CHAPTER 22

How is somatosensory information used to adapt to changes in the mechanical environment?

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Abstract: Recent studies examining adaptation to unexpected changes in the mechanical environment highlight the use of position error in the adaptation process. However, force information is also available. In this chapter, we examine adaptation processes in three separate studies where the mechanical environment was changed intermittently. We compare the expected consequences of using position error and force information in the changes to motor commands following a change in the mechanical environment. In general, our results support the use of position error over force information and are consistent with current computational models of motor learning. However, in situations where the change in the mechanical environment eliminates position error the central nervous system does not necessarily respond as would be predicted by these models. We suggest that it is necessary to take into account the statistics of prior experience to account for our observations. Another deficiency in these models is the absence of a mechanism for modulating limb mechanical impedance during adaptation. We propose a relatively simple computational model based on reflex responses to perturbations which is capable of accounting for iterative changes in temporal patterns of muscle co-activation.

Keywords: motor learning; error feedback; internal model; mechanical impedance

Introduction

One of the fundamental questions of motor learning is how adaptation to a changing mechanical environment occurs. By mechanical environment we mean the mechanical properties of any physical system with which a human interacts. This includes properties such as the stability of a support surface, the rigidity, dimensions and mass of manipulated objects and the dynamic characteristics of forces applied by the support surface or the manipulated object. If the mechanical environment changes in some way, performance of an activity will deteriorate unless motor commands to muscles are modified to compensate for these changes. Clearly, deterioration in performance is perceived through feedback from sensory receptors. Therefore, modification of motor commands must be linked to use of sensory information by the central nervous system. Since performance tends to improve incrementally with training, it is

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likely that perception of past poor performance (sensory error) is used to modify motor commands to muscles in a way that is expected to reduce sensory error on the next performance. Modification of motor commands results in modification of the forces applied to the environment and modification of the mechanical impedance presented to the environment. By mechanical impedance we mean properties which resist imposed motion, which in the case of muscles refers primarily to their viscoelastic properties. Mechanical impedance increases primarily by means of co-activation of antagonistic muscles. Any increase in the mechanical impedance of a limb will act to reduce the effect of perturbing forces applied by the environment to the limb. In particular, any generalized increase in the activation of elbow and shoulder muscles during reaching movements will reduce performance (sensory) error arising from a change in the mechanical environment. However, a change in the force applied to the environment will only reduce performance error if its magnitude and direction are appropriate. Inappropriate changes in the force will increase performance error. Consequently, the question posed initially should be reformulated as two questions. First, to what extent does the central nervous system increase mechanical impedance as opposed to modifying the applied force to adapt to changes in the mechanical environment? Second, when the applied force is modified what sensory information is used to compute the magnitude and direction of the change? The question marks in Fig. 1 identify

where these processes would occur in a feedforward learning scheme.

Until recently, models of motor learning required both sensory (performance) error signals and motor (command) error signals (Marr, 1969; Albus, 1971; Wolpert et al., 1998; Kawato, 1999). However, a recent computational model of the cerebellum (Porrill et al., 2004) suggests that the recurrent architecture of projections between motor cortex and cerebellum can be exploited in such a way that only sensory error information is required.

Sensory information about hand position and force are both available to the central nervous system and theoretically both could be used to represent sensory error (Fig. 1). It is possible to compare a sensory representation (visual or proprioceptive) of actual hand position with desired position, providing a position error signal. Indeed, there is convincing evidence that hand position error is critical for rapid adaptation to changes in the mechanical environment (Scheidt et al., 2000). One of the most prominent theories of motor learning involves the formation and refinement of an internal model of the interaction dynamics between the arm and the environment. The internal model is a neural representation of these dynamics that is used to compute the neural commands to control the movement. In the scheme shown in Fig. 1, these commands are implemented by an impedance controller and a force controller. In current models of motor learning under the internal model rubric, hand force rather than hand
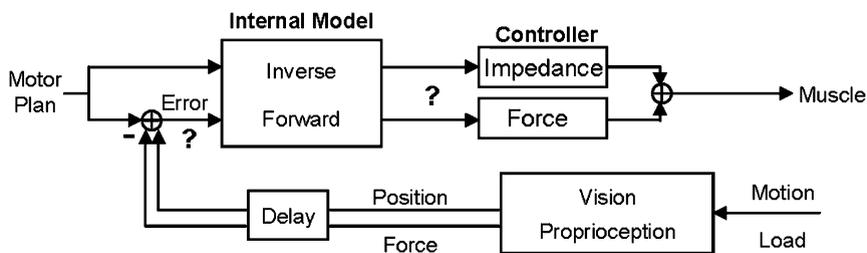

Fig. 1. Schematic representation of elements involved in modification of feedforward commands during learning. The motor plan is converted to feedforward commands to the impedance and force controllers by means of an internal model. The internal model also receives sensory information about performance error, which may include both position and force error. The internal model may include both inverse and forward models. The controllers issue activation commands to muscles which sum with feedback control signals (not shown) farther downstream. Question marks highlight the focus of our experimental investigations.

position is the output (Shadmehr, 2004). Consequently, learning involves the reduction of force error. Thoroughman and Shadmehr (2000) and Donchin et al. (2003) have proposed that hand position error can be used as a proxy for hand force error by transforming position error to force error. However, it is also possible that information about the force applied to the hand can be used to reduce performance error. We have recently examined the extent to which the central nervous system uses the strategy of increasing mechanical impedance to adapt to changes in the mechanical environment (Hinder and Milner, 2005; Milner and Franklin, 2005; Milner and Hinder, 2006). These studies also address the question of what type of sensory information is used to reduce performance error.

Methods

A total of 21 subjects participated in three experiments. Ten male subjects participated in the first experiment, six male and two female subjects participated in the second experiment and five male and four female subjects participated in the third experiment. Six of the subjects who participated in the second experiment also participated in the third experiment. All subjects gave informed consent prior to participating in the study. The protocol was approved by the institutional ethics review committee and conformed to the ethical standards set down in the Declaration of Helsinki.

In all three experiments, subjects adapted to changes in the dynamics of a robotic manipulandum during reaching movements away from the body. Movements began from a position about 30 cm in front of the shoulder and ended at a target 25 cm farther forward. We investigated both position-dependent and velocity-dependent changes in dynamics. More details of the methods can be found in previously published studies (Hinder and Milner, 2005; Milner and Franklin, 2005; Milner and Hinder, 2006).

In the first experiment presented here (Milner and Hinder, 2006), subjects adapted to a position-dependent force field for the first 125 trials. The force field acted purely in the x-direction and

pushed the subject's hand to the left $(-x)$

$$F_x = K(x + 0.032(y - y_s)(y - y_e)) \qquad (1)$$

with $K = 1.5$ N/cm on most trials. Occasionally, K was doubled for one (five times) or two trials (six times). Subjects were not informed that this would occur. When K was doubled for one trial, on the following trial only, a velocity-dependent force field was instituted, which also acted purely in the x-direction, but pushed the hand to the right $(+x)$

$$F_x = B\dot{y} \qquad (2)$$

with $B = 0.15$ N·s/cm. On three occasions during the training period (trials 3, 61 and 120), the force field was unexpectedly replaced by a virtual wall, i.e., the manipulandum acted like a stiff (10 N/cm) damped spring to lateral (x) displacement to the right. The wall effectively eliminated any rightward lateral error in hand position.

Following the 125 trials in the position-dependent force field, subjects adapted to the velocity-dependent force field for 50 additional trials. Hand position and force applied to the manipulandum were recorded at 1 kHz. We evaluated error by comparing the hand trajectory and force to the mean hand path and force at the end of the training period. Modification of the feedforward motor command during adaptation to the velocity-dependent force field was quantified by computing the lateral force impulse applied to the manipulandum between movement onset and peak tangential velocity.

In the second experiment presented here (Milner and Franklin, 2005), subjects intermittently adapted to a velocity-dependent force field given by

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -B & B \\ B & B \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \qquad (3)$$

with $0.09 \leq B \leq 0.15$ N·s/cm, dependent on the subject's capacity to adapt. This force field tended to push the subject's hand to the right and towards the target with the perturbing force increasing as a function of velocity. Subjects performed 27–28 sets of three consecutive trials in the velocity-dependent force field, each separated by a random number of between 4 and 8 null field (no force) trials. On several occasions (4–6), the third of the three force

field trials was unexpectedly replaced by a virtual channel, which created stiff elastic walls with a stiffness of 40 N/cm to lateral (x) displacement in either direction. On a similar number of occasions (4–5), the third of the three force field trials was omitted so that subjects performed only two force field trials before returning to the null field. Modification of the feedforward command undergone during the two or three force field trials was evaluated by comparing hand trajectory and force.

In the third experiment presented here (Hinder and Milner, 2005), subjects performed 150 trials in a position-dependent force field, that also pushed the hand to the right with the force increasing in a parabolic fashion during the first 5 cm of the movement and then decreasing symmetrically during the next 5 cm. The following equation describes the perturbing force, which was purely in the x-direction

$$F_x = -0.32(y_s - y)(y - y_e), \quad -(y_s - y)(y - y_e) \geq 0$$
$$F_x = 0, \qquad\qquad -(y_s - y)(y - y_e) < 0$$
(4)

where $y_s = 0$, $y_e = 10$ cm, y is the current location of the hand, giving a maximum force of 8 N when $y = 5$ cm. On every fifth trial, the force field was predictably replaced by a virtual channel (40 N/cm). Changes in the force measured on these trials indicated how subjects progressively adapted their lateral force to compensate for the perturbing effect of the force field. The effect of the virtual channel on the feedforward command was evaluated in terms of change in force applied to the channel and change in hand trajectory on the trial which followed the channel trial.

Results

The focus of the first study is on the performance error after a change in the mechanical environment and the type of sensory information used to modify the feedforward motor command on the following trial to reduce performance error. In the first study, the position-dependent force field produced a large deviation ($\sim$20 cm) to the left of the straight line joining the targets the first time it was

experienced, following a series of null field training trials. On the next trial (trial 2), the lateral deviation was dramatically reduced and eventually stabilized at $\sim\pm0.5$ cm after extensive training (Milner and Hinder, 2006). Trials 3, 61 and 120 were trials on which the force field was replaced by a virtual wall. Comparison of the trajectories on pre-wall trials 2 and 119 (Fig. 2A) and the lateral forces on wall trials 3 and 120 (Fig. 2B), provides insight into the adaptation process. There are only minor differences between the trajectories until after the midpoint of the movement (>13 cm). Yet, comparing the subsequent wall trials, the lateral force applied to the wall begins to differ shortly after movement onset and marked differences are already apparent 8 cm into the movement. This suggests that limb stiffness made an important
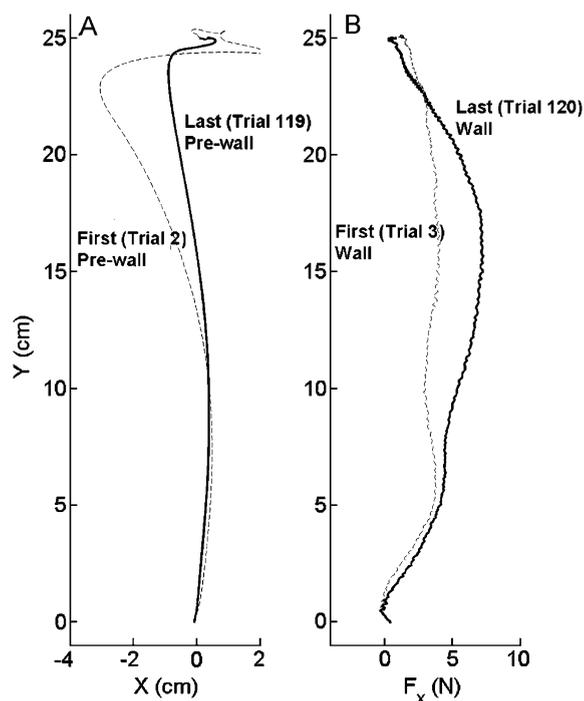

Fig. 2. (A) Mean hand paths across subjects ($N = 10$) early (dashed line) and late (solid line) during learning of the position-dependent force field. There is very little difference in the hand path until near the midpoint of the movement. (B) Mean lateral force across subjects on first wall trial (dashed line) and last wall trial (solid line) plotted as a function of forward position. Forces begin to differ well before the midpoint of the movement, indicating that the dynamics of the force field are not yet well compensated by trial 3.

contribution to reducing the performance error between the first and second trials otherwise greater initial deviation in the trajectories on trials 2 and 119 would have been expected based on differences in the profile of the applied lateral force recorded on the wall trials. Nevertheless, from Fig. 2B there is good evidence that subjects were already applying a substantial force to the right by trial 3. It seems clear that information about the direction and approximate magnitude of the force error must have been extracted from sensory information during the first two force field trials even though the profile of the force error was still inaccurate.

Observations from trials where the force field strength was doubled support this interpretation. Unexpected doubling of the force field strength from 1.5 N/cm to 3 N/cm for two trials in succession occurred on 5 occasions during training. This again produced a large lateral (x) deviation to the left on the first trial followed by a substantial reduction on the second trial, very similar to the first two force field trials (Milner and Hinder, 2006). On the following trial, the force field returned to its initial strength. Any increase in lateral force to compensate for doubling of the force field strength should have been evident as an aftereffect, i.e., a noticeable trajectory deviation to the right. Although the expected aftereffect was observed (Fig. 3A), the force applied to the manipulandum indicated that it was the result of a relatively small increase in force over the first 5 cm of the movement, relative to the force field trial which preceded doubling of the force field strength (Fig. 3B). This again suggests that although information about the direction and magnitude of the change in the mechanical environment was captured from sensory information when the force field strength was doubled, an important contribution to resisting the perturbing effect of the force field must have been derived from an increase in arm stiffness. It should be noted that the maximum force applied to the manipulandum on the aftereffect trial was substantially less than on the trial which preceded doubling of the force field strength. Because the force field drops to the right of the line joining the targets, subjects likely reduced their force by a combination of stretch reflexes in
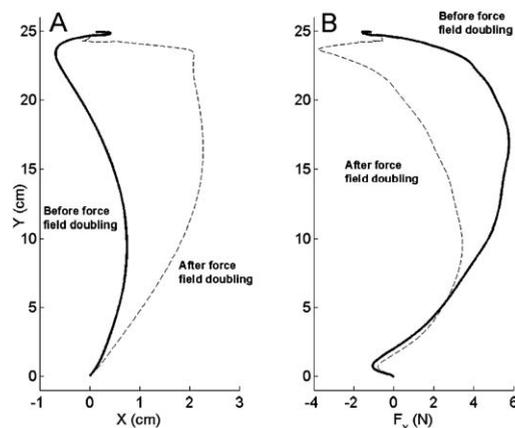

Fig. 3. (A) Mean hand paths across subjects ($N = 10$) for force field trials before (solid line) and after (dashed line) trials where the force field strength was doubled for two consecutive trials. There is a large aftereffect to the right after doubling of the force field strength, indicating that subjects increased their lateral force to the right. (B) Corresponding forces recorded at the hand, indicating that the aftereffect is created by a relatively small increase in rightward force applied to the manipulandum shortly after movement onset, during the initial 5 cm of the reach. The large negative force difference later occurs because deviation of the hand to the right results in lower forces due to the nature of the position-dependent force field (Milner and Hinder, 2006).

antagonist muscles and voluntary corrective action. It is also possible that high arm stiffness would limit the perturbing effect of the decline in force field magnitude to the right.

When a velocity-dependent force field (VF), which pushed subjects to the right, followed doubling of the force field strength, there was a large lateral deviation ($\sim$10 cm) to the right (Milner and Hinder, 2006). However, there was no evidence that subjects modified the direction of their lateral force. When the position-dependent dynamics of the initial force field was restored on the next trial all subjects initially applied a rightward force to the manipulandum, i.e., in the *same* direction as the perturbing effect of the VF. Although the trajectory of some subjects did deviate slightly to the left this occurred because they applied a lateral force to the right, which was now less than the magnitude of the leftward position-dependent force which they were opposing (Milner and Hinder, 2006).

The failure to use information about the direction of the change in the mechanical environment to reduce performance error was not a phenomenon related to one-trial learning. Following trial 125, the VF dynamics were maintained for 50 consecutive trials. We determined how soon after switching to the VF subjects changed the direction of lateral force applied to the manipulandum by comparing the force measured by the load cell attached to the manipulandum handle with the theoretical VF force calculated from Eq. (2). As long as the load cell force was less than the VF force, it indicated that subjects applied a force in the same direction as the VF, i.e., a rightward force, thereby unloading the load cell. A net rightward force over the acceleration phase of the movement (movement onset to peak y-velocity) was recorded even after 10 consecutive VF trials (Fig. 4A). Nonetheless, performance error was incrementally reduced over the first 30 VF trials (Fig. 4B). What this indicates is that subjects did not integrate information about the change in direction of force applied by the environment into the adaptation process. Otherwise, a change in the direction of initial force compensation would have been expected after one or two trials in the VF.

Previously published results of the second study (Milner and Franklin, 2005) confirmed that subjects stiffen the arm to reduce the perturbing effects of a change in the mechanical environment. Subjects normally performed movements in a null field, but intermittently, without prior warning, the null field changed to a VF [Eq. (3)] for the three consecutive trials. Increased activation of all recorded muscles, starting before movement onset, was found on the second VF trial. However, the changes in muscle activation patterns on the second VF trial also increased lateral force to partially counteract the VF force as inferred from aftereffects and channel trials. Occasionally, the third VF trial was omitted, i.e., it was replaced by a null field trial or by a virtual channel, to determine whether subjects were adapting by compensating the force produced by the force field. On trials where the third VF was replaced by the null field, there was a clear aftereffect, evident as deviation in the hand path, soon after movement onset, opposite to the direction of the lateral force
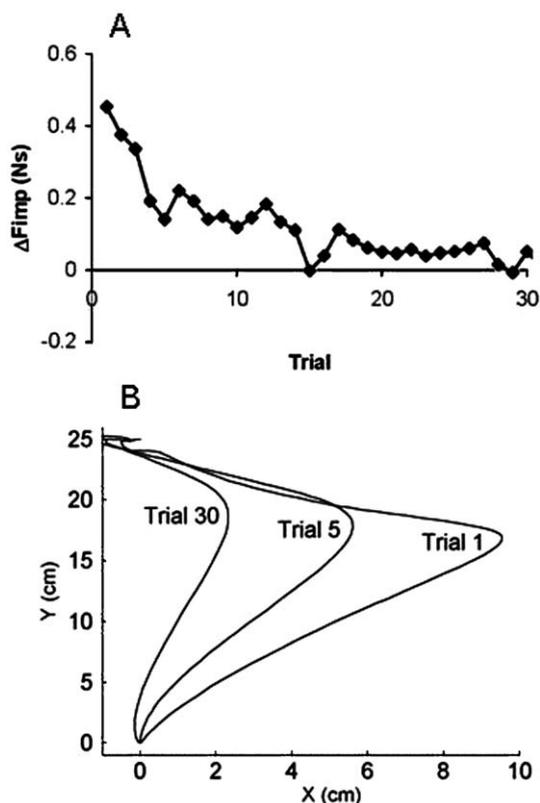

Fig. 4. (A) Difference between the force impulse generated by the velocity-dependent force field and the force impulse applied to the manipulandum by the subject, computed from movement onset to peak y-velocity, for the first 30 VF trials. Mean values for the 10 subjects are shown. (B) Mean hand paths across subjects ($N = 10$) during adaptation to the velocity-dependent force field, showing a gradual reduction in lateral error from trial 1 to trial 30.

created by the force field, i.e., to the left (Fig. 5A). This aftereffect was produced by a relatively small difference between the lateral force applied to the manipulandum on the null field trials preceding and following the three VF trials (Fig. 5B). Channel trials were also preceded by two VF trials and followed by a null field trial. The aftereffect of the VF trials following an intervening channel trial was only about half the size of the aftereffect observed when the null field trial occurred immediately after the second VF trial, despite a very small difference in the lateral force applied to the manipulandum (Fig. 5B). From this we can conclude that only small lateral forces are required to
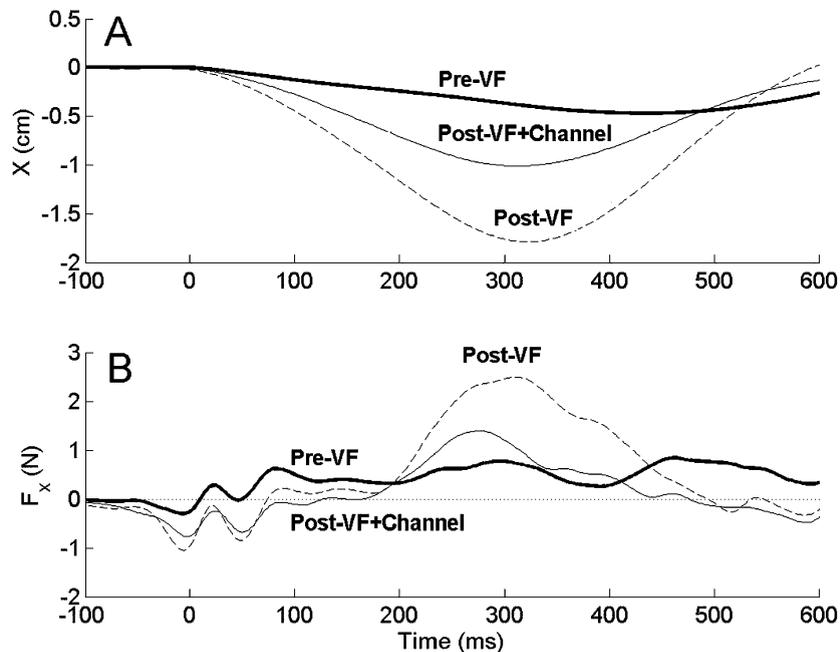
Fig. 5. (A) Mean lateral displacement from a straight line movement ($N = 4$) for null field trials prior to VF trials (Pre-VF, thick solid line), null field trials after two VF trials (Post-VF, dashed line) and null field trials after two VF trials and a channel trial, (Post-VF + Channel, thin solid line). (B) Corresponding forces applied to the manipulandum. A relatively large difference in lateral displacement is produced by relatively small differences in force during the first 200 ms of the movement (compare the thin solid line and dashed line).

produce aftereffects and that small differences in the lateral force can result in relatively large differences in aftereffect size.

In the third study, subjects adapted to a position-dependent force field (PF), which produced a lateral force to the right with a parabolic profile that peaked 5 cm from the start position and returned to zero 10 cm from the start position. The final 15 cm of each movement was performed in a null field. On the initial trial, the force field produced a lateral deviation of several centimeters to the right that reached its maximum during the null field portion of the movement. The lateral deviation was reduced to about a third of its initial value within five trials (Hinder and Milner, 2005). The strategy which subjects employed was to rapidly increase their lateral force at movement onset, pushing the manipulandum in the opposite direction to the force field, i.e., to the left. This resulted in a hand path that initially curved to the left, reaching maximum leftward deviation when

approximately a third the force field region had been traversed. During the portion of the movement beyond the boundary of the force field (> 10 cm), the hand path curved to the right of the straight line joining the targets before eventually coming back to the final target position (Fig. 6). The curvature to the right was the consequence of applying a smaller lateral force impulse to the manipulandum in the force field region than the force impulse created by the force field. On every fifth trial, the force field was replaced by a virtual channel. The focus of the current analysis is on what effect the channel trials during the last half of the training session had on the motor command. By this time, subjects had effectively adapted completely to the force field, as judged from the absence of changes in hand paths, lateral force profiles or muscle activation patterns (Hinder and Milner, 2005).

The effect of the channel trial was to increase the lateral deviation of the hand path on the force field
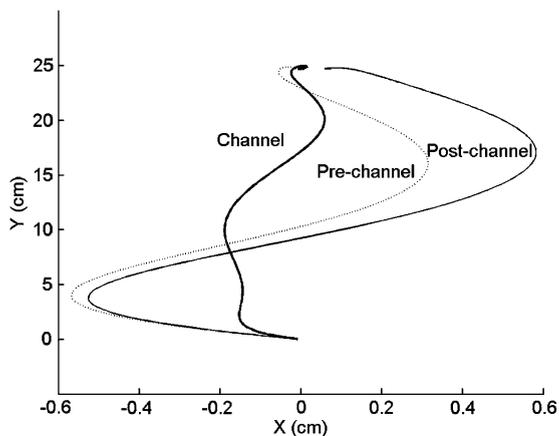
Fig. 6. Mean hand paths across subjects ($N = 9$) for position-dependent force field trials preceding (dotted line) and following (solid line) channel trials (thick solid line). Lateral displacement to the left is decreased and lateral displacement to the right is increased following the channel trial, indicating the subjects applied less leftward lateral force following the channel trial.

trial, which followed the channel trial, relative to the force field trial, which preceded the channel trial (Fig. 6). There were two distinct changes in the features of the hand path following the channel trial. Subjects produced less initial leftward curvature in the force field region and more rightward curvature beyond the force field boundary compared to the trial which preceded the channel trial. On channel trials, the manipulandum applied a lower peak (reaction) force to the hand than on force field trials. Position error on channel trials was reduced in both directions, i.e., both the initial curvature to the left and the later curvature to the right were effectively eliminated. Clearly, initial force was reduced on the trial following the channel trial compared to the trial preceding the channel trial because there was less initial displacement opposite to the direction of the force field. A reduction in force would also lead to a reduction in the stiffness of the arm, although stiffness may have also been reduced by a decrease in co-contraction of antagonistic muscles.

Discussion

Taken together the results of these studies suggest that any change to the mechanical environment, which increases lateral perturbing force, is resisted by a subsequent increase in the stiffness of the arm. However, the central nervous system also increments the lateral force opposing the perturbation if no lateral perturbing force existed previously or if the previously existing lateral force did not change direction. We have also demonstrated that muscle co-contraction is gradually reduced during training, decreasing arm stiffness if the lateral perturbing force does not change (Hinder and Milner, 2005; Milner and Franklin, 2005). This decrement in co-contraction apparently occurs in conjunction with incremental modification of the subject's lateral force profile such that the lateral force applied by the subject straightens the hand path. However, even after extensive training, the hand path is generally slightly curved, with the details of the curvature depending on the characteristics of the perturbing force.

In general, computational models of motor learning predict that if a reaching movement is repeatedly executed in the same environment, performance will improve incrementally, provided that the interaction between the arm and the environment is mechanically stable. Optimal control models such as those of Harris and Wolpert (1998) or Todorov and Jordan (2002) can be used to make general predictions about movement trajectories and movement variability at the end of learning, but are not structured to predict incremental changes from one trial to the next during learning. The most relevant learning models are those of Thoroughman and Shadmehr (2000) and Donchin et al. (2003). They predict that applied hand force will be iteratively modified in proportion to the position error, progressively reducing the error. Because they iteratively modify the internal model based on position error these models are consistent with the observation that reversing the direction of the environmental force does not immediately result in a reversal of the direction of the applied force, i.e., the models predict that the applied force will progressively decrement on successive trials until it eventually changes direction. However, they do not unequivocally predict an increase in performance error following a channel trial.

On trials following channel trials during the early phase of adaptation when position error was

expected (second study), the lateral force applied by the subject at movement onset (and possibly the amount of muscle co-contraction) was less than expected had there been no channel trial. The channel trial followed a trial with a relatively large performance error. If the central nervous system interprets somatosensory information during the channel trial as indicating that this performance error has been eliminated then the learning models of Thoroughman and Shadmehr (2000) and Donchin et al. (2003) would not predict any change in the motor command on the subsequent trial; in particular, no reduction in lateral force, which is inconsistent with our observations. However, this interpretation ignores prior expectation. Since it is likely that the force field was expected rather than the channel, elimination of performance error by the channel created a discrepancy. At this early stage of learning, the discrepancy would have most likely been interpreted as a decrease in force field strength. The appropriate response to a decrease in force field strength would be to reduce lateral force, as observed. This could be accommodated in the learning models by including a term in the computation of the update to the internal model which incorporates the statistics of prior experience, e.g., Bayesian statistics (Kording et al., 2004; Krakauer et al., 2006).

Once subjects have adapted completely to a persistent change in the mechanical environment position error may be very small so the constrained trajectory imposed by the channel may not be perceived as a perturbation. Indeed, the work of Scheidt et al. (2000) suggests this to be the case for a velocity-dependent force field. However, if hand paths are sufficiently curved after adaptation, as in the case of adaptation to the parabolic force field of our third study (Hinder and Milner, 2005), the channel might be perceived as a perturbing force opposite to the direction of curvature. This would be the case if the desired trajectory changed during adaptation, a possibility raised by Donchin et al. (2003). This might explain why subjects reduced their leftward lateral force after channel trials in our third study, resulting in greater curvature to the right during the latter portion of the movement. As is evident from Fig. 6, the channel effectively eliminated the normal rightward curvature during the latter portion

of the movement. Assuming that the desired trajectory includes rightward curvature, the channel creates a position error to the left. Since adaptation to the force field involved applying force to the left, the learning models would predict that following a channel trial this force should be reduced which would increase curvature to the right, consistent with our observations. Therefore, it seems that the desired trajectory can change during adaptation, depending on the nature of the change in the mechanical environment.

Because a reversal of the direction of the perturbing force does not evoke an immediate reversal of the direction of the applied force the question arises as to whether sensory receptors sensitive to force provide unambiguous information about force direction. Force-sensitive sensory receptors in muscle, Golgi tendon organs, probably cannot unambiguously signal the direction of the external force. A reduction in force field strength or a change in force field direction would both unload the Golgi tendons organs of contracting muscles, resulting in a similar change in their output. Signals from other force-sensitive receptors, cutaneous mechanoreceptors in the hand, could resolve the ambiguity, but only if the assisting force exerted by the subject was less than the external force. In this case, pressure sensitive mechanoreceptors in the hand would detect a force being applied by the manipulandum in the direction of the force field due to the decelerating effect of the inertia of the arm. On the other hand, if the subject exerted an assisting force that was larger than the external force, these mechanoreceptors would experience a force due to the decelerating effect of the inertia of the manipulandum, which would not indicate a change in force field direction. To avoid making potentially larger errors by misinterpreting such ambiguous information, the central nervous system may rely only on information about position error for incrementally reducing performance error. Therefore, computational models of motor learning that use position error to drive learning are likely to more closely reflect physiological reality than models which use force error.

There is one aspect of control which none of the current learning models addresses and that is the modulation of mechanical impedance. There is no

mechanism in any of these models that can explain the large feedforward increase in muscle co-contraction that is frequently observed after introducing a perturbing force nor the iterative reduction in co-contraction that occurs during adaptation to the perturbing force. We have developed a computational model that can account for these processes (Milner et al., 2006). The model uses reflex responses to the perturbation as a template for changes to feedforward motor commands. By taking a proportion of the reflex response, i.e., scaling it by a learning factor, shifting the result forward in time and adding it to the previous motor command, iterative changes in temporal patterns of muscle activation observed during learning can be reproduced. Once performance error is reduced below some threshold, a second learning factor is applied which incrementally reduces the muscle activation, reproducing the gradual reduction in co-contraction until a steady-state is achieved around the performance error threshold.

In summary, our results provide support for the computation models of motor learning developed by Shadmehr and Thoroughman (2000) and Donchin et al. (2003). In addition, they suggest that position error is the primary driving signal for modifying the internal model. We also have evidence for the speculation by Donchin et al. (2003) that the desired trajectory can be altered during adaptation to certain types of changes in the mechanical environment. These models do have several limitations though, that need to be addressed. In particular, incorporating the statistics of prior experience may be necessary, as Krakauer et al. (2006) suggest. As well, a mechanism for the modulation of limb mechanical impedance through adjustments in co-contraction levels of antagonistic muscles is required. To rectify this limitation, we propose a model in which reflex responses to perturbations serve as time-delayed templates for iterative adjustments to motor commands that result in improved performance (Milner et al., 2006).

Acknowledgments

References

Albus, J.S. (1971) A theory of cerebellar function. Math. Biosci., 10: 25–61.

Donchin, O., Francis, J.T. and Shadmehr, R. (2003) Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. J. Neurosci., 23: 9032–9045.

Harris, C.M. and Wolpert, D.M. (1998) Signal-dependent noise determines motor planning. Nature, 394: 780–784.

Hinder, M.R. and Milner, T.E. (2005) Novel strategies in feedforward adaptation to a position dependent perturbation. Exp. Brain Res., 165: 239–249.

Kawato, M. (1999) Internal models for motor control and trajectory planning. Curr. Opin. Neurobiol., 9: 718–727.

Kording, K.P., Ku, S. and Wolpert, D.M. (2004) Bayesian integration in force estimation. J. Neurophysiol., 92: 3161–3165.

Krakauer, J.W., Mazzoni, P., Ghazizadeh, A., Ravindran, R. and Shadmehr, R. (2006) Generalization of motor learning depends on the history of prior action. PloS Biol., 4: e316.

Marr, D. (1969) A theory of cerebellar cortex. J. Physiol., 202: 437–470.

Milner, T.E. and Franklin, D.W. (2005) Impedance control and internal model use during the initial stage of adaptation to novel dynamics. J. Physiol., 567: 651–664.

Milner, T.E. and Hinder, M.R. (2006) Position information but not force information is used in adapting to changes in environmental dynamics. J. Neurophysiol., 96: 526–534.

Milner, T.E., Ng, B. and Franklin, D.W. (2006) Learning feedforward commands to muscles using time-shifted sensory feedback. In: Ishii K., Natsume K. and Hanazawa A. (Eds.), Brain-Inspired IT II Decision and Behavioral Choice Organized by Natural and Artificial Brains. Elsevier, Amsterdam, pp. 113–116.

Porrill, J., Dean, P. and Stone, J.V. (2004) Recurrent cerebellar architecture solves the motor-error problem. Proc. R. Soc. Lond. B, 271: 789–796.

Scheidt, R.A., Reinkensmeyer, D.J., Conditt, M.A., Rymer, W.Z. and Mussa-Ivaldi, F.A. (2000) Persistence of motor adaptation during constrained, multi-joint, arm movements. J. Neurophysiol., 84: 853–862.

Shadmehr, R. (2004) Generalization as a behavioral window to the neural mechanisms of learning internal models. Hum. Mov. Sci., 23: 543–568.

Thoroughman, K.A. and Shadmehr, R. (2000) Learning of action through adaptive combination of motor primitives. Nature, 407: 742–747.

Todorov, E. and Jordan, M.I. (2002) Optimal feedback control as a theory of motor coordination. Nat. Neurosci., 5: 1226–1235.

Wolpert, D.M., Miall, R.C. and Kawato, M. (1998) Internal models in the cerebellum. Trends Cogn. Sci., 2: 338–347.