

Learning and Memory Formation of Arm Movements

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Introduction

Learning a motor task is characterized by a gradual transition from a high demand on attention to the task becoming automatic and non-attentive. Studies that have recorded limb movements during learning of a motor task have shown that this increase in automaticity of movements is accompanied by key kinematic features: (1) Stiffness of the limbs decrease (Milner and Cloutier, 1993), as evidenced by a decreased co-activation of the muscles and an increased compliance in response to a perturbation. (2) Movements become smoother (Hreljac, 1993), as evidenced by a reduction in a cost function that scales with the jerkiness of the movement (second derivative of velocity). (3) Motion of the joints become decoupled (Vereijken et al., 1992), as evidenced by a reduction in the cross-correlation between patterns of joint rotations. The central hypothesis is that these kinematic features result from the formation of motor memory: the content of motor memory is called an “internal model” of the task. Formation of the internal model allows the nervous system to reduce the dependence of the motor program on the visual and proprioceptive feedback. This leads to a reduction in the attention requirements of the task and increases the reliance of the motor output on an internal model that predicts motor patterns that should be produced in order to execute a desired movement.

Although this description of an internal model brings to mind learning of complex motor skills, it is equally valid for simple tasks. This can be illustrated by an example: if one is asked to rapidly pick up an empty bottle of milk that has been painted white, the arm exhibits a flailing like motion. This is an indication that in programming the motor output to the muscles, the nervous system predicts and attempts to compensate for the mechanical dynamics of the perceived full bottle. In a control theory framework, the internal model (IM) is an association from a desired trajectory for the hand to a set of muscle torques (Shadmehr and Mussa-Ivaldi, 1994a). Since in principle this map is unique for the objects and tools which we have learned to interact with, “motor memory” may be thought to contain, at least in part, a collection of IMs where visual information serves as an identifying cue that allows for binding of an appropriate association, i.e., recall. We learn these IMs with experience (Gordon et al., 1992), and they are an integral part of our ability to interact with the objects and systems in our environment. Yet we know little about the neural substrate of motor memory or the processes that culminate in its formation. The objective of this chapter is to review as well as present some new results on psychophysics of learning to make arm movements, and then put these results in perspective of what we know about memory systems of the brain.

Learning novel dynamics

As one learns to control their arm to perform a novel motion, the motor output begins to rely on an IM. The evidence for this comes from two directions. In the first approach, changes in

the motor output have been recorded as some aspect of a well-learned task has been altered (Milner and Cloutier, 1993; Gottlieb, 1994). For example, Gottlieb (1994) trained subjects to make elbow movements against various loads. He found that after a number of practice movements, the EMG had changed in such a way as to suggest that the motor output was being pre-programmed before the onset of movement based on the expected behavior of the load. Milner and Cloutier (1993) quantified changes in EMG during practice and observed that initially, when presented with a novel load, subjects tended to co-contract antagonist muscles, increasing stiffness of the arm. An increase in stiffness is a reasonable way of dealing with an unknown load: the arm will show less deviations from the desired kinematic behavior for a given disturbing force. With practice, there was a decrease in the level of co-contraction. This decrease paralleled an increase in the reliance of the motor output on a pattern of muscle torques which specifically compensated for the imposed load.

In the second approach, the formation of the internal model has been inferred by what is termed “after-effects”: novel forces were imposed on the arm by having subjects move a manipulandum (Fig. 1) (Sanes, 1986; Shadmehr and Mussa-Ivaldi, 1994a), or by positioning a subject at the center of a rotating room (Lackner and Dizio, 1994) so that strong coriolis forces acted on the arm during multi-joint reaching movement. The imposed forces perturbed the trajectory of the arm and required the subject to use visual and proprioceptive feedback to correct errors in hand path (Fig. 1C). With practice, subjects were able to make accurate and smooth reaching movements without visual guidance (Fig. 1D). It is suggested that the IM functions as a mapping from a desired arm movement (i.e., plan) to a prediction of the forces that will be encountered during the movement (Shadmehr and Mussa-Ivaldi, 1994b). As a consequence, because of the reliance of the motor output on the IM, removal of the imposed forces should lead to after-effects: in the absence of forces, the hand trajectory should be a mirror image of that observed before adaptation (one can describe a mathematical model and make exact predictions of this trajectory, see Shadmehr and Mussa-Ivaldi, 1994). This prediction has been experimentally confirmed (Fig. 1F).

We have recently developed a tool that gives a fairly direct measure of the IM constructed by the subject’s motor system (Shadmehr et al., 1995). The idea is to measure the change in the mechanical impedance of the arm (i.e., how the arm’s neuro-muscular system reacts to a perturbation). Consider the equations of motion for the robot-human system of Fig. 1:

$$I_r(p)\ddot{p} + G_r(p, \dot{p})\dot{p} = E(p, \dot{p}) + J_r^T F \quad (1)$$

$$I_s(q)\ddot{q} + G_s(q, \dot{q})\dot{q} = C(q, \dot{q}, q^*(t)) - J_s^T F \quad (2)$$

where I and G are inertial and coriolis/centripetal matrix functions, E is the torque field produced by the robot’s motors, i.e., the environment, F is the force measured at the handle of the robot, C is the controller implemented by the motor system of the subject, $q^*(t)$ is the reference trajectory planned by the motor control system of the subject, J is the Jacobian

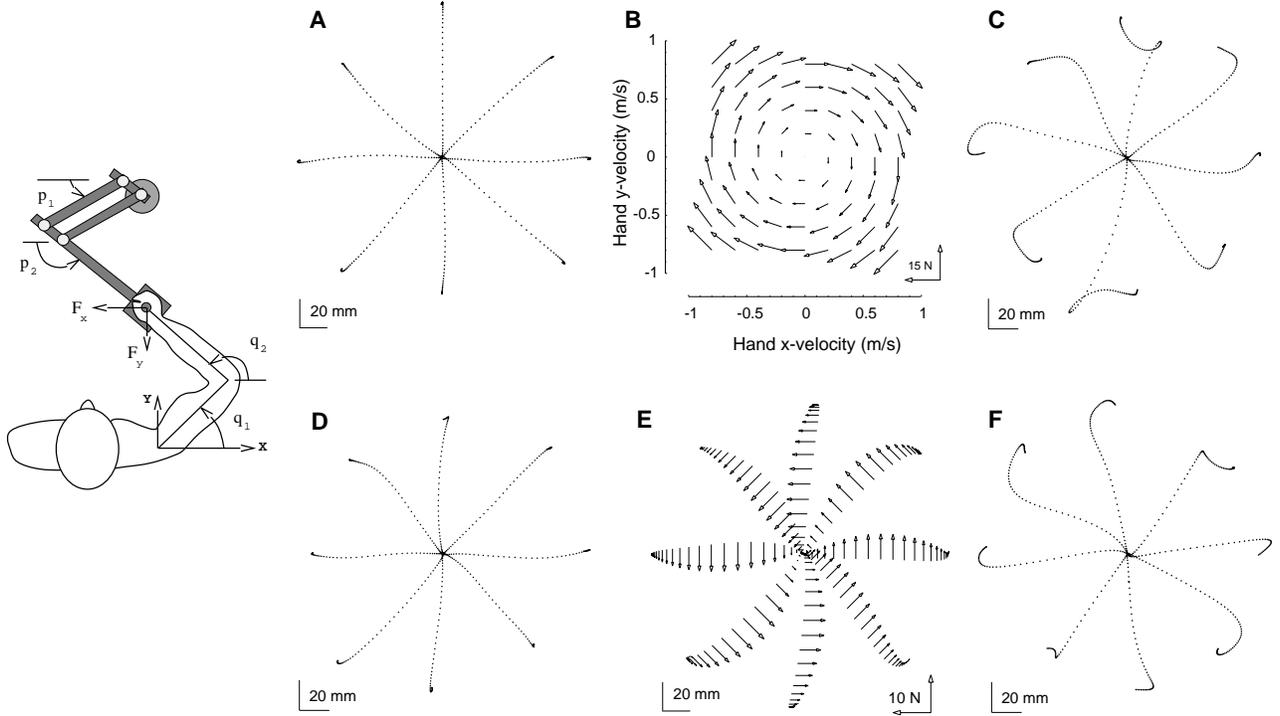


Fig. 1: The robot manipulandum and the experimental setup. The manipulandum is a very low friction, planar mechanism powered by two high performance torque motors. Subject grips the handle of the robot. The handle houses a force transducer. The video monitor facing the subject displays a cursor corresponding to the position of the handle. A target position is displayed and the subject makes a reaching movement. With practice, subject learns to compensate for the forces produced by the robot. **A**, Hand path of a typical subject in the null field (i.e., no forces being produced by the robot). **B**, An example of a force field produced by the robot, $F = B\dot{x}$, where \dot{x} is the hand velocity vector. **C**, Resulting hand path of an untrained subject in the field. **D**, Hand path after 300 movements in the field. The trajectory in the field converges to the trajectory observed in the null field. **E**, Forces produced by a typical trained subject to counter the effect of the force field as a function of hand position for each movement. These forces are the projection of the forces measured at the interaction point between the subject and robot onto a direction perpendicular to the direction of target. **F**, While training in the field, random targets are presented with null field conditions. The result are after-effects. The points in all hand paths are 10 msec apart.

matrix describing the differential transformation of coordinates from endpoint to joints, q and p are column vectors representing joint positions (e.g., q_1 and q_2) of the subject and the robot (Fig. 1), and the subscripts s and r denote subject or robot matrices of parameters. In the null field, i.e., $E = 0$ in Eq. (1), assume that a solution to this coupled system is $q = q^*(t)$, i.e., the arm follows the reference trajectory (typically a straight hand path with a Gaussian tangential velocity profile). Let us name the controller which accomplishes this task $C = C_0$ in Eq. (2). When the robot motors are producing a force field, i.e., $E \neq 0$, the arm's motion converges back to the reference trajectory if the new controller in Eq. (2) is $C = C_1 = C_0 + J_s^T J_r^{-T} \hat{E}$. The internal model composed by the subject is $C_1 - C_0$, i.e., the change in the controller after some training period. We can estimate this quantity by measuring the change in the interaction force along a given trajectory before and after training. If we call these functions F_0 and F_1 ,

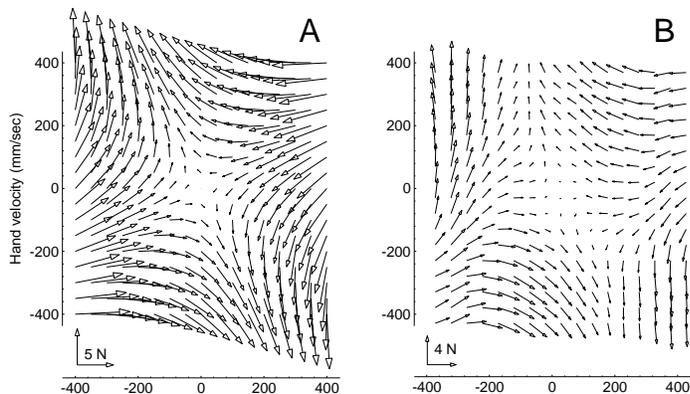


Fig. 2: Quantification of the change in impedance of a subject’s arm after learning a force field. **A:** The force field produced by the robot during the training period. **B:** The change in the subject’s arm impedance after the training period, i.e., the internal model.

then we have:

$$F_0(q, \dot{q}, \ddot{q}, q^*(t)) = J_s^{-T}(C_0 - I_s \ddot{q} - G_s \dot{q}) \quad (3)$$

$$F_1(q, \dot{q}, \ddot{q}, q^*(t)) = J_s^{-T}(C_0 + J_r^T J_r^{-T} \hat{E} - I_s \ddot{q} - G_s \dot{q}) \quad (4)$$

The functions F_0 and F_1 are impedances of the subject’s arm before and after training in a field. By approximating the function $F_1 - F_0$, we have an estimate of the change in the output of the human arm’s adaptive controller, which we have defined to be the internal model. In order to measure F_0 , we had the subjects make movements in a series of environments. The environments were unpredictable (no opportunity to learn) and their purpose was to perturb the controller about the reference trajectory so we could measure F_0 at states neighboring the reference trajectory. Next, the environment in Fig. 2A was presented and the subject given a practice period to adapt. After training, F_1 was estimated in a similar fashion as F_0 . The difference between these two functions was calculated along all measured arm trajectories and the results were projected onto the hand velocity space. The resulting pattern of forces were interpolated via a sum of Gaussian radial basis functions, and are shown in Fig. 2B. This is the change in the impedance of the arm and estimates the input–output property of the internal model that was learned by this subject. We found that subjects learned to change the effective impedance of their arm in a way that approximated the imposed force field.

We also recorded EMG activity during learning of the reaching task. Figure 3 shows the root-mean squared EMG from four arm muscles during movements in the null field (no forces) and those in field of Fig. 1B. The particular movement shown is to a target at 90 degrees (at 12 o’clock). The force field would tend to push the hand in a clock-wise direction, causing a shoulder and elbow extension. After practice, the learned response is an increase in activation of all muscles, but this increase is particularly strong in the elbow and shoulder flexors. In effect, the subjects learn to make a movement which is primarily an elbow extension with strong activation of the elbow and shoulder flexors. The EMG activity of the biceps suggests that for this movement, practice results in generation of compensatory flexor torques that correlate with hand velocity.

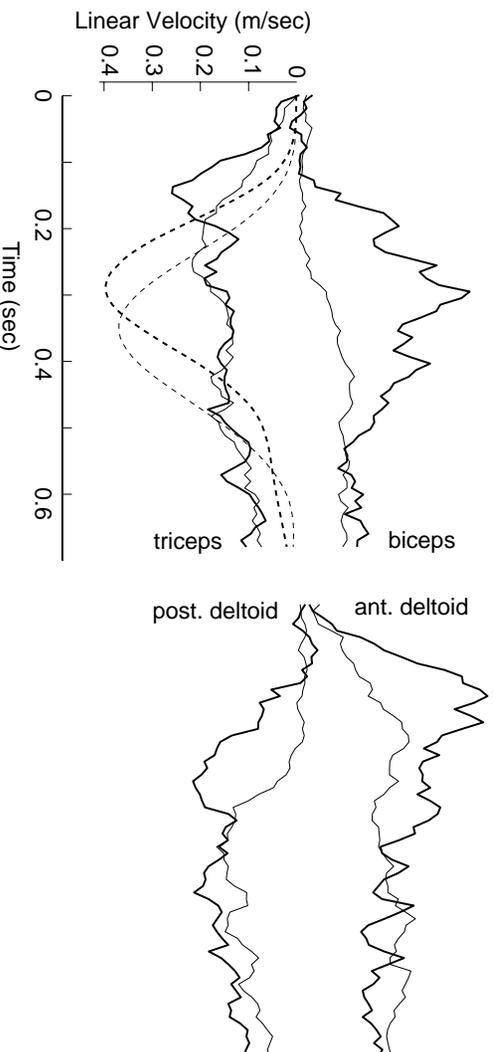


Fig. 3: Root-mean squared, averaged ($n=14$ subjects), bandpass filtered (17–530 Hz) EMG from four arm muscles during motion of the hand to a target location at 10 cm and 90 degrees (12 o'clock). The thin line is the EMG during movements in the null field, and the heavy line is the EMG in the force field of Fig. 1B, after subjects had adapted. Movement kinematics are super-imposed on the triceps EMG: thin and thick lines are the linear velocities ($\sqrt{x^2 + y^2}$) in the null and force fields, respectively. The pattern of forces (Fig. 1B) for this movement imposes an extension torque on the elbow and shoulder joints. The torque will be proportional to hand velocity. Effect of training is an increase in the activity of all muscles, but the magnitude of the increase is particularly large for the biceps and the ant. deltoid (elbow and shoulder flexors). With training, subjects learn to significantly increase activity of the flexors for a movement which is essentially an extension of the elbow joint. Note that after adaptation, biceps EMG is essentially proportional to hand velocity, compensating for the imposed force field.

Representation of memory changes with time

Once the pattern of muscular activity that was necessary to make smooth reaching movements in the force field was learned, it became available for recall: performance in the same environment was significantly improved (compared to initial practice) when tested 24 to 48 hours later (Shadmehr et al., 1995). In comparison, performance in an untrained environment remained at naive levels. Recent experiments show that the improvement in performance persists without further practice for at least 5 months (Shadmehr and Brashers-Krug, 1996). This suggests that practicing arm movements with a novel mechanical environment sets in motion processes that result in long-term motor memories.

Unfortunately, we know little about the processes that culminate in motor memory formation (Salmon and Butters, 1995; Halsband and Freund, 1993). However, a feature of memory across the animal kingdom is that it continues to develop long after practice has stopped: in general, memory appears to functionally progress from a short-lived fragile form to a long-lasting stable form (DeZazzo and Tully, 1995). For example, a person who has been knocked unconscious will have memory loss for the events that occurred just before the blow. Severely depressed patients who undergo electric shock therapy show a significant (and sometimes transient) reduction in their ability to recall items they recently learned (Squire et al., 1975). The

progression to long-term memory, which is referred to as consolidation, is a time dependent process that is initiated during the practice session but continues long after completion of practice. The time during which information becomes consolidated has been used to functionally define short-term memory (Fuster, 1995).

Does formation of motor memory progress from a short-term, fragile form to a long-term stable form? Is there a distinct short-term motor memory phase? Until recently, there was little evidence to support the notion of motor memory consolidation. For example, severely depressed patients receiving electric shock therapy 24 hours after acquiring a visuo-motor skill showed no loss of the skill (Squire et al., 1984). However, the same patients had little recollection of having practiced the task before. In other words, the intervention appeared to have stopped the consolidation process of one type of information (the memory of the episode), but not of the visuo-motor memory. This and a lack of evidence regarding a functional transformation of motor memory from a fragile to a stable form had suggested that the distinction between short-term and long-term memory did not apply to learning of visuo-motor skills (Squire, 1987).

However, we know that representation of memory of certain skills also changes with time: in a perceptual discrimination task, it was observed that subjects rapidly improved with training, and continued to improve at a slower rate after completion of practice and without further training (Karni and Sagi, 1993). The fast learning took place with the presentation of the stimulus, but further, slower learning took place hours after the end of the training session and was critically dependent on a component of sleep (Karni et al., 1994). In another set of experiments it was shown that motor memories are not permanent and may be vulnerable to experimental intervention: Lewis and co-workers (Lewis and Miles, 1956; Lewis et al., 1951) demonstrated that association of visual stimuli to specific motor actions could be learned and subsequently “unlearned” when a second task required subjects to associate similar visual stimuli to different motor actions. However, these studies did not investigate whether the vulnerability of the original learning changed with the passage of time.

If a newly acquired motor memory gradually (and without further practice) becomes stable with time, then one would expect that an appropriate intervention will eventually have little effect on the ability to recall a previously learned IM. Using the paradigm of learning to control arm movements in a force field (Fig. 1), this idea was recently tested. We asked subjects to practice movements in field B_1 , and then gave them a period of rest, varying from 5 minutes to 24 hours (during which subjects were free to do what they wished). After this period of rest, subjects trained in field B_2 , where $B_2 = -B_1$, i.e., the forces in B_2 were in the opposite direction of B_1 . We then tested for retention of the skill acquired in practicing in B_1 some days later (Fig. 4). Our results showed that retention of the IM for B_1 could be disrupted when a second, anti-correlated to the first, IM for B_2 was learned (Brashers-Krug et al., 1995). We theorized that this disruption occurred because the adaptive system was attempting to

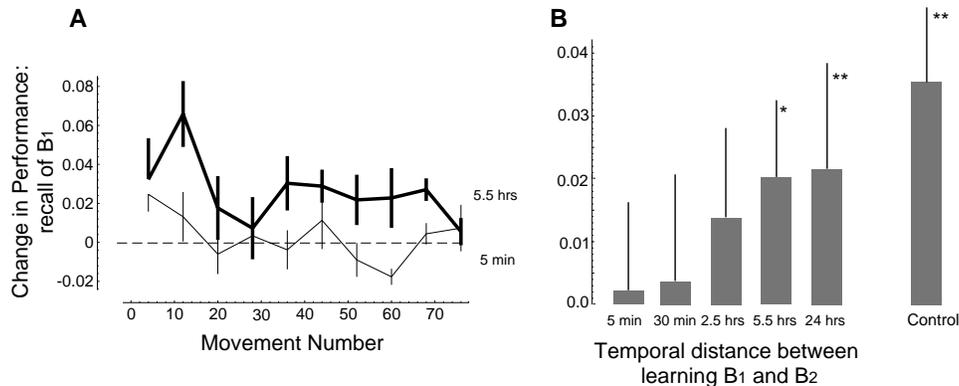


Fig. 4: Performance during the test of recall for B_1 as a function of temporal distance between learning of B_1 and B_2 . B_1 was tested for recall one week after B_1 and B_2 were learned. The performance measure is a correlation between a typical hand trajectory of the subject in the null field before introduction of the forces (as in Fig. 1A) and the trajectory in the field. **A**, Mean improvement in performance \pm SE for two groups of subjects. Thin line is for the group ($n=9$) that practiced in B_2 five minutes after completion of practice in B_1 . Thick line is for the group ($n=10$) that practiced in B_2 5.5 hours after B_1 . **B**, Ability to recall B_1 is significantly dependent on temporal distance between B_1 and B_2 . Each bar is the mean \pm 95% confidence interval of change in performance as measured for a target set during the recall test vs. during initial practice.

associate the same visual target to two very different muscular force patterns: learning of IM_2 was causing an “unlearning” of IM_1 . However, if IM_2 was learned beyond a critical time window (approximately 4-5 hours) after acquisition of IM_1 , it had little effect on recall of IM_1 (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1996). In other words, within hours, the representation of IM_1 became gradually less vulnerable to the “intervention” caused by learning of IM_2 . This suggested that the memory representation of IM_1 rapidly underwent a process of consolidation.

The main mechanisms currently believed to underlie memory formation in the central nervous system is long-lasting changes in synaptic efficacy (Bliss and Collingridge, 1993). A prominent example of synaptic plasticity is long-term potentiation (LTP) or depression (LTD), both of which have been observed in the motor areas of the cortex (Asanuma and Keller, 1991) and cerebellum (Castro-Alamancos et al., 1995). With regard to neural basis of consolidation, it has been shown that after inducing LTP (in the hippocampus), certain low frequency stimuli can de-potentiate the synapse (Fujii et al., 1991), effectively reducing the synapse’s efficacy to near baseline levels. These stimuli, however, are only effective if they are given within a small time window after potentiation of the synapse: 20 minutes after induction of LTP, the low-frequency stimuli depotentiate the synapse by 70%, while at 100 minutes, the depotentiation is only at 30%. This suggests that one mechanism for consolidation might be changes in the resistance of LTP or LTD to events that might reverse the potentiation. Recently, it was reported that a molecule that participates in long-term synaptic remodeling of Purkinje cells in the cerebellum was highly expressed only during the 1 to 4 hours after completion of a motor

learning task. This suggests that within a short time window after completion of practice of a motor task, there may be critical events taking place in representation of the learned skill in the central nervous system. The time course of these neurophysiological changes are similar to the functional changes that we have observed in our subjects.

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