



1996 SPECIAL ISSUE

## Forward Models for Physiological Motor Control

R. C. MIALL AND D. M. WOLPERT

University Laboratory of Physiology, Oxford; and Sobell Department, Institute of Neurology, London

(Received 10 November 1995; revised and accepted 1 March 1996)

**Abstract**—Based on theoretical and computational studies it has been suggested that the central nervous system (CNS) internally simulates the behaviour of the motor system in planning, control and learning. Such an internal “forward” model is a representation of the motor system that uses the current state of the motor system and motor command to predict the next state. We will outline the uses of such internal models for solving several fundamental computational problems in motor control and then review the evidence for their existence and use by the CNS. Finally we speculate how the location of an internal model within the CNS may be identified. Copyright © 1996 Elsevier Science Ltd.

**Keywords**—Motor control, Internal Models, Forward Models, Arm movement, Cerebellum.

### 1. BACKGROUND

The topic for this section of the special issue of *Neural Networks* is whether the CNS makes use of internal models. Although shown to be of potential use in motor control, and finding applications in fields such as robotics, neural network and adaptive control, until recently there had been little evidence for control strategies used in man that are based on internal models. There is now growing support amongst researchers in human motor control that model-based strategies are used in the control of multi-joint movements. The purpose of this paper is therefore to review the concept and the uses of internal models within physiological motor systems. We will then review the recent lines of evidence that most strongly argue for the presence of these models in man. In general we will limit our discussion to forward models, and restrict our evidence to that covering voluntary control of the human arm and hand.

#### 1.1. Internal Models of Motor Systems

Over recent years the concept of an internal model, a

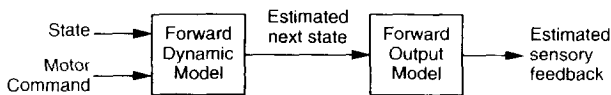
system which mimics the behaviour of a natural process, has emerged as an important theoretical concept in motor control (Kawato et al., 1987; Jordan, 1995). Internal models can be classified into three conceptually distinct groups.

The first type is a causal representation of the motor apparatus, sometimes known as a forward model (Jordan & Rumelhart, 1992). Such a model would aim to mimic or represent the normal behaviour of the motor system in response to outgoing motor commands. For example, a forward model of the arm's dynamics might have as input the current state (e.g., joint angles and velocities) and motor commands being issued by a controller, and produce as output an estimate of the new state. This model therefore captures the state transition behaviour of the arm in response to the motor outflow. By state, we refer to the current position and velocity of the motor apparatus, or in more general terms, to a set of parameters which when taken together with knowledge of the inputs and dynamics of the system determine its future behaviour. However, the state may or may not be accurately known by the controller (or the internal model), and so one needs to separate the state variables from the sensed variables. These can differ widely in physiological systems: the position and velocity of the human arm are sensed principally by muscle spindles, which signal changes in muscle length rather than in joint angles. So, one can also propose a forward sensory output model of the arm that might predict the sensory signals (from sensory ending in the muscles,

---

Acknowledgements: RCM is supported by a Wellcome Senior Research Fellowship. We would like to acknowledge the support of the Wellcome Trust; we also thank the McDonnell-Pew Foundation and the MRC for support.

Requests for reprints should be sent to R. C. Miall, University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK; email: rcm@physiol.ox.ac.uk.



**FIGURE 1.** Forward dynamic models and forward output models can be cascaded to generate an estimate of the sensory consequences of motor commands.

joints and skin) which would be consequent on a particular state. Such a sensory output model would therefore have as input the current state and as output the predicted sensory feedback. By cascading a forward dynamics and forward sensory output model, an estimate of the sensory consequences of a motor command can be achieved (Figure 1). In the kinematic domain the forward model is taken as the mapping between joint co-ordinates and the endpoint co-ordinates of the hand. As forward models are causal they are well-defined functions in that the mappings are either one-to-one or many-to-one. Thus although the same hand endpoint may be reached with many different arm configurations (because of the redundant degrees of freedom of the primate arm), there is no ambiguity about the hand's location given any particular arm configuration.

The second group of internal models are conceptually similar to the forward model of the motor system, but instead model the behaviour of the external environment. Such a cognitive model would encapsulate knowledge of the physical properties of the environment, and predict the behaviour of the external world. We understand the normal behaviour of the physical world, and for example, can predict accurately the trajectory of a ball we wish to catch (Lacquaniti & Maioli, 1989); we are shocked when the physical world breaks the normal behavioural patterns (e.g., Spelke et al., 1992). This knowledge is based on our forward models of the cause and effect. Although these models are likely to be useful for motor planning (e.g., McIntyre et al., 1995), we will discuss them no further in this review.

The third group of models are known as inverse models (Atkeson, 1989), which invert the causal flow of the motor system. These models therefore also encapsulate knowledge about the behaviour of the motor system, but generate from inputs about its state and state transitions an output representing the causal events that produced that state. For example, an inverse dynamic model of the arm would estimate the motor command that caused a particular movement. The input might therefore be the current and the desired state of the arm; the output would be the motor command which would cause the arm to shift from the current state to this desired state. An inverse sensory output model would predict the changes in state that corresponded to a change in sensory inflow. In the kinematic domain the inverse kinematic model again inverts the forward kinematic model to produce

a set of joint angles which achieve a particular hand position. However, as a forward model may have a many-to-one mapping, there is no guarantee that a unique inverse will exist, because the inverse may be a one-to-many mapping. This can be seen for the human arm in which the inverse mapping between hand position and joint angles is non-unique (Craig, 1986).

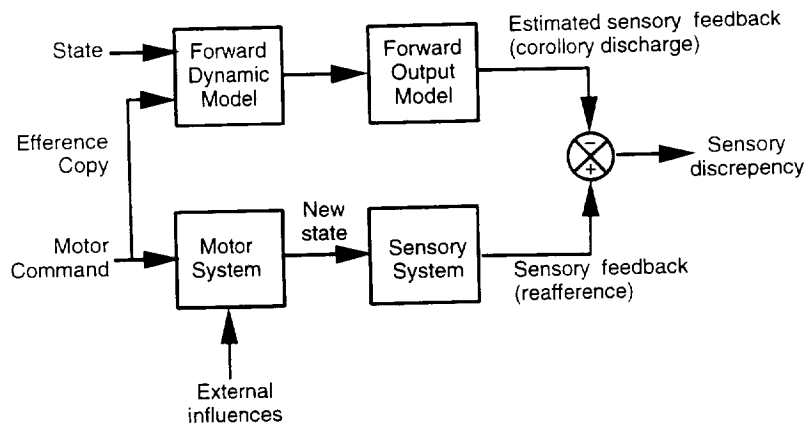
These models have been proposed by engineers, and have been demonstrated to be highly advantageous in a range of motor control situations (Craig, 1986; Lacquaniti et al., 1992). We will discuss forward models in more detail from now on, as the discussion of and evidence for inverse models would require a separate paper (Lacquaniti et al., 1992; Cruse & Steinkuehler, 1993; Wada & Kawato, 1993; Shadmehr & Mussa-Ivaldi, 1994; Imamizu et al., 1995). However, it is worth describing in some detail how these models might be employed in a physiological context, before considering evidence that points to their existence and their use. As mentioned above, we are limiting ourselves mainly to discussion of the voluntary control of the human arm.

## 2. POTENTIAL USES OF FORWARD MODELS

### 2.1. Cancelling Sensory Reafference

A forward model is a key ingredient in a system that uses motor outflow (also called efference copy: Sperry, 1950; Festinger & Cannon, 1965; Kelso, 1977) to anticipate and cancel the sensory effects of movement. Sensory signals arise in the periphery from two causes: those as a result of environmental influences on the body, and those resulting from self-generated movement. The first are termed afference, while the second type of sensory signals are known as refference as they are the sensory consequences of movement (Figure 2). Although the afferent and refferent signals have distinct causes they are carried by the same sensory channels. From a behavioural viewpoint it may be necessary to distinguish between signals from the two causes especially to monitor changes in the external world separate from those resulting from self-movement.

As an example consider the problem of moving the hand over an object on a table and estimating without the aid of vision whether the object is itself moving. The slip velocity (the velocity of the object across the palm of the hand) is the sum of the velocity of the hand and the velocity of the object in the outside world. So to decide if the object is moving, the component of its slip due to self-generated arm movement must first be removed. However, an efference copy cannot itself provide this information, as it is a motor signal predictive of muscle activation, rather than of sensory input. By generat-



**FIGURE 2.** Forward models are necessary to cancel reafferent inputs. The forward dynamic and output models (upper row) generate an estimate of reafference; the difference between this estimate and the actual reafferent inputs signals (bottom row) can inform the CNS about external events. This sensory discrepancy signal is also useful for training models.

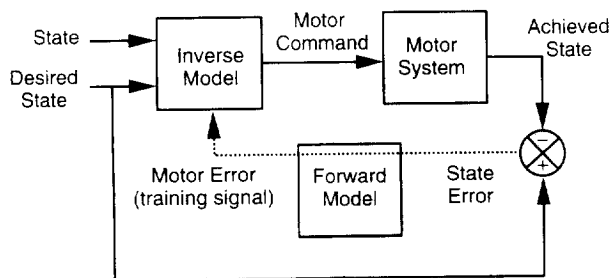
ing an estimate of the sensory consequences of a motor command, an internal forward model can be used to cancel reafferent sensory signals, and thus allow the external environment-related signals to be recovered. Robinson has proposed just such a model for the ocular motor system (Robinson et al., 1986), allowing the generation of a true target velocity signal (retinal slip of a visual object plus eye velocity) to drive smooth pursuit movements of the eyes.

The internal sensory signal needed to cancel reafference has been labelled corollary discharge (Sperry, 1950), although the distinction between efference copy (a motor signal: Festinger & Cannon, 1965) and corollary discharge (an internal sensory signal) is not always made clear.

### 2.2. Distal Supervised Learning

One fundamental problem which the CNS faces in the context of control is that the goal and outcome of a movement are often defined in task-related coordinates. For example, when we reach a visual target the goal is initially specified in a visual framework. During the movement, any error in the motor command causes a visual error. A second example (Jordan & Rumelhart, 1992) is the control of speech,

where our training is based on hearing words spoken and where the error signals available during speaking are auditory, whilst the controller needs to adjust motor commands to the vocal apparatus. A basic problem therefore exists in translating these task-related (visual or auditory) goals and errors into the appropriate intrinsic signals (motor commands and motor errors) which are required to update the controller. The forward relationship between motor signals and sensory signals can be captured by a forward model (Figure 3). Jordan and Rumelhart (1992) have shown how such a forward model can then be used to estimate the motor errors during performance, by the backpropagation of sensory errors through the model. They called this approach distal supervised learning because the supervision of the task—the detection of performance errors in task-related co-ordinates—is distal to the desired detection of motor signal errors. They demonstrated that a forward model could be used to transform errors between the desired and actual sensory outcome of a movement into the corresponding errors in the motor command, thereby providing appropriate signals for motor learning. While it is not clear how this error backpropagation might be achieved in the CNS, the theory is attractive and addresses some important questions in motor learning.



**FIGURE 3.** Forward/inverse learning. A forward model can be used to translate errors measured in the state of the motor system into motor command errors needed to train an inverse model.

### 2.3. State Estimation

During reaching movements, information about the location of the hand is essential for accuracy; subjects deprived of proprioceptive and cutaneous cues are very disabled (Rothwell et al., 1982; Cody et al., 1990; Ghez et al., 1990; Hasan, 1992; Teasdale et al., 1993; Ghez et al., 1995; Gordon et al., 1995; Sainburg et al., 1995; Miall et al., 1996), and even in normal subjects, it is necessary to have recent sensory information from the hand to allow an accurate movement to be executed (Ghez et al., 1995; Miall et al., 1996). We

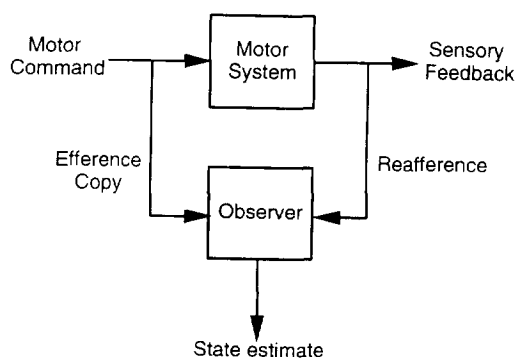


FIGURE 4. An observer model.

will focus here on the computations involved in integrating sensory and motor information to provide an estimate of the state of the arm (e.g., arm position and velocity). Observer models (Figure 4) from engineering formalise the sources of information which the CNS could use to construct such an estimate of the state of the arm during movement (Goodwin & Sin, 1984). This framework consists of a state estimation process, the observer, which monitors the motor commands sent to the arm (efference copy) and the returning sensory feedback. As mentioned previously, the available sensory signals (visual and proprioceptive) may not directly provide an adequate state estimate. However, based on these sensory and motor sources, the observer estimates the arm's state, integrating the multiple sources of information to reduce the overall uncertainty in its estimate (Abidi & Gonzalez, 1992). Observer models generally use a recursive update formulation to estimate the state of the arm as it evolves over time. A central component of the observer model is often an internal forward dynamic model of the arm, which provides an estimate of the next state of the arm given the current state and action. Such a state estimation process can be used to maintain an optimal estimate of the state of the hand during movement. The Kalman filter (Kalman & Bucy, 1961) is an example of an observer model. It provides a method for obtaining state estimates by combining two processes. The first process is based upon internal simulation of the motor system while the second uses sensory feedback to correct the internal simulation. The relative contributions of the internal simulation and sensory correction processes to the final estimate are modulated across time so as to provide optimal state estimates. Thus, Kleinman et al. (1971) were able to use a Kalman-Bucy filter and internal model to fit manual tracking data from trained observers.

Such a state estimate could be used in motor coordination. Consider the problem of coordinating the motion of two different parts of the body: these could be the two hands, or the hand and arm, or perhaps the hand and eye. When using both hands,

the control of one obviously must depend on the current state (location and velocity) of the other. In reach and grasp tasks there is a close link between the aperture of the hand and the hand's transport towards the target. Haggard and Wing (1995) have suggested a feedback model for this coordination based on a state-space model, which can account for observed responses to imposed perturbations of the arm. However, as we will mention in the following section, temporal delays in the sensory and motor pathways suggest that for many movements, this coordination needs to depend on a state estimate, rather than on proprioceptive signals. Such an estimate can be produced by a forward model. Thus a coordination scheme could be envisaged almost identical to Haggard and Wing's, based on feedforward motor commands and a state estimate from a forward model. For other tasks, such as the eyes following the motion of the hand in the dark, then there must be the requisite translation of the spatial location of the hand into the motor coordinates of the ocularmotor system.

#### 2.4. Internal Feedback to Overcome Time Delays

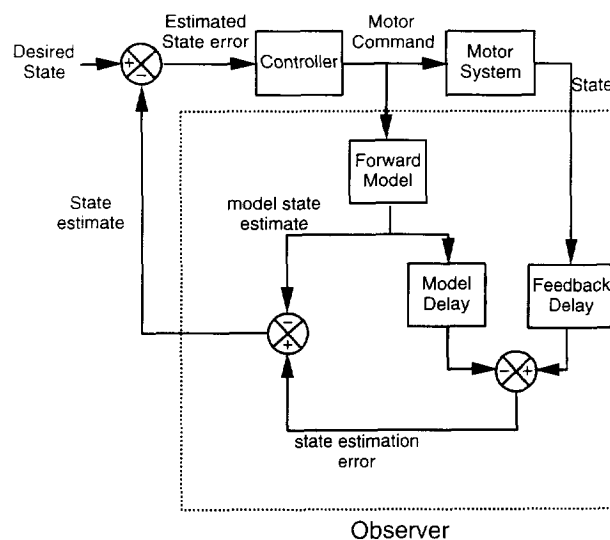
Physiological control can be divided into feedforward and feedback control strategies. Feedforward control embraces all techniques for controlling a motor apparatus (the effector organs, for example, muscle) without reference to one or more controlled variables (possibly muscle length or joint angles) describing the current state of the motor system. In contrast, feedback control uses some knowledge of the controlled variables to determine the outgoing motor commands. For example, the controller could assess the difference between the sensed state of the motor apparatus (e.g., sensed changes in muscle length as signalled by the muscle spindles) and a reference value for that variable. The controller could then seek to minimise the difference by negative feedback. Such negative feedback control is robust, as the controller need not be precisely matched to the motor apparatus—any errors in the motor output or external disturbances will be sensed and corrected. Its principal disadvantage is that feedback control is sensitive to intrinsic delays in the sensorimotor loop. A well designed feedback control system operates at its highest possible open loop gain. However, at the frequency at which the feedback delay introduces a phase lag of  $180^\circ$ , the open loop gain must be kept below unity to avoid instability. Therefore, feedback controllers are extremely sensitive to delays, and must be designed to avoid high gain at high frequencies. This reduces the speed of their responses: a stable feedback controller cannot respond at a speed which is high with respect to the overall feedback delay.

In motor control delays arise in sensory transduc-

tion, central processing, and in the motor output. Sensor transduction latencies are most noticeable in the visual system where the retina introduces a delay of 30–60 ms, but sensory conduction delays can also be appreciable. Central delays are also present due to such ill-defined events such as neural computation, decision making and the bottlenecks in processing commands. Delays in the motor output result from motorneuronal axonal conduction delays, muscle excitation–contraction delays, and phase lags due to the inertia of the system. These delays combine to give an unavoidable feedback delay within the negative feedback control loop, and can lie between about 30 ms for a spinal reflex up to 200–300 ms for a visually guided response. (The actual loop delay is difficult to measure exactly, as it depends on factors such as the type of perturbation and the task demands: Keele & Posner, 1968; Zelaznik et al., 1983; Barrett & Glencross, 1989; Miall, 1996.)

As fast arm movements can last less than 200 ms, feedforward controllers must be used which issue motor commands based on sensory inputs, but that do not use feedback of the controlled variable. Another physiological example would be the control of human saccadic eye movements; although the extra-ocular muscles do have muscle spindles, they do not have a demonstrable stretch reflex, and the spindles do not seem to be used in feedback control of eye movement. Hence these extremely fast eye movements are under feedforward control. However, the main disadvantage of feedforward control is the need to issue accurate and appropriate motor commands to effect the desired outcome. This implies detailed knowledge of the response characteristics of the motor apparatus. Although this is possible for structures such as the eye which has relatively simple dynamics it is unlikely to be the case for the multi-joint arm.

Hence another proposed use of internal forward models is to assist in feedforward control by providing an estimate of the outcome of a motor command which can be used for negative feedback control. In other words, by including the forward model within an internal negative feedback loop, it provides an internal feedback signal that is available much more rapidly than the actual feedback signals resulting from the movement. We have proposed a particular form of this control strategy, known as a Smith predictor (Miall et al., 1993). This includes a forward model (Figure 5), servicing a rapid high-gain internal feedback loop whose output can drive the arm towards the desired state. The feedback controller therefore compares the reference value of a controlled variable with an estimate of the state of the motor system, as provided by the forward model, and corrects the estimated error signal. As the internal forward model avoids the feedback delays



**FIGURE 5.** The Smith predictor model. A forward model and model time delay are used to generate a state estimate (thus the modules within the dotted square form an observer). The Smith predictor is designed for control of systems with significant feedback delays.

in the real motor apparatus, this internal feedback loop can have a high open-loop gain, and function as a near-optimal feedforward controller. Note that although a forward model cannot avoid some intrinsic delays due to neural processing and conduction times (let us assume perhaps 50 ms in total) it would be easy to develop a forward model that predicted the motor system output 50 ms into the future, and thus effectively cancelled these intrinsic delays. In the limit, a negative feedback controller with no feedback delay could have an open loop gain of near infinity, and its output would be functionally equivalent to that of an inverse model. The Smith predictor also includes an explicit delay mechanism, that delays a copy of the rapid sensory estimate to allow temporally synchronous comparison with the actual sensory consequences of the movement. This is important to allow any errors in the internal estimate to be detected and corrected. By ensuring synchrony between the delayed output of the forward model and the actual feedback, the Smith predictor effectively isolates the feedback delays from the control loop. Without this delay, a controller using a forward model within an internal feedback loop must operate in purely feedforward mode (without any actual feedback from the movement) or with only very low feedback gain to avoid instability. Hence the Smith predictor combines the advantages of feedforward control (although based on an internal feedback mechanism) with those of feedback control.

### 2.5. State Prediction

In a manner similar to estimation of the current state of the motor apparatus, a forward model can be used

to estimate its state some time into the future. Such a prediction could be used in at least two contexts.

**2.5.1. Model Predictive Control.** One can take the basic idea of an internal feedback loop (as described above) and extrapolate it into the future behaviour of the plant. If the reference value that the controller is seeking to reach is known in advance (either a constant target value or a predictable signal), then the state estimate of the future performance of the system can be compared in advance, and predicted errors corrected before they occur. This theory has been developed as model predictive control (Garcia et al., 1989), and conceptually shifts the control strategy from negative feedback correction of errors towards control based on anticipation of future events. In principle it completely negates the delays in the motor pathway, unlike the Smith predictor which can only shift them outside of the control loop. Humans can achieve zero-lag in tracking tasks in which the target is predictable (Weir et al., 1989), and while this could be due simply to anticipation of the target, model predictive control might also be employed.

**2.5.2. Mental Practice and Planning.** Mental practice can be thought of as rehearsing movements without moving. It is known that mental practice can lead to improved performance, and it is suggested that the mental rehearsal allows performance to be monitored and motor learning to take place in the absence of real action (Hall et al., 1992; Yue & Cole, 1992). During such mental practice a forward model could be used to predict the outcome of one or a series of actions: an estimate of a future state (which of course could be generated by a forward model) and the appropriate motor commands could be directed to the model and yet blocked before reaching the motor apparatus. Hence an iterative or recursive use of forward models could allow mental practice and mental imagery of arbitrarily distant motor states. Based on the relationship between the desired movement and its predicted outcome given by the model, a controller could select between possible actions, or the controller could itself adapt. Hence, a forward model could also be involved in motor planning. For example, in order to pick up a cup, the planner must develop a suitable motor program involving movement of the hand and arm. However, if the cup is too far away from the body, the plan might also include forward motion of the trunk and possibly even locomotion. By internally testing the developing plan, or alternative plans, via a forward model, it would be possible to assess their utility. Hence, the planner might initially test the plan "extend arm", but when the forward model predicted that the hand would fall short of the cup's position, the planner could at least reject that plan,

even though the forward model cannot by itself provide a better plan.

### 3. LEARNING AND REPRESENTATION OF INTERNAL MODELS

In this section we focus on two attributes of forward models: adaptability and representation. As we grow many of the parameters of the motor system, such as link lengths and inertias, which govern the dynamics of the motor system change dramatically. Hence, a forward model which captures the dynamics of a three-year-old child's arm is unlikely to be of use to the fully grown adult. Similarly, on a shorter time scale the dynamics of the motor system change when we pick up an object or even change the body's orientation with respect to gravity. Therefore, to be useful the forward model needs to be adaptable. In general the signals which are required to train or update an internal model can be readily generated. In the kinematic domain the forward model which relates the sensed joint angles (inputs) to hand location (outputs) can be trained by the monitoring of synchronous input-output pairs. Any discrepancy between the model output and the actual output of the system can be used to update the model using any of a number of supervised learning techniques [for a review see Hertz et al. (1991)]. Similarly in the dynamic domain the output is the predicted state which can be compared to the actual state to produce an error signal—any discrepancy can then be used to update the forward model. Such a supervised learning strategy has been shown to be effective in artificial neural networks for producing reasonably accurate forward models (Jordan & Rumelhart, 1992). Supervised learning does not imply that one needs goals for the movement, however, and models have been proposed that correlate the estimated and actual outcome of random motor commands (Kuperstein, 1991; Bullock et al., 1993; see also Konczak et al., 1995).

By regarding forward models as function approximators it is possible to explore the representation or basis functions used to construct the model. Such a representation can span a range of possibilities from local to global. At one extreme, a function approximator can be represented as a look-up table in which corresponding input-output pairs are stored (Atkeson, 1989; Rosenbaum et al., 1993). Thus, the forward kinematic model could be represented as a set of pairs of visual and motor co-ordinates. At the other extreme of the range from local to global representation is a model whose parameters are defined by the physical attributes of the system. Thus, the forward kinematic model could be represented by the trigonometric equations relating hand position to joint angles. Within the model

would be parameters representing the link lengths and in these models adaptation generally occurs through tuning of the parameters (e.g., Harris, 1965). Intermediate in the range of representation ability are function approximators such as neural network models (Hertz et al., 1991). Neural network models fall into the general class of function approximation models that are defined by a large number of variables (e.g., the weights in a neural network) that do not necessarily correspond to the physical parameters of the system. For example, in Albus' (1971) CMAC (cerebellar model articulatory controller) model of co-ordinate transformations, input-output pairs are stored in a distributed fashion over a set of weights. There is a storage-flexibility payoff where local representations require more storage but are flexible to the class of functions that can be approximated, whereas global representations require little storage but are less flexible to the functions that can be represented.

The way in which a training signal alters the input-output relationship of the internal model reflects its underlying representation. Therefore, one way which can be used to probe the type of representation used is through generalisation studies (for a review of this technique see Bedford, 1989). This generalisation technique has been applied to a variety of internal models, although primarily to inverse models. In this technique an altered relationship is introduced locally between the normal inputs and outputs of a system, and after learning the generalisation pattern is assessed. Studies in the kinematic domain have investigated pointing behaviour before and after an altered local remapping (Bedford, 1989; Ghahramani et al., 1995; Imamizu et al., 1995) and have shown that the local remapping generalises substantially to points remote from the remapped locations. These results rule out a look-up table representation in which only visited cells in the table are adjusted. A study of pointing in the plane shows that the generalisation to a one point remapping shows a Gaussian-like decay in generalisation which is well captured by a Gaussian radial basis function network (Ghahramani et al., 1995). These studies suggest that kinematic generalisation is best explained in terms of visual or Cartesian space. Shadmehr and Mussa-Ivaldi (1994) have studied generalisation in the dynamic domain. Subjects held a robotic manipulator and were exposed to altered dynamic environments which thereby changed the normal input-output dynamics of the arm. Subjects learned to achieve pre-perturbation performance in one part of the workspace and then were tested for after effects in another region. The after effects were indicative that generalisation was based on intrinsic joint coordinates rather than on the Cartesian coordinates of the workspace.

#### 4. EVIDENCE FOR FORWARD MODELS

We now turn to the evidence for forward models. As before we intend to restrict ourselves mainly to considering the human control of arm movement, but of course, we will also draw on animal studies providing electrophysiological evidence supporting internal models.

##### 4.1. Behavioural Evidence for State Estimation

Although many studies have examined integration among purely sensory stimuli (for a psychophysical review see Welch and Warren, 1986) little is known of how information is integrated during movement. In Section 2.3 it was suggested that a forward model could be used in an observer based system to estimate the arm's state. For example, when we move our arm in the absence of visual feedback, there are three basic methods the CNS can use to obtain an estimate of the current state, the position and velocity, of the hand. The system could make use of sensory inflow (the information available from proprioception), it could make use of integrated motor outflow (the motor commands sent to the arm), or it could combine these two sources of information via the use of a forward model. Recently Wolpert et al. (1995) studied a sensorimotor integration task in which subjects estimated the location of their hand at the end of movements made in the dark, with or without externally-imposed forces. The subjects typically made small errors in reporting the position of the hand (they used a computer mouse with the other hand to line up a cursor with the estimated position of the moving hand). The errors varied with movement duration. The temporal propagation of the bias and variance of this state estimate was therefore analysed as a function of movement and compared to errors predicted within the observer model framework (Figure 6a), making a simple assumption about the accuracy of the internal model. The bias of the subjects' estimates showed two distinct phases as a function of movement duration, with an initial increase reaching a peak of 0.9 cm after 1 s followed by a sharp transition to a region of gradual decline (Figure 6b). The variance of the estimate also showed an initial increase during the first second of movement after which it stabilised at about 2 cm<sup>2</sup>. External forces applied to the manipulator also had distinct effects on the bias and variance propagation. Wolpert and colleagues showed that these results could be accounted for by a Kalman filter model which combined both an imperfect internal forward model simulation with sensory correction, whereas sensory feedback or internal simulation alone could not capture the data. The internal model was set to slightly over-

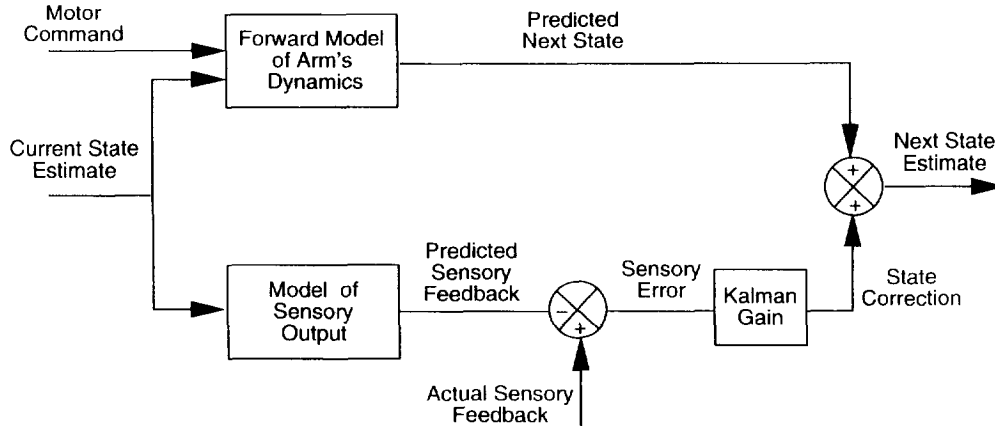


FIGURE 6a. A recursive observer model for estimating the state of the arm during movement.

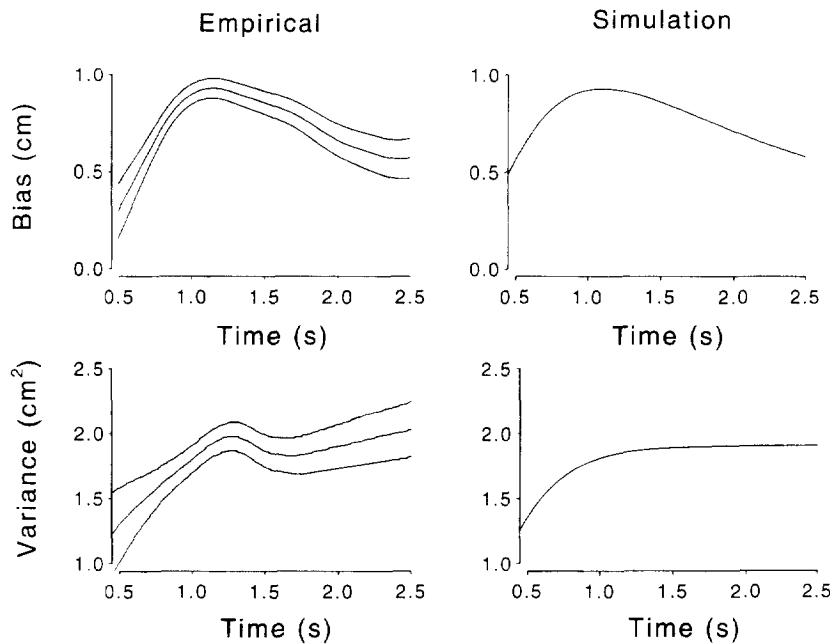


FIGURE 6b. Measured and simulated bias and variance propagation curves for human state estimates. The left panels are the mean bias and variance ( $\pm$  SE,  $n=8$  subjects) of subjects' estimates of their hand position after an unseen movement. The right curves are predictions based on the observer model illustrated in Figure 6a. From Wolpert et al. (1995).

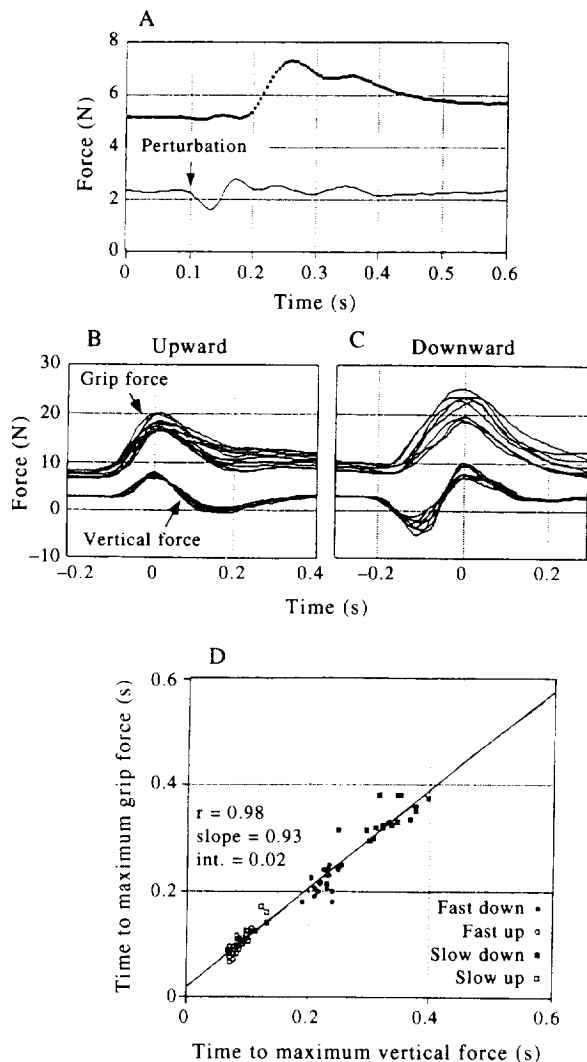
estimate the motion of the hand for a given force from the muscular system. This result is a clear demonstration of the use of an internal model for state estimation.

#### 4.2. Coordination and Timing

In Section 2.3 we also discussed the use of a forward model for coordination between movements of different effectors. There are at least two lines of evidence that support this suggestion. The first is the study of the temporal relation between hand kinematics and grip force when moving an object. When subjects lift an object they modify their grip force, and this grip force closely tracks the acceleration of the object (Johanssen & Westling, 1984). This is not unexpected, as acceleration of the object would increase the load on the hand, and

unless the grip force was sufficient, the object would slip between the fingers. Johanssen and Westling (1984) showed that the latency between peak load force and peak grip force is essentially zero. More recently, Flanagan and Wing (1993) report that this synchronicity remains whether the movements are made in the vertical or horizontal axes (where here the relevant comparison was between grip force and inertial force due to lateral acceleration), and at a range of speeds (Figure 7). This close relationship between load force and grip force was also seen in even the first movement made by each subject lifting a load. Clearly this implicates feedforward control. If the subjects used a feedback based strategy, there would be measurable delays between the increase or decrease in load force measured at the hand, and the corrective adjustment in grip forces. Furthermore, the apparent generalisation of coordination between grip





**FIGURE 7.** Recordings of grip and load forces during lift of a small object. Perturbation of the object evokes an increase in grip force after about 100 ms (A), but during spontaneous lift, grip force modulates synchronously (B,C). The regression of peak vertical force latency to peak grip force latency has an intercept of almost zero (D). All data from one subject; modified from Flanagan and Wing (1993) with permission.

and hand across different directions and speeds rules out simple synergies between muscles. Accurate coordination between hand movement and grip force requires knowledge of the distal effects measured at the hand of the motor commands moving the arm. So any effective synergy would need to be based on knowledge of the limb's dynamics. Hence it seems likely that an internal model was used to predict the actual movement of the arm from the descending motor commands, and that this estimate was used to compute and issue in time the necessary commands to adjust the grip force, negating the sensory-motor delays.

The second line of evidence comes from studies by Vercher and colleagues (Vercher & Gauthier, 1988, 1992) of ocular tracking of the unseen hand. They

reported that the eye followed the hand (actually following a cursor driven by the hand) with no delay. Again, this implies feedforward control, because of the inherent delays in the system. When an additional delay was interposed by computer between motion of the hand and the observed motion of the cursor, Vercher and Gauthier (1992) observed smooth pursuit tracking that followed the hand motion and preceded the cursor motion. This temporal coordination could not be achieved using feedback signals.

We would like to raise an additional, spatial argument to the interpretation of these results. If the grip force in Flanagan and Wing's task can be accurately adjusted for expected changes in load at the hand, then the CNS must be able to calculate those load forces at the hand. Hence the brain must be able to assess the hand's motion with respect to the external gravitational field, and also estimate the forces at the hand when the carried object is accelerated laterally. These estimates would not be easy without a forward model, and it would not be sufficient just to be able to scale and time the grip forces by an efferent copy of the descending motor command. A critical test here would be to determine that the grip and load forces were both synchronous and accurately scaled even in movements which lead to measurable different load forces at the hand, and that had not been rehearsed. Recent data from those authors points to this (Wing, 1996). In considering the results presented by Vercher et al., we do not know of any published data on the spatial accuracy of the eyes' tracking of the hand in the dark, but we would offer the same argument as for grip forces. If, as we predict, the eyes can accurately follow the position of the unseen hand with zero latency, even when the arm configuration makes the hand's position vary with respect, say, to shoulder position, then the ocular controller must have access to an estimate of the hand's spatial position. Again, to estimate the hand's position accurately in space, and to predict this position such that the eye can be commanded in time to track that position with zero lag requires a forward model. We are currently testing this hypothesis.

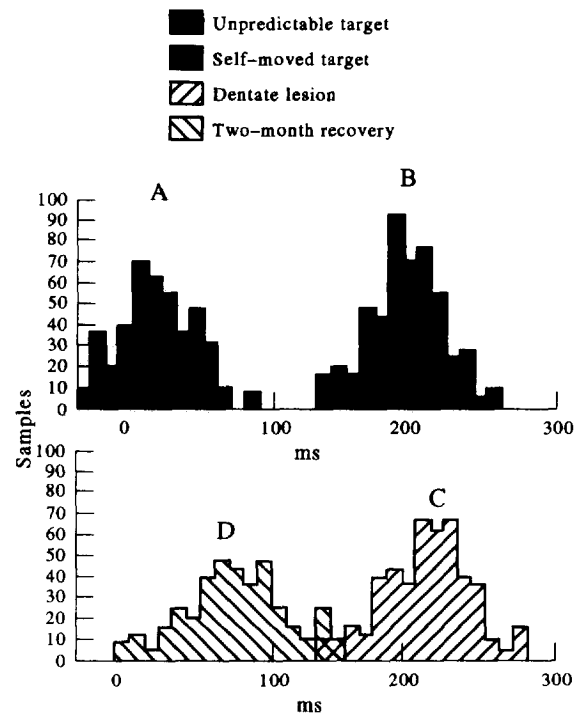
## 5. LOCALISATION OF A FORWARD MODEL

We now turn to the question of where these forward models may be found. Of course, it will be clear from the previous sections that forward models could be used within a number of motor systems, in a number of different ways. There might be several forward models in different brain sites. For example, a forward model has been proposed for ocularmotor control, and would be expected to be in brain stem circuits; a forward model used for high level motor planning is more likely to be found in association

areas of the cerebral cortex. However, a strong contender for the forward models used in internal feedback control of movement (either for state estimation or for state prediction) must be the cerebellum. This structure is known to be involved in motor coordination, although its precise role is far from clear. We have reviewed recently the reasons why we believe it forms a forward model, and will not repeat those reasons here (Miall et al., 1993). To summarise, we argued from comparative anatomy, from data on inactivation of the cerebellum, and from electrophysiology, that the cerebellum contains one, if not several, forward models in the form of Smith predictors.

We have recently shown that patients with damage to the outflow of the cerebellum are poor at tracking tasks in which they are deprived of visual feedback of hand position (Cody et al., 1991; Haggard et al., 1995). Denial of visual feedback helps these patients to reduce hand oscillations (which probably arise from instability in the visual feedback loop), as expected from a controller with long time delays. However, without visual feedback they cannot control the velocity of their wrist movements, which we suggested implies the cerebellum in state estimation during the movements.

In Section 4.2 we suggested that a forward model would be used for coordination between different motor systems. To support the suggestion that this function requires the cerebellum, Vercher and Gauthier (1988) have shown that monkeys, like humans, can make eye movements to follow movement of a cursor controlled by the hand with very low latency. However, inactivation of the cerebellum impaired this ocular-manual coordination, so that the latency of the eye movements rose to a level normally seen when tracking an external, unpredictable, target (Figure 8). They have also recently demonstrated that sensory afferents are not required for the temporal linking of ocular and manual systems, whilst motor outputs are required (Vercher et al., 1996). This confirms that efferent copy is an important part of the coordination process. Likewise, van Donkelaar and Lee (1994) have shown that cerebellar patients have impaired ocular tracking of the cursor moved by the hand, and suggest that the cerebellum normally mediates ocular-manual coordination. It has also been demonstrated that cerebellar patients are impaired in the precision grip tasks studied by Flanagan and Wing, losing the close relationship between load forces and grip forces (Hermsdorfer et al., 1994), and Muller and Dichgans (1994) report that cerebellar patients lose the low-latency coupling between grip and load forces. Furthermore, single unit recording studies show that the cerebellum is highly active in such tasks (Espinoza & Smith, 1990; Dugas & Smith, 1992). Thus there



**FIGURE 8.** Ocular to manual tracking latencies measured in monkeys. The intact animals could make short latency smooth pursuit of a self moved target (A), but unpredictable targets were followed with a mean latency of 210 ms (B). In the days immediately after a lesion of the dentate nucleus, the monkeys initially followed the self-moved target with similar long latencies (C); after 2 months recovery the latencies had again reduced (D). Modified from Vercher and Gauthier (1988), with permission.

seems a body of evidence that the cerebellum may be critical for all these coordination tasks. It seems likely to us, although we accept that we are extrapolating beyond the data, that the cerebellum's role in these diverse tasks is to provide the forward model estimates and predictions of the state of the motor system.

## 6. PHYSIOLOGICAL IDENTIFICATION OF AN INTERNAL MODEL IN THE BRAIN

In this final section, we ask how a forward (or inverse) model might be detected electrophysiologically, or by some physiological interventions. It is perhaps best to split this problem into several parts.

### 6.1. Input Signals

First, one could record the inputs to the putative forward model, and test whether they conform to those required. For a forward model, two major inputs would be a set of sensed state signals, necessary to update the forward model, and the efferent copy of motor commands, from which the state estimate is generated. The cerebellum certainly

receives both of these. It receives a large input from fibres descending from the motor cortex, via the pons, and it is thought that these represent the efferent copy of outgoing motor commands. The cerebellum also receives a vast amount of proprioceptive information directly from the ascending dorsal spinocerebellar tracts, which provide an update on the state of the motor apparatus. Remember that these sensory signals are delayed, and in different coordinate systems from the required information of the current state; they cannot be used instead of the forward model. The ventral spinocerebellar tracts are not purely sensory, however, and carry ascending information even in the absence of muscular activity (if the muscles are blocked). This may represent efferent copy from the spinal circuitry, updating the cerebellum on those motor outputs being controlled at a spinal level.

## 6.2. Output Signals

One could also test the outputs of a forward model, which should correlate with the expected state of the motor apparatus. This is rather difficult, however, as one would need to distinguish between internal predicted state signals arising from the model, the external sensory signals from the periphery, and motor commands. For the ocular system, especially during movement in a single dimension, it might be difficult to disentangle sensory and motor signals. The dynamics of the eye are quite straightforward, and the temporal envelope of motor commands to the eye has strong similarities to feedback signals from the resultant motion of the eye. Thus it is not straightforward to decide if a central neural signal represents a motor command (on an efferent copy), a sensory estimate, or peripheral sensory signal. This has been undertaken by Shidara et al. (1993), however, who were able to predict the firing rate of cells in the cerebellar cortex from measurements of the acceleration and velocity of the eye. They propose, in contrast to our hypothesis, that the cerebellum generates a signal close to the output expected from an inverse dynamics model driving the recorded eye movements. They also argue, because the parameters from their regression equations which predict the firing rate at one eye velocity can also match the firing rates measured at other velocities, that this implies that the model is indeed a parametric inverse model.

The difficulty of separating state signals from motor commands can also be raised for the manual motor system, although because of the much greater complexity of the kinematics and dynamics of the arm, it should be possible to separate the signals unambiguously. The human arm has redundancy in the number of degrees of freedom of its joints. We

can position a fingertip on a target, and adopt a wide range of arm configurations without lifting the finger from its fixed location. Thus if a forward model represented the state of the hand (or fingertip) location in extrinsic coordinates, its output could be independent of the differing arm configurations (a many-to-one mapping of motor commands to state estimates). One can also cause the same motion of the hand with very widely different muscle torques (with more or less co-contraction about each joint); these again should separate the motor and sensory signals. It would also be easier in the slower moving manual system to temporally separate out motor and sensory signals. A central signal that coded for hand motion (as tested by the criteria just mentioned) with zero or negative latency to the actual movement could only arise from an internal model. There have been many reports, of course, that neural signals co-vary with parameters of the movement, and have negative latencies. But one needs to demonstrate that the neural signal correlates better with the motor outcome than the estimated motor commands (e.g., with different levels of co-contraction) before this can be definite.

Blocking sensory inputs (by peripheral denervation) would likely disrupt the forward model, so this intervention might not make the model output more easy to identify. Hence, it seems likely that the best one could do would be to identify an internal signal that co-varied with state, and not motor outflow. Inactivating the outputs of the forward model may be more hopeful. As Haggard et al. (1995) reported, head injured ataxic patients suffer selective damage to the superior cerebellar peduncle, carrying the cerebello-cerebral fibres, and display manual tracking behaviour consistent with loss of a forward model (Section 5).

## 6.3. Neural Codes

One can add to these experimental problems the fact that we do not know what the neural code for an internal model will be. At the periphery of the nervous system it has proved quite straightforward to identify sensory afferent signals, and to identify the neural codes for different aspects of the sensory stimulus. Likewise, in later stages of the motor system, the relationships between efferent motor signals and muscle activity are quite clear. It is in the central nervous system, where these internal models are proposed, that the coding is less obvious. It is not clear, therefore, whether neurons in the input or output layers of an internal model will code, as one example, movement amplitude temporally or spatially, in parallel or individually, in extrinsic or intrinsic co-ordinates. It will therefore be quite difficult to be certain of the presence of an

internal model just on electrophysiological grounds. Alternative techniques, using fMRI or PET scanning may prove equally difficult, because of their current temporal limits set by the dynamics of changing cerebral blood flow. MEG technology may therefore be a useful tool, perhaps combined with the high spatial resolution of fMRI.

#### 6.4. Training Signals

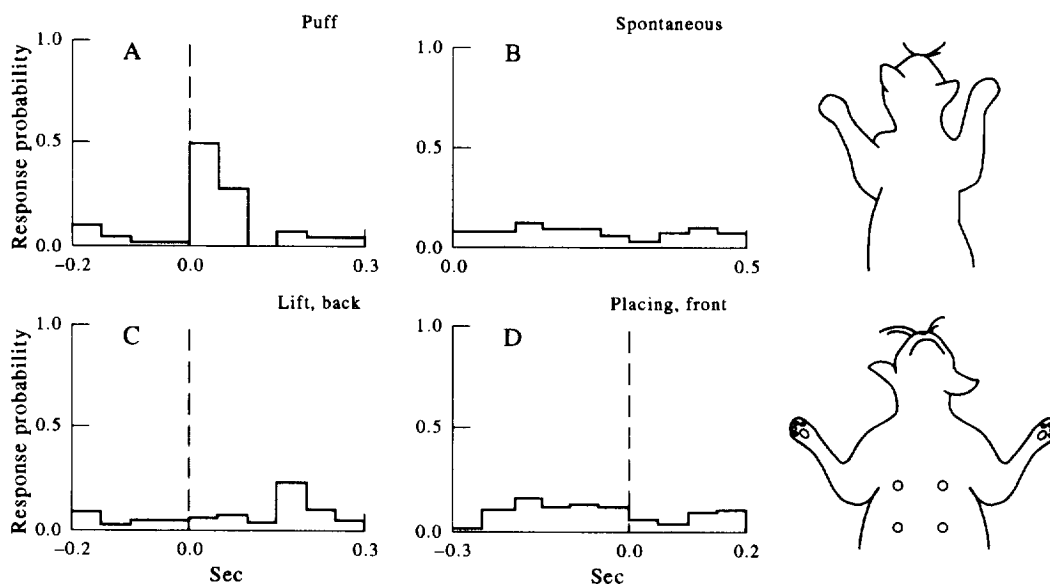
However, it may be fruitful to try to record those signals used to develop and adapt these internal models, rather than the input or output of the model itself. Neural networks can be trained with any number of different training algorithms, but there is always a fundamental relationship between the training signal and the developing neural representation. To develop an inverse model, the training signal must inform the model about its desired behaviour in terms of the outgoing motor commands. For a forward model, the training signal must inform about the desired sensory estimate. Hence one could test candidate training signals for their correlation with sensory or motor errors. It is possible to develop tasks in which the relationships between movement errors and the associated sensory or motor signals are unambiguous (Kawato & Gomi, 1993), and thus determine whether the training signal coded for a motor error (i.e., an error in the motor command) or a sensory error (an error in the prediction of the movement's outcome). The most obvious candidate signal so far studied is the climbing fibre input to the cerebellum. Although there is still debate about it (e.g., the forthcoming issue of *Behavioural Brain Sciences on Motor Learning*), many workers have

argued that these climbing fibres carry a training or instruction signal. Gellman et al. (1985) showed that climbing fibres could be reliably activated by cutaneous inputs on the paws of a walking cat, but were inactive if the animal actively used that foot (Figure 9). Thus they suggested the climbing fibres signalled unexpected sensory events. This is exactly what would be expected of a sensory error signal. Andersson and Armstrong (1987) have reported similar results. These sets of evidence indicating that the climbing fibres are sensitive to passive stimulation could reflect the situation in which a sensory prediction fails: sensory inputs are received that are not expected, based on the normal expectation of sensory input in the absence of movement. They again suggest that the cerebellum may be responsible for the development of a forward model: if the climbing fibres were a motor error signal [responsible for training an inverse model (Gomi & Kawato, 1992; Kawato & Gomi, 1992)], this sensitivity to passive stimulation would be difficult to explain.

#### 7. CONCLUSIONS

The evidence for internal models in physiological motor systems is still indirect. However, there are a number of experiments that point to the existence and use of internal forward models. Of course, many problems remain to be resolved.

Where in the brain are these models held? Localisation of internal models will likely come about through investigation such as neuronal recording, stimulation, lesioning, and functional imaging. We believe that several such lines of evidence point to the cerebellum as the most



**FIGURE 9.** Inferior olivary responses from the cat to touch to the forepaw. The upper left panel shows that passive stimulation of the paw invokes responses with high probability (82% within 100 ms); the bottom panels indicate that active placing of the paw by the cat does not evoke a response. The top right panel shows very low spontaneous activity in this cell. From Gellman et al. (1985) with permission.

probable site of the forward models for limb movement (Miall et al., 1993).

How are these models represented? Behavioural tests of generalisation may well illuminate this question. One can explore how well subjects generalise across the full parameter space in which their learning takes place, and thus gain insight into the representation of the stored knowledge. As an example, the evidence of Ghahramani et al. (1995) points to a representation with large functional receptive fields rather than a local look-up table. The further step of identifying the actual neural code used will certainly require an electrophysiological approach.

What are the learning rules governing their development and the physiological mechanisms allowing their adaptation? Again, it seems possible that the rules could be identified behaviourally, by limiting the control signals available to the subjects, or by studying the rate and extent of learning in different contexts. Great strides have already been made in understanding synaptic mechanisms that could underlie long-term learning; a major challenge remains to definitively link these synaptic mechanisms to learning measured at the level of motor psychophysics.

Are there many separate models for different modes of motor control or a few generalised models? We have suggested that a forward model can be used in many different ways. It is not known whether a single model would subserve several different purposes, or whether several independent models would be used in parallel (Jacobs et al., 1991; Jordan & Jacobs, 1992). If there are multiple models, will they reside in one site perhaps co-localised because they all depend on a common neural substrate, or will they be found in separate sites closer to their functional role?

Are there several models in a hierarchy, coding for sensory predictions in different coordinate frames? We have suggested this might be possible within the cerebellum (Miall et al., 1993), with models predicting the outcome of movement within visual (or kinematic frameworks) and within motor (or dynamic) frameworks.

We look forward to the next few years to bring clear resolutions to some of these questions.

## REFERENCES

- Abidi, M. A., & Gonzalez, R. C. (1992). *Data fusion in robotics and machine intelligence*. San Diego, CA: Academic Press.
- Albus, J. S. (1971). A theory of cerebellar function. *Mathematical Bioscience*, **10**, 25–61.
- Andersson, G., & Armstrong, D. M. (1987). Climbing fibre input to b zone Purkinje cells during locomotion in the cat. *Journal of Physiology (London)*, **385**, 107–134.
- Atkeson, C. G. (1989). Learning arm kinematics and dynamics. *Annual Review of Neuroscience*, **12**, 157–183.
- Barrett, N. C., & Glencross, D. J. (1989). Response amendments during manual aiming movements to double-step targets. *Acta Psychologica*, **70**, 205–217.
- Bedford, F. L. (1989). Constraints on learning new mappings between perceptual dimensions. *Journal of Experimental Psychology*, **15**, 232–248.
- Bullock, D., Grossberg, S., & Guenther, F. H. (1993). A self-organising neural model of motor equivalent reaching and tool use by a multijoint arm. *Journal of Cognitive Neuroscience*, **5**, 408–435.
- Cody, F. W. J., Schwartz, M. P., & Smit, G. P. (1990). Proprioceptive guidance of human voluntary wrist movements studied using muscle vibration. *Journal of Physiology (London)*, **427**, 455–470.
- Cody, F. W. J., Lovgreen, B., & Schady, W. (1991). Human visuo-motor tracking in cerebellar dysfunction. *Journal of Physiology (London)*, **446**, 449P (Abstract).
- Craig, J. J. (1986). *Introduction to robotics*. Reading, MA: Addison-Wesley.
- Cruse, H., & Steinkuehler, U. (1993). Solution of the direct and inverse kinematic problems by a common algorithm based on the main multiple computations. *Biological Cybernetics*, **69**, 345–351.
- Dugas, C., & Smith, A. M. (1992). Responses of cerebellar Purkinje cells to slip of a hand-held object. *Journal of Neurophysiology*, **67**, 483.
- Espinoza, E., & Smith, A. M. (1990). Purkinje cell simple spike activity during grasping and lifting objects of different textures and weights. *Journal of Neurophysiology*, **64**, 698–714.
- Festinger, L., & Cannon, L. K. (1965). Information about spatial location based on knowledge about efference. *Physiological Review*, **72**, 705–384.
- Flanagan, J. R., & Wing, A. M. (1993). Modulation of grip force with load force during point-to-point arm movements. *Experimental Brain Research*, **95** 131–143.
- Garcia, C. E., Preit, D. M., & Morari, M. (1989). Model predictive control: Theory and practice—a survey. *Automatica*, **25**, 335–348.
- Gellman, R. S., Gibson, A. R., & Houk, J. C. (1985). Inferior olivary neurones in the awake cat: Detection of contact and passive body displacement. *Journal of Neurophysiology*, **54**, 40–60.
- Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1995). Computational structure of coordinate transformations: A generalization study. In G. Tesauro, D. S. Touretzky and T. K. Leen (eds.), *Advances in neural information processing systems 7* (pp. 1125–1132). Cambridge, MA: MIT Press.
- Ghez, C., Gordon, J., Ghilardi, M. F., Christakos, C. N., & Cooper, S. E. (1990). Roles of proprioceptive input in the programming of arm trajectories. *Cold Spring Harbor Symposium on Quantum Biology*, **55**, 837–847.
- Ghez, C., Gordon, J., & Ghilardi, M. F. (1995). Impairments of reaching movements in patients without proprioception. II. Effects of visual information on accuracy. *Journal of Neurophysiology*, **73**, 361–372.
- Gomi, H., & Kawato, M. (1992). Adaptive feedback control models of the vestibulocerebellum and spinocerebellum. *Biological Cybernetics*, **68**, 105–114.
- Goodwin, G. C., & Sin, K. S. (1984). *Adaptive filtering prediction and control*. Englewood Cliffs, NJ: Prentice-Hall.
- Gordon, J., Ghilardi, M. F., & Ghez, C. (1995). Impairments of reaching movements in patients without proprioception. I. Spatial errors. *Journal of Neurophysiology*, **73**, 347–360.
- Haggard, P., & Wing, A. (1995). Coordinate responses following mechanical perturbation of the arm during prehension. *Experimental Brain Research*, **102**, 483–494.

- Haggard, P. N., Miall, R. C., Wade, D. T., Fowler, S., Richardson, A., Anslow, P., & Stein, J. F. (1995). Damage to cerebello-cortical pathways following closed head injury: an MRI and behavioural study. *Journal of Neurology, Neurosurgery and Psychiatry*, **58**, 433–438.
- Hall, C., Buckholz, E., & Fishbourne, G. J. (1992). Imagery and the acquisition of motor skills. *Canadian Journal of Sports Science*, **17**, 19–27.
- Harris, C. S. (1965). Perceptual adaptation to inverted, reversed and displaced vision. *Psychological Review*, **72**, 419–444.
- Hasan, Z. (1992). Role of proprioceptors in neural control. *Current Opinions in Neurobiology*, **2**, 824–829.
- Hermesdorfer, J., Wessel, K., Mai, N., & Marquardt, C. (1994). Perturbation of precision grip in Friedreich's ataxia and late-onset cerebellar ataxia. *Movement Disorders*, **9**, 650–654.
- Hertz, J., Krogh, A., & Palmer R. G. (1991). *Introduction to the theory of neural computation*. Redwood City, CA: Addison Wesley.
- Imamizu, H., Uno, Y., & Kawato, M. (1995). Internal representations of the motor apparatus: Implications from the generalization in visuo-motor learning. *Journal of Experimental Psychology*, **21**, 1174–1198.
- Jacobs, R. A., Jordan, M. I., Nowlan, S. J., & Hinton, G. E. (1991). Adaptive mixture of local experts. *Neural Computation*, **3**, 79–87.
- Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, **56**, 550–564.
- Jordan, M. I. (1995). Computational motor control. In M. S. Gazzaniga (Eds.), *The cognitive neurosciences*. (pp. 597–609). Cambridge, MA: MIT Press.
- Jordan, M. I., & Jacobs, R. A. (1992). Hierarchies of adaptive experts. In J. Moody, S. Hanson, & R. Lippmann (Eds.), *Advances in neural information processing systems 4* (pp. 985–993). San Mateo, CA: Morgan Kaufmann.
- Jordan, M. I., & Rumelhart, D. E. (1992). Forward models: Supervised learning with a distal teacher. *Cognitive Science*, **16**, 307–354.
- Kalman, R. E., & Bucy, R. S. (1961). New results in linear filtering and prediction. *Journal of Basic Engineering (ASME)*, **83D**, 95–108.
- Kawato, M., & Gomi, H. (1992). A computational model of four regions of the cerebellum based on feedback-error-learning. *Biological Cybernetics*, **68**, 95–103.
- Kawato, M., & Gomi, H. (1993). Feedback-error-learning model of cerebellar motor control. In N. Mano, I. Hamanda, & M. R. DeLong (Eds.), *Role of the cerebellum and basal ganglia in voluntary movement* (pp. 51–61). Amsterdam: Elsevier Science Publishers.
- Kawato, M., Furukawa, K., & Suzuki, R. (1987). A hierarchical neural network model for control and learning of voluntary movement. *Biological Cybernetics*, **57**, 169–186.
- Keele, S. W., & Posner, M. I. (1968). Processing of visual feedback in rapid movements. *Journal of Experimental Psychology*, **77**, 155–158.
- Kelso, J. A. S. (1977). Planning and efferent components in the coding movement. *Journal of Motor Behaviour*, **9**, 33–47.
- Kleinman, D. L., Baron, S., & Levinson, W. H. (1971). A control theoretic approach to manned-vehicle systems analysis. *IEEE Transactions Automatic Control*, **AC-16**, 824–832.
- Konczak, J., Borutta, M., Topka, H., & Dichgans, J. (1995). The development of goal-directed reaching in infants: hand trajectory formation and joint-torque control. *Experimental Brain Research*, **106**, 156–168.
- Kuperstein, M. (1991). INFANT neural controller for adaptive sensory-motor coordination. *Neural Networks*, **4**, 131–145.
- Lacquaniti, F., & Maioli, C. (1989). Adaptation to suppression of visual information during catching. *Journal of Neuroscience*, **9**, 149–159.
- Lacquaniti, F., Borghese, N. A., & Carrozzo, M. (1992). Internal models of limb geometry in the control of hand compliance. *Journal of Neuroscience*, **12**, 1750–1762.
- McIntyre, J., Gurfinkel, E. V., Lipshits, M. I., Droulez, J., & Gurfinkel, V. S. (1995). Measurements of human force control during a constrained arm motion using a force-actuated joystick. *Journal of Neurophysiology*, **73**, 1201–1222.
- Miall, R. C., (1996). Task dependent changes in visual feedback control: A frequency analysis of human manual tracking. *Journal of Motor Behaviour*, in press.
- Miall, R. C., Weir, D. J., Wolpert, D. M., & Stein, J. F. (1993). Is the cerebellum a Smith Predictor? *Journal of Motor Behaviour*, **25**, 203–216.
- Miall, R. C., Haggard, P. N., & Cole, J. D. (1996). Evidence of a limited visuo-motor memory used in programming wrist movements. *Experimental Brain Research*, **107**, 267–280.
- Muller, F., & Dichgans, J. (1994). Dyscoordination of pinch and lift forces during grasp in patients with cerebellar lesions. *Experimental Brain Research*, **101**, 485–492.
- Robinson, D. A., Gordon, J. L., & Gordon, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics*, **55**, 43–57.
- Rosenbaum, D. A., Engelbrecht, S. E., Bushe, M. M., & Loukopoulos, L. D. (1993). Knowledge model for selecting and producing reaching movements. *Journal of Motor Behaviour*, **25**, 217–227.
- Rothwell, J. C., Traub, M. M., Day, B. L., Obeso, J. A., Thomas, P. K., & Marsden, C. D. (1982). Manual motor performance in a deafferented man. *Brain*, **105**, 515–542.
- Sainburg, R. L., Ghilardi, M. F., Poizner, H., & Ghez, C. (1995). Control of limb dynamics in normal subjects and patients without proprioception. *J. Neurophysiology*, **73**, 820–835.
- Shadmehr, R., & Mussa-Ivaldi, F. (1994). Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience*, **14**, 3208–3224.
- Shidara, M., Kawano, K., Gomi, H., & Kawato, M. (1993). Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum. *Nature*, **365**, 50–52.
- Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychology Review*, **99**, 605–632.
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual invasion. *Journal of Comparative Physiology and Psychology*, **43**, 482–489.
- Teasdale, N., Forget, R., Bard, C., Paillard, J., Fleury, M., & Lamarre, Y. (1993). The role of proprioceptive information for the production of isometric forces and for handwriting tasks. *Acta Psychologica*, **82**, 179–191.
- Van Donkelaar, P., & Lee, R. G. (1994). Interactions between the eye and hand motor systems: disruptions due to cerebellar dysfunction. *Journal of Neurophysiology*, **72**, 1674–1685.
- Vercher, J. L., & Gauthier, G. M. (1988). Cerebellar involvement in the coordination control of the oculo-manual tracking system: effects of cerebellar dentate nucleus lesion. *Experimental Brain Research*, **3**, 155–166.
- Vercher, J. L., & Gauthier, G. M. (1992). Oculo-manual coordination control: Ocular and manual tracking of visual targets with delayed visual feedback of the hand motion. *Experimental Brain Research*, **90**, 599–609.
- Vercher, J., Gauthier, G. M., Guedon, O., Blouin, J., Cole, J., & Lamarre, Y. (1996). Self-moved target eye tracking in control and deafferented subjects: roles of arm motor command and proprioception in arm-eye coordination. *Journal of Neurophysiology*, in press.
- Wada, Y., & Kawato, M. (1993). A neural network model for arm trajectory formation using forward and inverse dynamics models. *Neural Networks*, **6**, 919–932.

- Weir, D. J., Miall, R. C., & Stein, J. F. (1989). Cues and control strategies in a visuo-motor tracking task. *Journal of Motor Behaviour*, *21*, 185–204.
- Welch, R. B., & Warren, D. H. (1986). Intersensory interactions. In K. R. Boff, L. Kaufmann, & J. P. Thomas (Eds.), *Handbook of perception and human performance. Volume I: Sensory processes and perception*. New York: John Wiley.
- Wing, A. M. (1996). Anticipatory control of grip force in rapid arm movement. In A. Wing, P. Haggard, & R. Flanagan (Eds.), *Hand and brain: neurophysiology and psychology of hand movement*. (Chap. 15). San Diego, CA: Academic Press, in press.
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, *269*, 1880–1882.
- Yue, G., & Cole, K. J. (1992). Strength increases from the motor program: Comparison of training with maximal voluntary and imagined muscle contractions. *Journal of Neurophysiology*, *67*, 1114–1123.
- Zelaznik, H. N., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single aiming movements. *Journal of Motor Behaviour*, *15*, 217–236.