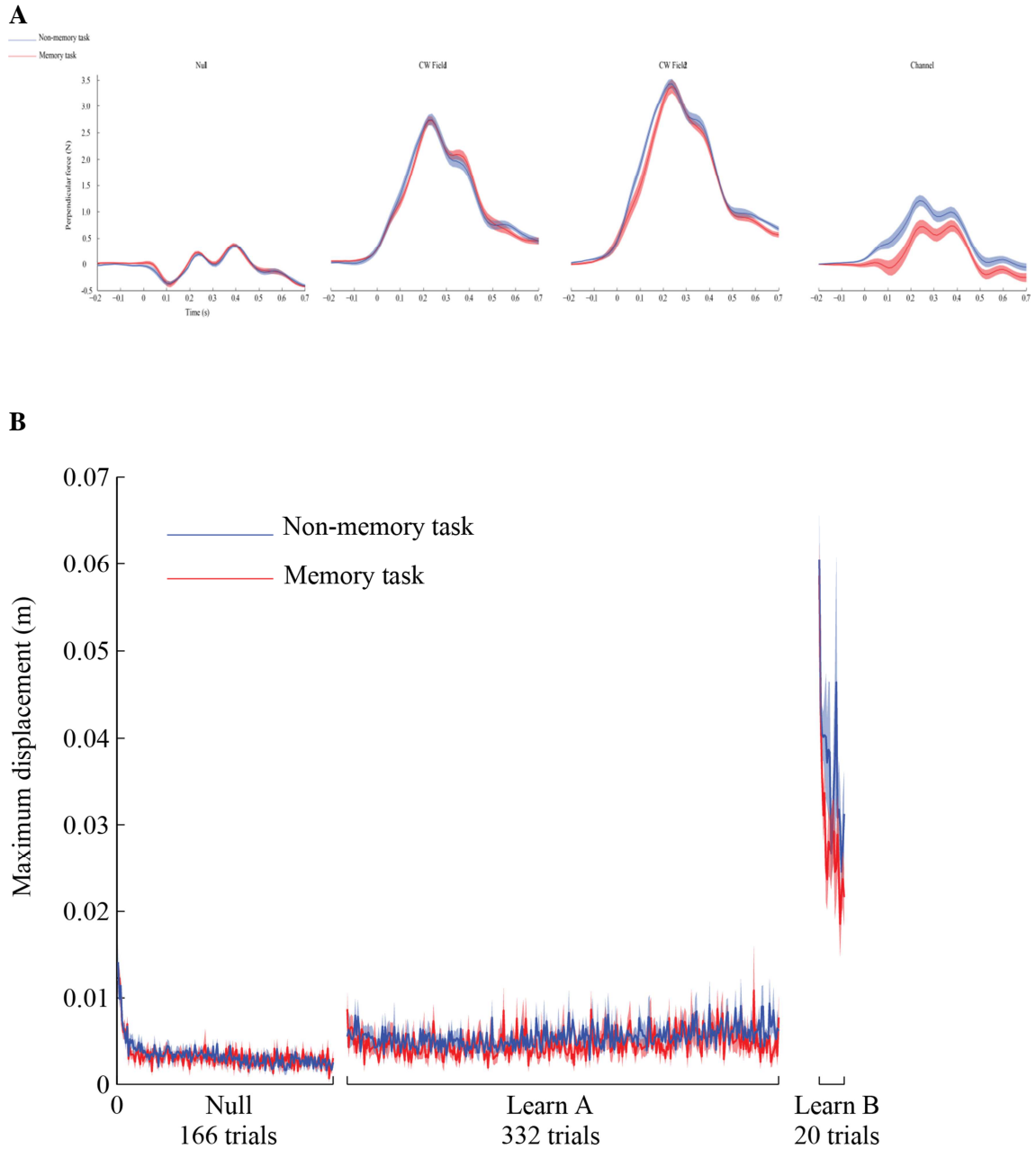
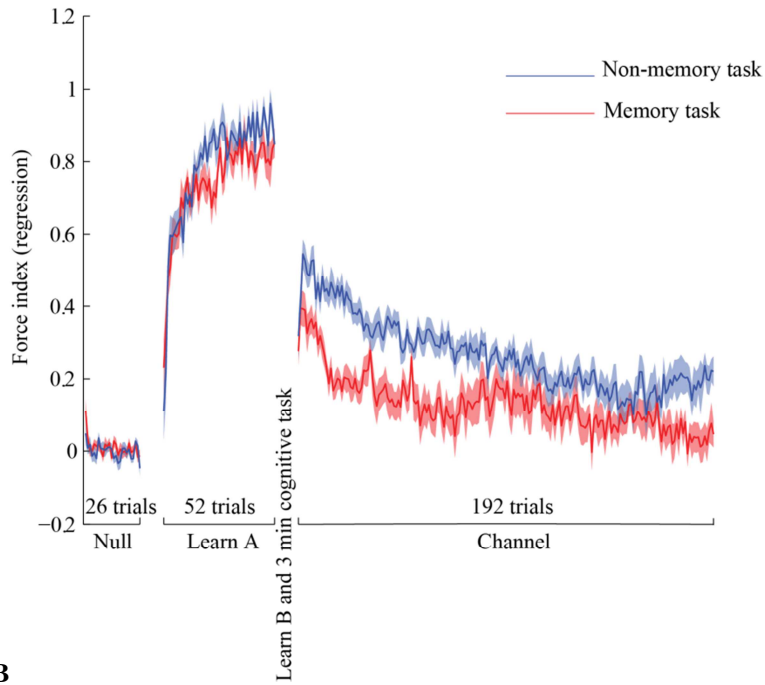


Figure 4: **A**: Perpendicular force profiles throughout the movement for channel trials, averaged over each block. The first learning block for the A field is divided into two equal parts (CW1 and CW2). A difference in the groups appears in the channel block, the word group's output is much lower than the vowel group's, showing interference. **B**: Maximum perpendicular displacement, taken as the maximum horizontal distance between the trajectory and a straight line between the start and end points. Both groups show the same behavior.

**A**



**B**

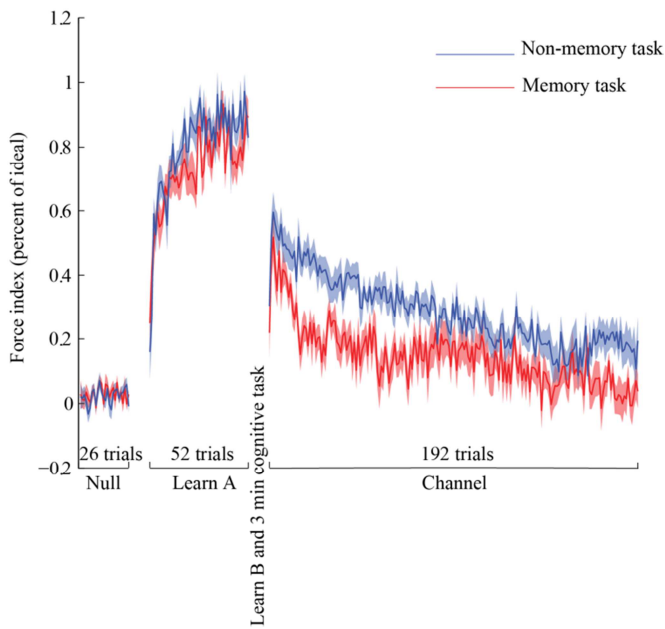


Figure 5: Force index, **A** using the regression of the force profile on the velocity profile and **B** calculated at maximum velocity. A difference in the groups appears in the channel block, the word group's output is much lower than that of the vowel group, showing interference.

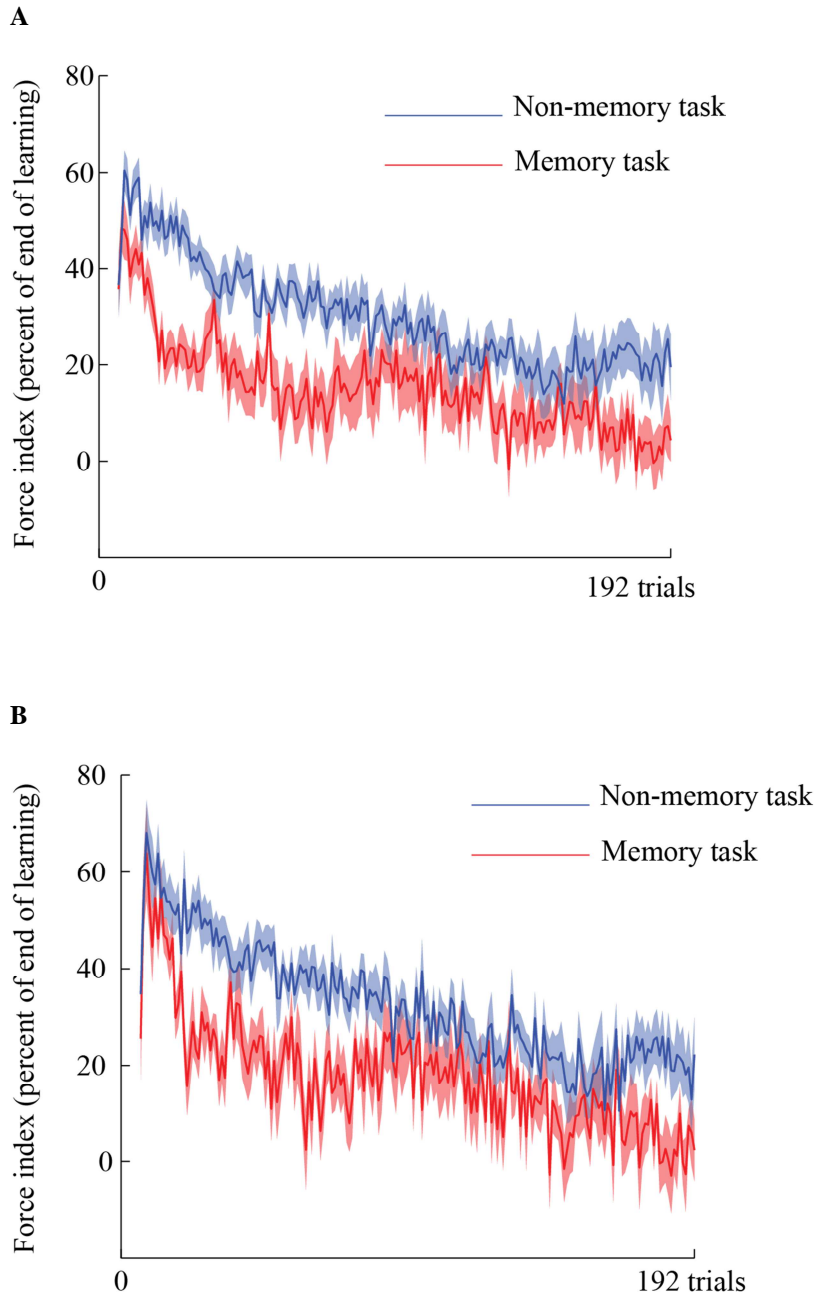


Figure 6: Force index as a percentage of the end of learning (see text). **A** using the regression of the force profile on the velocity profile and **B** calculated at maximum velocity. A difference in the groups appears in the channel block, the word group's output is much lower than that of the vowel group, showing interference.

## Experiment 2

Our aim here was to look at the anterograde interference of the declarative memory onto the motor memory. 20 participants were distributed in two groups: a memory task (word: 11 people) and a non-memory task (vowel: 9 people). No significant result was found.

First of all, subjects did indeed follow the cognitive task: performance for the memory task was 10.7 words remembered on average (for the sum of both lists, out of 24; STD = 7.44), and the non-memory task had a mean of 42.9 correct answers (out of 48; STD = 2.89). For motor performance, we looked at trajectories averaged for each block for both groups, not considering the channel trials, and the traces looked the same (Figure 7B). We checked that parallel velocities were the same for each group during both blocks (Figure 8A). For kinematics, we plotted the perpendicular velocity (Figure 8B) and the perpendicular force profiles with respect to time, for each block (Figure 9A). Then again, there was no difference in the results. Another parameter of interest was the maximum perpendicular displacement, taken as the maximum absolute horizontal distance from the straight line joining the starting position and the target. The traces were on top of one another (Figure 9B). Finally, the main parameter was the force index during channel blocks, which was calculated using two methods. The first one was estimating the ratio of the force produced at maximum velocity. More specifically, we took the average of the last 7 channel trials in the baseline block, and subtracted that profile to all profiles, including the baseline block. We then took the force at maximum velocity of the resulting profile, and divided it by the ideal force, i.e. the maximum velocity times the viscosity of the velocity-dependent field. The second was simply calculating the regression of the force profile onto the velocity profile. The traces are shown in Figure 10. To check for potential differences, we ran a one-way ANOVA on the mean of the force index of each block: for the baseline block,  $F_{(1,18)} = 0.04$ ,  $p = 0.843$ ; for the learning

block,  $F_{(1,18)} = 0.775$ ,  $p = 0.391$ . We also ran repeated-measures ANOVAs, binning trials by groups of 13 for values of the force index. For a group by block interaction: for the baseline block,  $F_{(1,18)} = 2.256$ ,  $p = 0.15$ ; for the learning block,  $F_{(1,18)} = 0.298$ ,  $p = 0.592$ . For the learning block there was indeed learning, shown by a significant effect of block:  $p = 0.001$ .

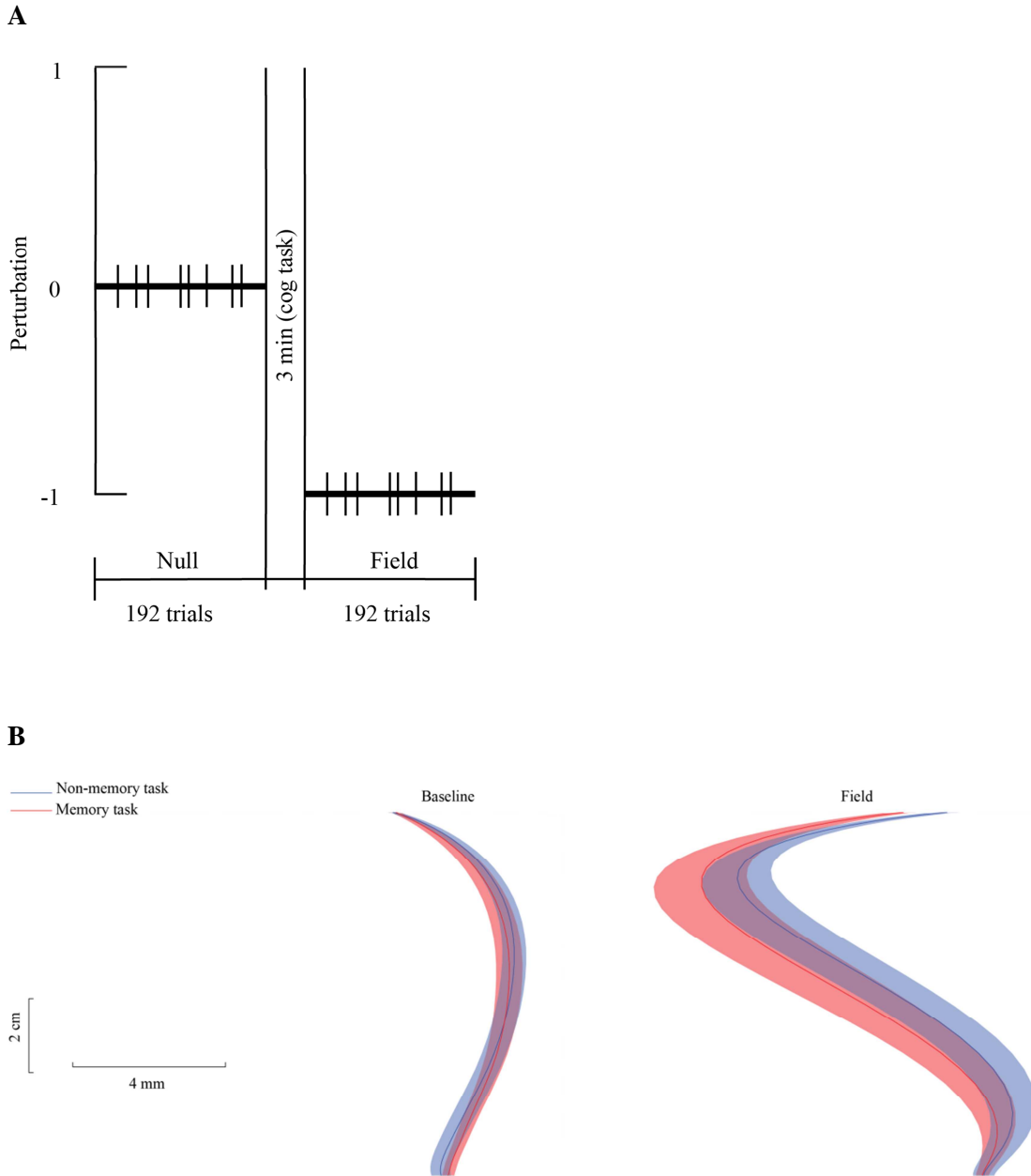
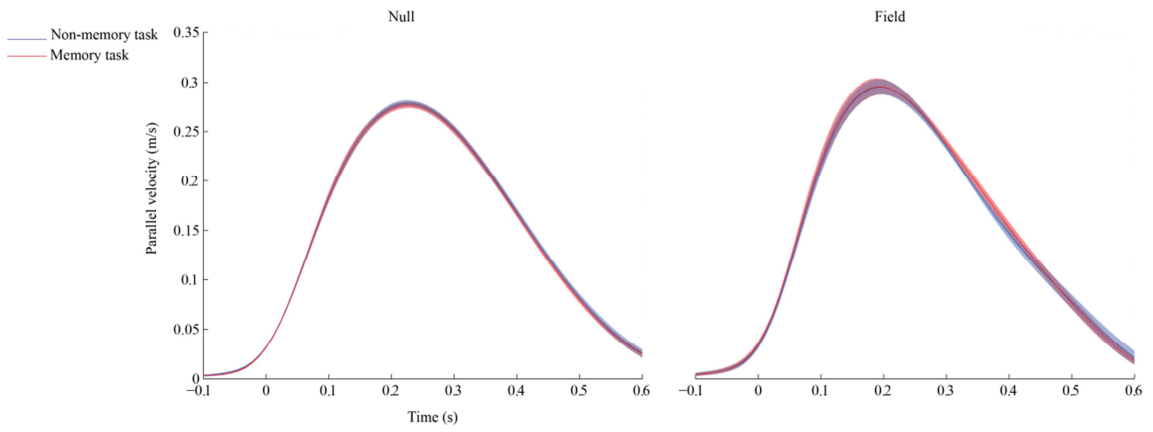


Figure 7: **A:** Experiment design: participants trained in a null field (no perturbation, 192 trials including 26 interspersed error-clamp trials), then performed a 3 minute cognitive task (either memory task (word) or non-memory task (vowel)), followed by a learning block in a B field of 192 trials containing 26 error-clamp trials. Vertical ticks indicate error-clamp trials during baseline training and learning.

**B:** Trajectories from starting to end point. Both groups show the same behavior. The main line is the average value across subjects, the shaded areas around it are standard errors (SEM).



**A**



**B**

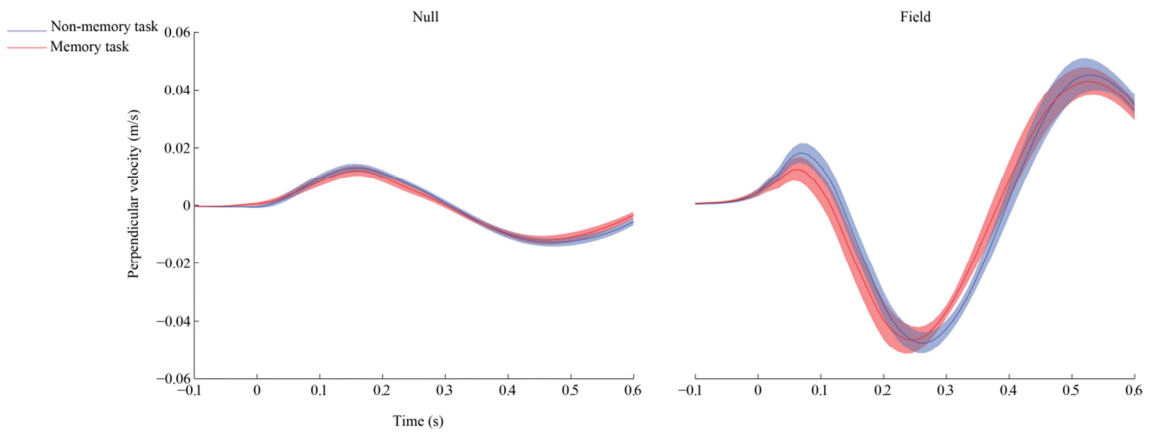


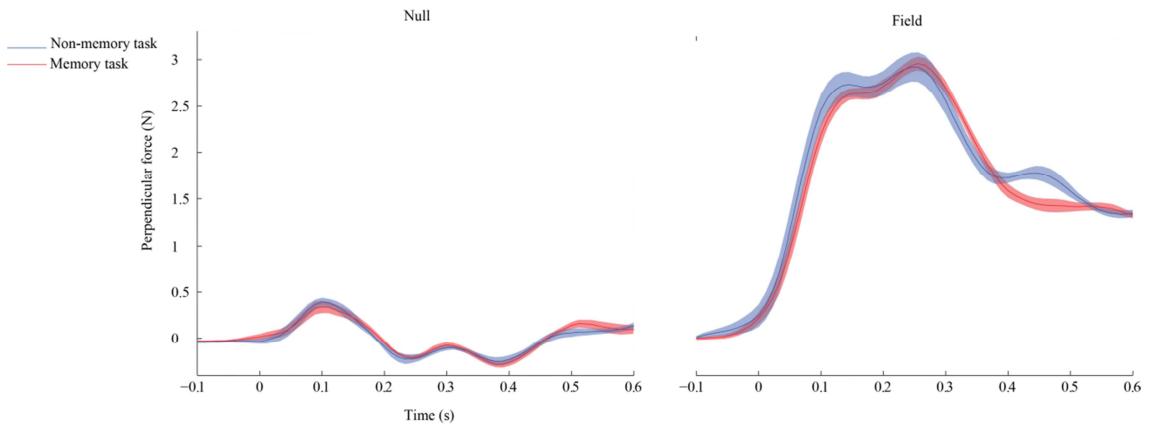
Figure 8: **A**: Parallel velocity profiles throughout the movement for field trials, averaged over each block.

Both groups show the same behavior.

**B**: Perpendicular velocity profiles throughout the movement for field trials, averaged over each block.

Both groups show the same behavior.

**A**



**B**

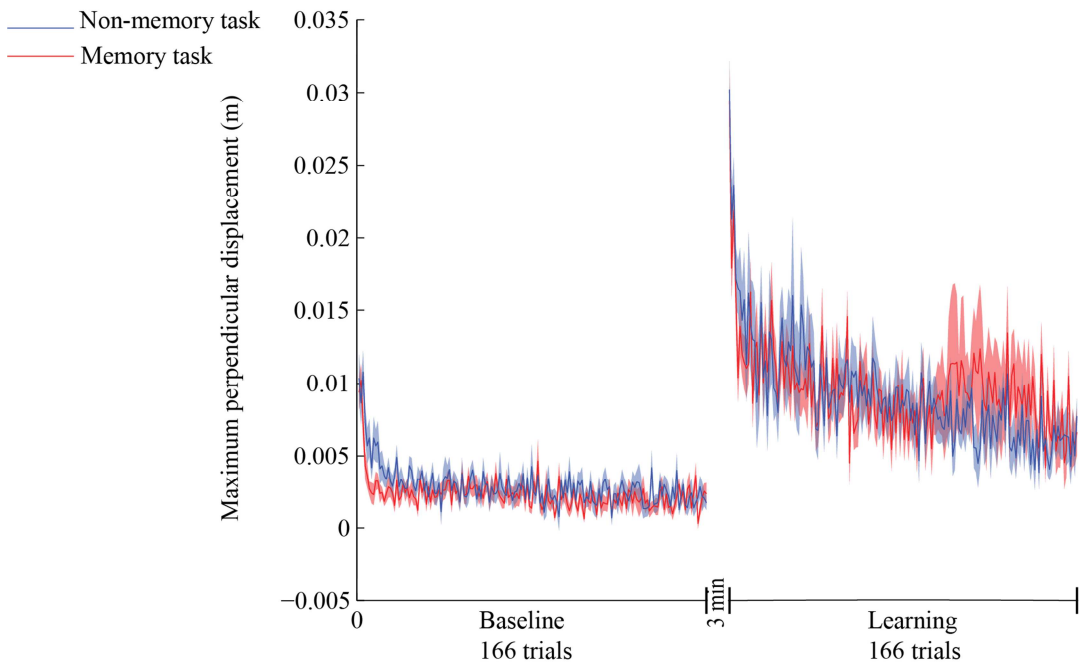
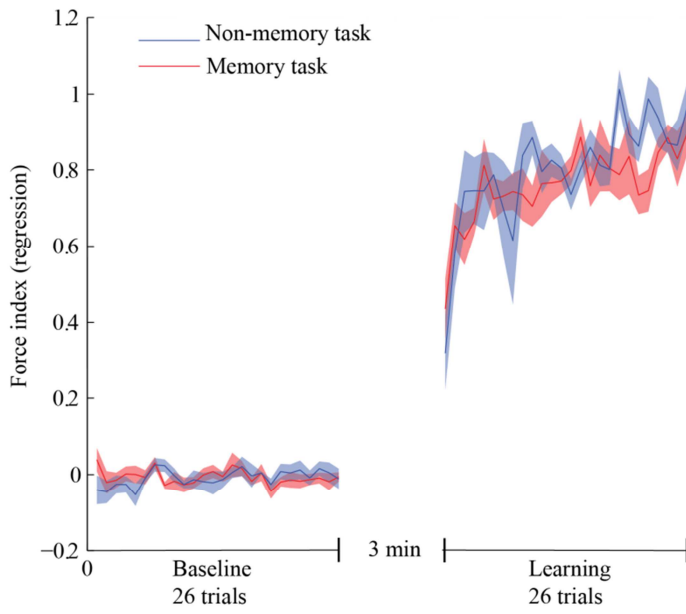


Figure 9: **A**: Perpendicular force profiles throughout the movement for channel trials, averaged over each block. Both groups show the same behavior. **B**: Maximum perpendicular displacement, taken as the maximum horizontal distance between the trajectory and a straight line between the start and end points. Both groups show the same behavior.

**A**



**B**

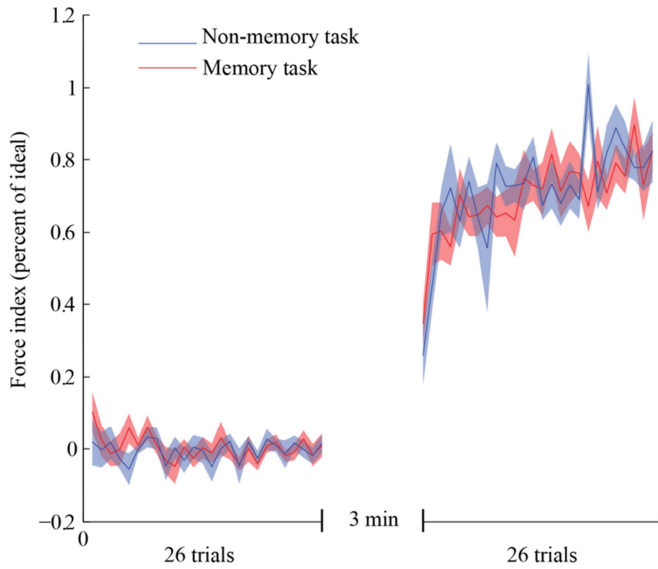


Figure 10: Force index, **A**: using the regression of the force profile on the velocity profile and **B**: calculated at maximum velocity. Both groups show the same behavior.

### Experiment 3

Our aim here was to 1) study the retrograde interference from the declarative memory onto the motor memory after training simply in one field and 2) assess whether the interference would decrease after doing the task multiple times in a row. 34 participants were first distributed in three groups: a memory task group (word: 13 people), a non-memory task group (vowel: 11 people), and a no task (wait: 10 people) group. We did obtain a significant effect of blocks but not of groups, in other words practice made the performance change, but all the groups were the same.

First of all, subjects did indeed follow the cognitive task: performance for the memory task was 124.8 words remembered on average (for the sum of the 20 lists, out of 240; STD = 45.6), and the non-memory task had a mean of 443.6 correct answers (out of 480; STD = 37.89). For motor performance, we specifically looked at trajectories during all blocks, not considering the channel trials, and the traces looked the same (Figure 12). We checked that parallel velocities were the same for each group during different blocks (Figure 13A). For kinematics, we plotted the perpendicular velocity (Figure 13B) and the perpendicular force profiles (Figure 14A) with respect to time, for each block. Another parameter of interest was the maximum perpendicular displacement, taken as the maximum absolute horizontal distance from the straight line joining the starting position and the target. The traces were on top of one another (Figure 14B), suggesting no difference between the groups. Finally, the main parameter was the force index during channel blocks, which was calculated using the two methods described in experiment 2. Traces are shown in Figure 15. We assessed the force index during the learning and relearning blocks, but again there was no main effect. We also fitted a line between the first and last data point of the force index in each channel block, and considered the slope as a measure of the decay

in each block. No significance was found. A repeated-measures ANOVA was conducted on this decay; there was an effect of block ( $F_{(9,18)} = 2.802, p = 0.004$ ), but there turned out to be no group-by-block interaction ( $F_{(18,279)} = 1.265, p = 0.210$ ). A repeated-measures ANOVA on the mean of the maximum displacement per block showed no difference (no effect of group:  $F_{(2,31)} = 1.504, p = 0.238$ , and no group-by-block interaction: using the Greenhouse-Geisser correction for sphericity,  $F_{(8.225,127.494)} = 1.610, p = 0.126$ ). The regression force index gave the same profile, and plotting the mean of the force index per channel block with standard errors confirmed the results. Repeated-measures ANOVAs on the mean of the force index for the baseline block and the learning block showed no difference for either block (for baseline: with the Greenhouse-Geisser correction for sphericity, group-by block  $F_{(10.106,156.639)} = 0.650, p = 0.771$ ; for learning: with the Greenhouse-Geisser correction for sphericity, group-by block  $F_{(12.818,198.683)} = 0.772, p = 0.688$ ). We also wanted to consider the effect of the cognitive task itself, therefore we ran a repeated-measures ANOVA on the difference in force index apart from the cognitive task, that is the difference between the first value of the force index right after the cognitive task and the last value of the force index right before the cognitive task. The results were not significant (using the Greenhouse-Geisser correction for sphericity:  $F_{(9.640,154.244)} = 1.012, p = 0.435$ ). The difference between the mean of the force index for the last block and for the first block was of interest as well, but the one-way ANOVA showed no significance either ( $F_{(2,32)} = 1.825, p = 0.178$ ). Since all those results were negative, we decided to consider only the first block of the experiment. This was reproducing the second experiment as reported in Keisler & Shadmehr (2010). There was a slight difference though: the block of learning did not include any channel trial then, whereas here five out of those twenty were error-clamp trials. The previous results mainly showed an effect when binning the first two trials of the block following the cognitive task together, running a Kruskal-Wallis test on that data. We ran a one-way ANOVA and a Kruskal-Wallis test on the same binning of results, but instead of reproducing those results the results were negative again

( $F_{(2,31)} = 1.72$ ,  $p = 0.196$  for the one-way ANOVA;  $\chi^2_{(2,34)} = 2.195$ ,  $p = 0.334$  for the Kruskal-Wallis test).

Since those results were not in accordance with the previous results reported, we decided to look at the likelihood of obtaining the previous results with the currently collected data. We had 13 people in the memory task group, 11 in the non-memory task group, and 10 in the no task group. The previous results had been obtained with 6 people in each group. We randomly drew 6,000 sets of groups of 6 people in each group, and ran the one-way ANOVA and Kruskal-Wallis test on the first two trials of the channel block binned together, to compare the distribution of the p-values and assess how likely it was to get a significant result from the current data (Figure 16). For the one-way ANOVA p-value distribution, about 5.1% were below 0.05; around 3.3% of the p values for the Kruskal-Wallis showed significance. This suggests that it was somewhat unlikely but not impossible to get significant results from this data, when the total data shows no significant difference.

However, when gauging correlations between motor performances and performance in the memory task, a trend seemed to appear. Therefore we added ten people to the memory task group (reaching 23 participants), in order to have a better idea of whether those correlations showed any significant trend. To assess performance in the memory task, we simply counted the number of words remembered. For the motor task, we considered the force index of the first two trials of the block binned together, the difference in force index across the cognitive task, and the mean of the block. All of those were calculated for block 1, block 10, and the mean for all blocks, and then compared respectively to the cognitive performance in block 1, block 10, and across the whole experiment. All correlations did not reach significance.

Overall, this experiment suggests that there is no interference from the declarative memory onto the motor memory, when learning and relearning only one field for a short amount of time at a time.

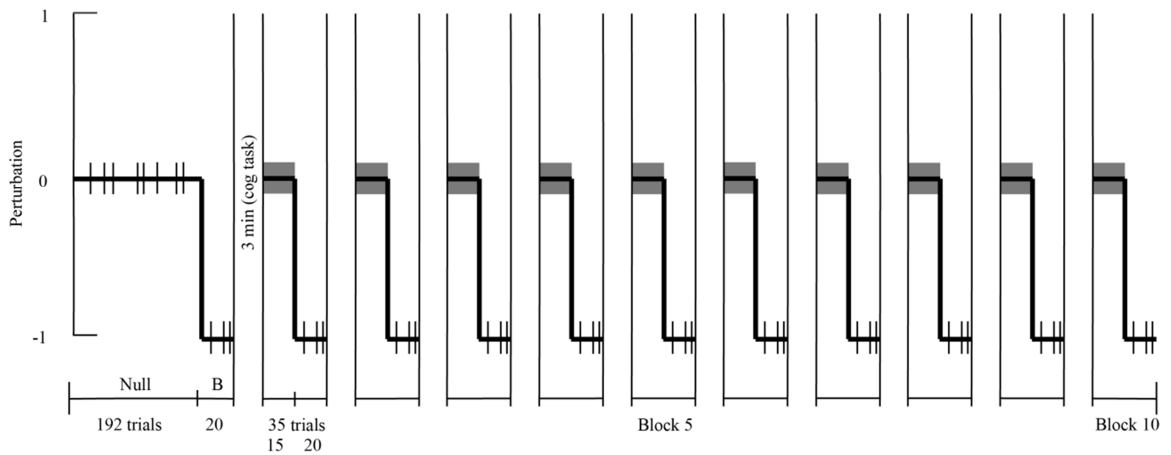


Figure 11: Experiment design: participants trained in a null field (no perturbation, 192 trials including 26 interspersed error-clamp trials), then in a counterclockwise (B) field for 20 trials (including 5 interspersed error-clamp trials), followed by a sequence repeated ten times: a 3 minute cognitive task (either memory task (word), non-memory task (vowel) or no task (wait)), a probing block of 15 error-clamp trials and a new learning block of the B field of 20 trials (including 5 interspersed error-clamp trials). Vertical ticks indicate error-clamp trials during baseline training and learning.

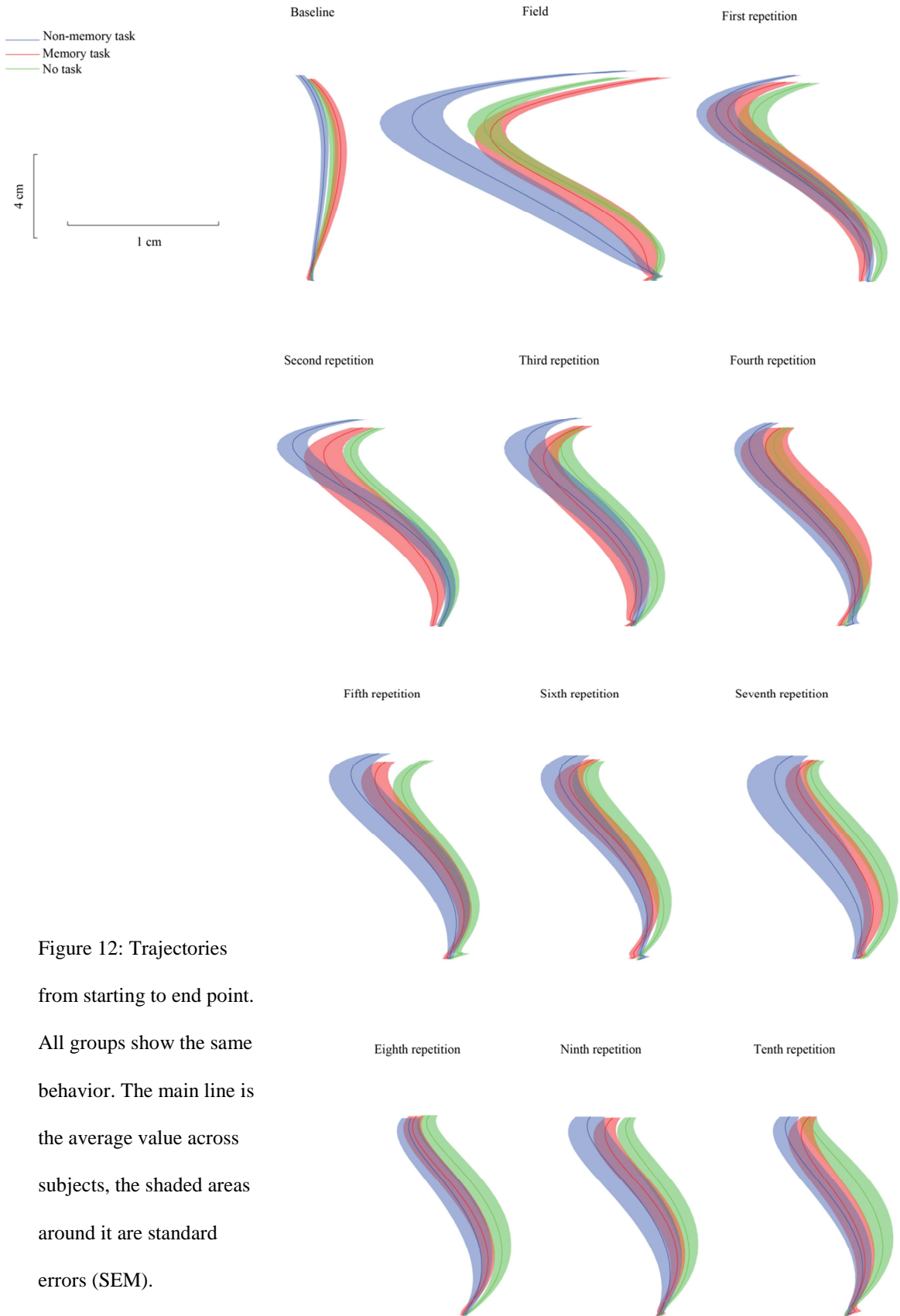


Figure 12: Trajectories from starting to end point. All groups show the same behavior. The main line is the average value across subjects, the shaded areas around it are standard errors (SEM).



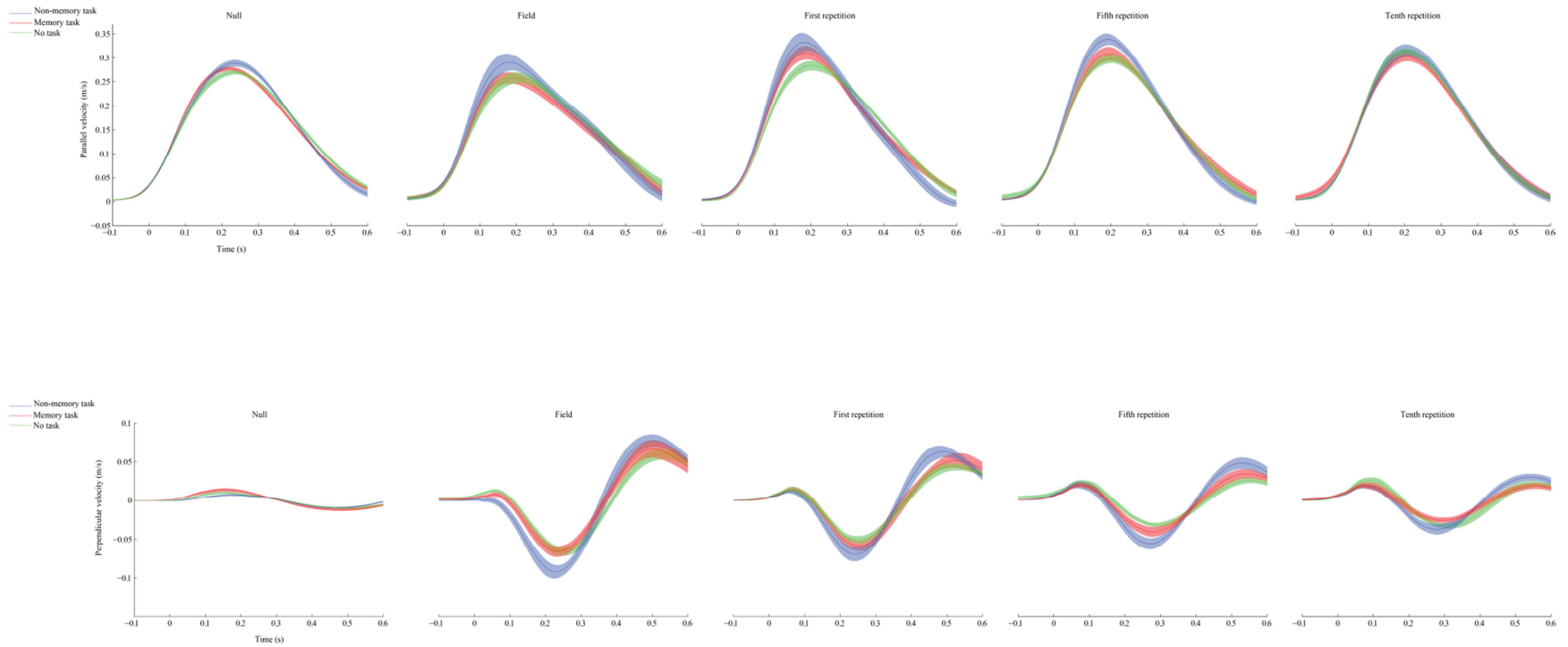


Figure 13: **A:** Parallel velocity profiles throughout the movement for field trials, averaged over each block. All groups show the same behavior.

**B:** Perpendicular velocity profiles throughout the movement for field trials, averaged over each block. All groups show the same behavior.

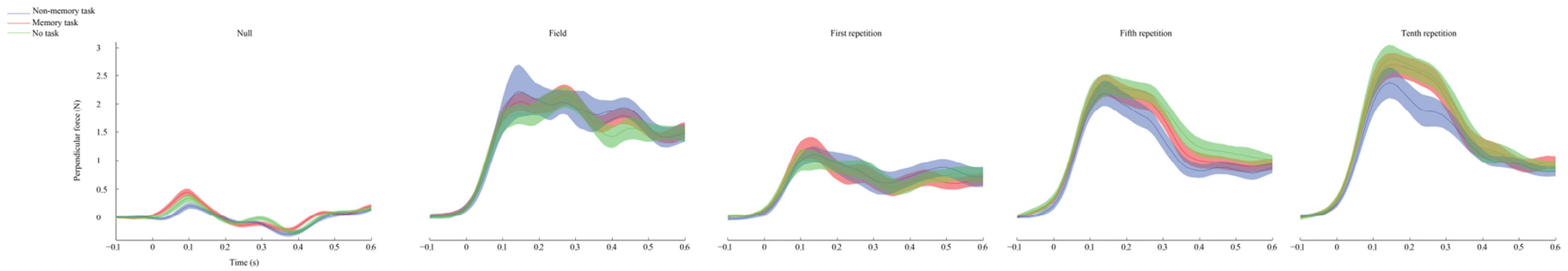
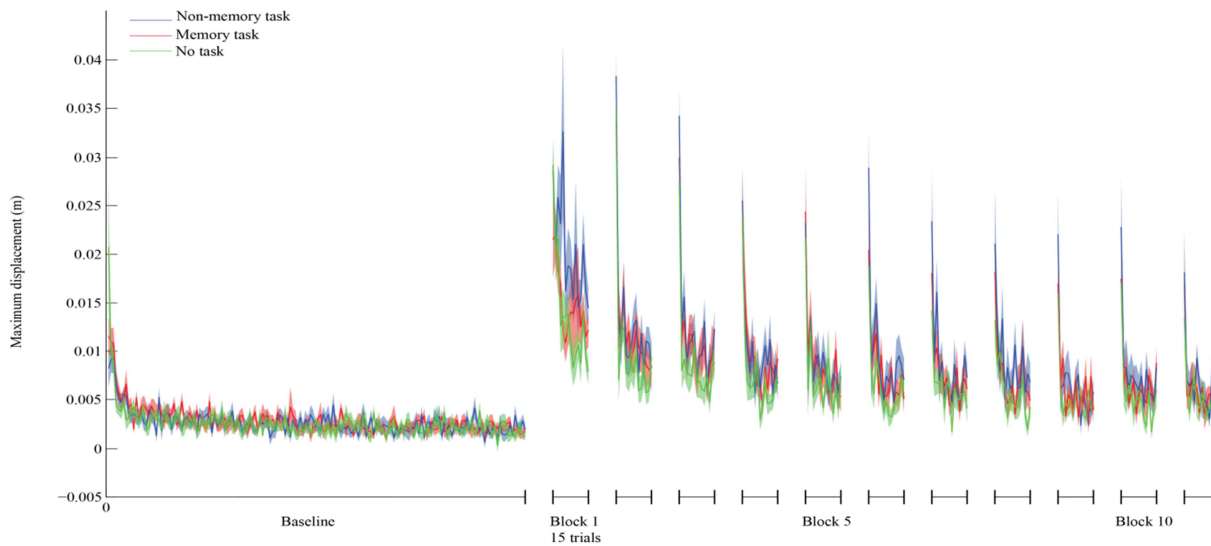
**A****B**

Figure 14: **A:** Perpendicular force profiles throughout the movement for channel trials, averaged over each block. All groups show the same behavior. **B:** Maximum perpendicular displacement, taken as the maximum horizontal distance between the trajectory and a straight line between the start and end points. All groups show the same behavior.

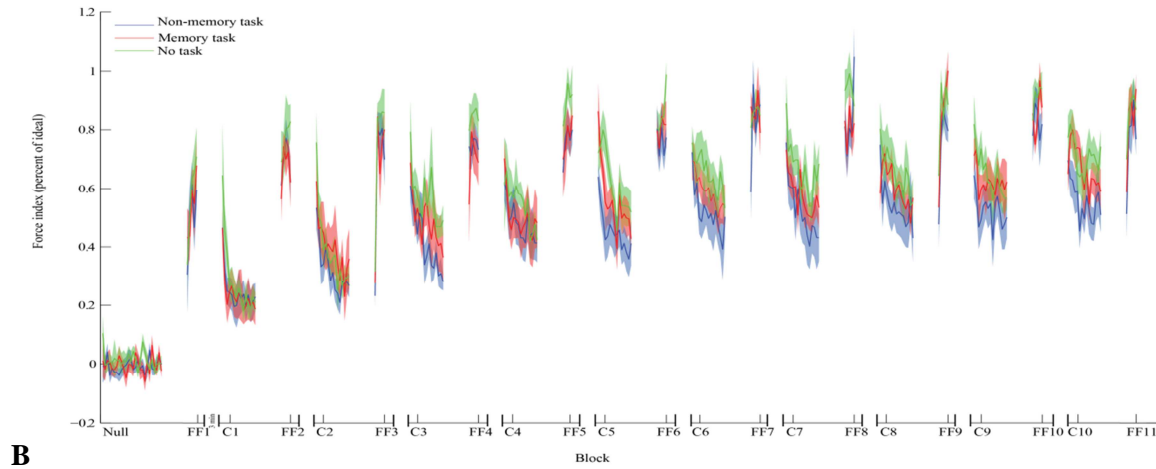
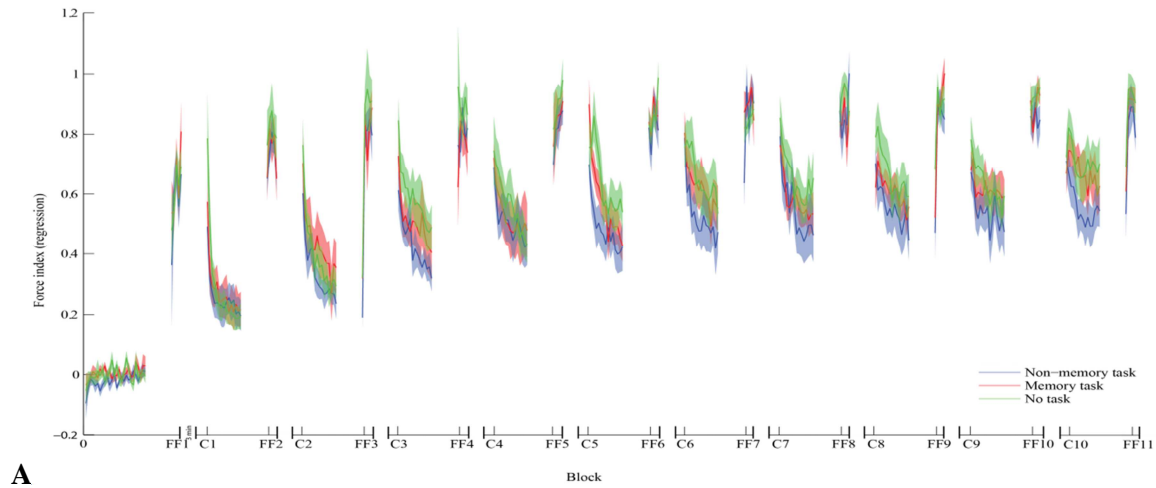


Figure 15: Force index, **A**: using the regression of the force profile on the velocity profile and **B**: calculated at maximum velocity. All groups show the same behavior.

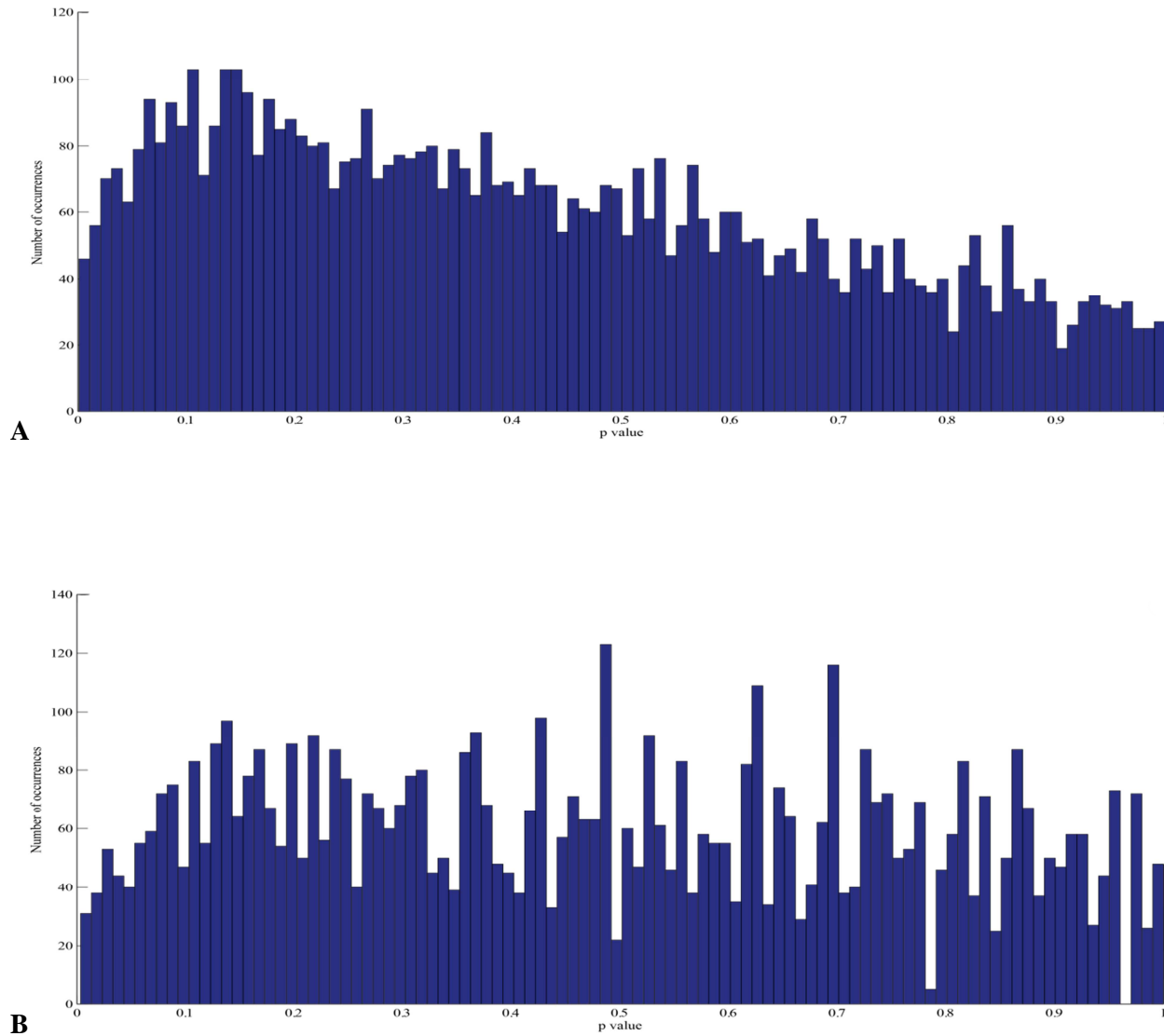


Figure 16: Distribution of p values for **A**: a one-way ANOVA and **B**: a Kruskal-Wallis test. 6,000 groups of 6 people each were randomly taken from the data, and the two tests were performed on the first two trials of the first channel block binned together. This shows the likelihood of obtaining significant results from this dataset.

## Discussion

Previous studies have shown interference between cognitive tasks involving the declarative memory system and motor tasks, in both sequence learning (Brown & Robertson, 2007a and 2007b) and in reach adaptation (Keisler & Shadmehr, 2010), specifically retrograde interference. In this study we examined anterograde interference and the retention that can take place in the retrograde interference process. We found that after learning opposite fields for different amounts of time, a declarative task could interfere with the subsequent recall of the motor memory, but no interference was apparent when learning only one field, or relearning it multiple times in a row. We also found no presence of anterograde interference of the declarative task on the subsequent learning of a motor memory when training in a field, which is in contrast to what had been found in sequence learning tasks, where interference happened both in a retrograde and an anterograde fashion (Cohen & Robertson, 2011).

Keisler & Shadmehr (2010) examined the effect of a cognitive task, either a memory task, a non-memory task or no task, and found that the memory task interfered with the recall of a motor memory. The first part of our experiment 3 reproduced this protocol, however we found no group differences. The previous results had been explained by the two-state model from Smith et al. (2006), which predicts interference between the declarative memory system and the fast process of motor memory in this paradigm. The fact that there was no interference here could potentially be explained with results by Vaswani & Shadmehr (2013), which demonstrated that during error-clamp trials a motor memory does not decay, but is rather disengaged while still being protected to be recalled if the perturbation appears again. Given that only one field was experienced by the subject, disengagement of the motor memory is likely the same for all groups, and therefore we see no difference in the output during recall of the motor memory between

groups. The same explanation goes for experiment 2, where only one field is experienced, thus no interference is seen.

Experiment 1 showed retrograde interference from the declarative memory on the motor memory, but in a different way than was previously reported. Indeed, Keisler & Shadmehr had shown that a cognitive memory task can interfere with spontaneous recovery of a motor memory. However, here we see spontaneous recovery for both the memory (word) task and the non-memory (vowel) task, but the output of the word group is substantially lower than that of the vowel group. A potential explanation comes from studies of extinction. Ghazizadeh et al. (2012) showed that the ventromedial prefrontal cortex (vmPFC) is involved in the suppression of unreinforced actions. That is, when learning competing memories, the first memory is protected while learning a new one (Pekny et al., 2011). During error-clamp trials, one memory is chosen to be re-expressed, and in this case it was the memory of A as that was primarily reinforced. Presumably, spontaneous recovery occurs as a result of vmPFC suppression of memory B, before the memory is disengaged during the block of error-clamp trials. However, one can imagine that that declarative task interferes with the vmPFC to prevent the suppression of expression of B, which may explain the decreased motor output of the word group, relative to the vowel group.

The role of the PFC is yet unclear however, as shown with unpublished results from Dr Bastian's laboratory, that give more credence to the belief that the PFC is required for protection of memories. They found that children of all ages were capable of showing savings in a motor task across two days without washout in between sessions. However, when day 2 began with a washout block, the youngest children failed to show savings upon relearning, whereas the older children showed savings comparable to adults. This may relate to the developmental time course of the PFC. Younger children may not be able to protect the initial memory from washout as a result of their yet-undeveloped PFC.

Whether the PFC is involved in protection of memories, their suppression, or both, its role seems to explain the results we see here. Indeed, if the vmPFC is involved mainly in protection of memories, we can imagine that the declarative task would interfere with that ability to decrease the protection of the memory of field A, showing a lower output. If it is mostly involved in the suppression of memories, the word task could prevent the extinction of the memory of the B field, again lowering the output. Trying to distinguish between the two explanations and the exact role of PFC requires further studies.

It would also be interesting to know if interference would occur when doing both the motor task and the declarative task simultaneously. There is evidence that performance is lowered in some cases (Taylor & Thoroughman, 2007, 2008), but when participants are able to verbally describe the perturbation the learning is better (Hwang et al., 2006). Further work could also be made to study whether the interaction between the memories is bidirectional, i.e. whether the motor memory can interfere with the recall of previously learned words, or with the subsequent learning of words.

In conclusion, our data provide evidence for retrograde interference between the declarative memory and the motor memory systems, when learning opposite fields for different amounts of time, but not when learning only one field for a short period of time. There was no anterograde interference either. These results might be due to an interaction with the prefrontal cortex, involved in the protection and suppression of memories.

### **Appendix: Median deviation of the medians: MDM**

To find an outlier, one method that has been shown to be efficient at labeling outliers is called the median deviation of the medians, and was described in Rousseeuw and Croux in 1993. It basically rejects data points that are too far away from the median of the distribution. For experiment 1, we used this criterion to look for outliers at the subject level, taking the distribution of all subjects for the experiment (both groups together). We considered the mean of the force index for the learning block for each participant, and used the MDM criterion to decide whether there was an outlier, and found one that we discarded from the analysis. We then used the same criterion on a trial-by-trial basis to remove outlier trials.

The first part is to define the median deviation of the medians (MDM): for each data point, the absolute distance with every other point in the distribution is calculated, and the median of that distribution is computed. Doing this for all  $n$  data points, we get a  $n$  different medians, and evaluate the median of that distribution of those medians. The MDM is proportional to this median:

$$MDM = C \cdot \text{median}_i(\text{median}_j(|x_i - x_j|_{j \neq i}))$$

where  $C$  is any constant. It has been shown that, if it is assumed that the true underlying distribution of the dataset is a Gaussian distribution, setting  $C = 1.1926$  makes the MDM a robust estimate of the standard deviation of the distribution. Any data point is then defined as an outlier when further away than 3 times the MDM from the median, i.e. greater than  $\text{median} + 3 * \text{MDM}$  or lower than  $\text{median} - 3 * \text{MDM}$ .



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### **Scholarly life**

Aymeric Blanc was born in Clamart, France on February 12, 1988. After going to high school around Paris, he entered the lycée Louis-le-Grand for a 3-year preparatory program in Mathematics and Physics that led to getting into Ecole Polytechnique, where he turned to Biology. He then enrolled in the Master of Science in Biomedical Engineering program at Johns Hopkins University in 2011, where his research focused on the interference between declarative memories and motor memories, working specifically on arm reaching movements.