An Internal Model for Sensorimotor Integration

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On the basis of computational studies it has been proposed that the central nervous system internally simulates the dynamic behavior of the motor system in planning, control, and learning; the existence and use of such an internal model is still under debate. A sensorimotor integration task was investigated in which participants estimated the location of one of their hands at the end of movements made in the dark and under externally imposed forces. The temporal propagation of errors in this task was analyzed within the theoretical framework of optimal state estimation. These results provide direct support for the existence of an internal model.

The notion of an internal model, a system that mimics the behavior of a natural process, has emerged as an important theoretical concept in motor control (1). There are two varieties of the internal model: (i) forward models, which mimic the causal flow of a process by predicting its next state (for example, position and velocity) given the current state and the motor command; and (ii) inverse models, which invert the causal flow by estimating the motor command that caused a particular state transition. Forward models have been shown to be of potential use for solving four fundamental problems in computational motor control. First, the delays in most sensorimotor loops are large, making feedback control too slow for rapid movements. With the use of a forward model for internal feedback, the outcome of an action can be estimated and used before sensory feedback is available (2, 3). Second, a forward model is a key ingredient in a system that uses motor output (also called efference copy) to anticipate and cancel the sensory effects of movement (also called reafference) (4). Third, a forward model can 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 (5). Similarly, by predicting the sensory outcome of the action without actually performing it, a forward model can be used in mental practice to learn to select between possible actions (6). Finally, a forward model can be used for state estimation in which the model's prediction of the next state is combined with a reafferent sensory correction (7). Although shown to be of theoretical use, the existence of an internal forward model in the central nervous system (CNS) is still a topic of debate.

When we move an 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 can make use of sensory inflow (the information available from proprioception), it can make use of integrated motor outflow (the motor commands sent to the arm), or it can combine these two sources of information by use of a forward model. To test between these possibilities, we carried out an experiment in which participants, after initially viewing one of their arms in the light, made arm movements in the dark. Three experimental conditions were studied, involving the use of null, assistive, and resistive force fields. We assessed the participants' internal estimate of hand location by asking them to localize visually the position of their hand at the end of the movement (8). The bias of this condition estimate, plotted as a function of movement duration, shows a consistent overestimation of the distance moved (Fig. 1). This bias shows two distinct phases as a function of movement duration: an initial increase reaching a peak of 0.9 cm after 1 s followed by a sharp transition to a region of gradual decline. The variance of the estimate also shows an initial increase during the first second of movement after which it plateaus at about 2 cm². External forces had distinct effects on the bias and variance propagation. Whereas the bias was increased by the assistive force and decreased by the resistive force, the variance was unaffected.

These experimental results can be fully accounted for if we assume that the motor control system integrates the effluent outflow and the reafferent sensory inflow. To establish this conclusion, we developed an explicit model of the sensorimotor integration process, which contains as special cases all three of the methods referred to above (9). This model is based on the observer framework (7) from engineering in which the state estimator (or observer) has access to both the inputs and outputs of the system. Specifically, the input to the arm is the

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motor command and the output is the sensory feedback that, in the absence of vision, consists solely of proprioception. On the basis of these two sources, the observer produces an estimate of the state of the system. In particular, we chose to use a Kalman filter (10) observer, which is a linear dynamical system that produces an estimate of the location of the hand by using both the motor outflow and sensory feedback in conjunction with a model of the motor system. Using these sources of information, the model estimates the arm’s state, integrating sensory and motor signals to reduce the overall uncertainty in its estimate.

The model is a combination of two processes that together contribute to the state estimate. The first process (upper part, Fig. 2A) uses the current state estimate and motor command to predict the next state by simulating the movement dynamics with a forward model. The second process (lower part, Fig. 2A) uses a model of the sensory output process to predict the sensory feedback from the current state estimate. The sensory error—the difference between actual and predicted sensory feedback—is used to correct the state estimate resulting from the forward model. The relative contributions of the internal simulation and sensory correction processes to the final estimate are modulated by the Kalman gain so as to provide optimal state estimates. By making particular choices for the parameters of the Kalman filter, we were able to simulate motor outflow–based estimation (11), sensory inflow–based estimation, and forward model–based sensorimotor integration. Moreover, to accommodate the observation that participants generally tend to overestimate the distance that their arm has moved, we set the gain that couples force to state estimates to a value that is larger than its veridical value (12). All other components of the internal model were set to their veridical values.

The Kalman filter model demonstrates the two distinct phases of bias propagation observed (Fig. 2, B through E). By overestimating the force acting on the arm, the forward model overestimates the distance traveled, an integrative process eventually balanced by the sensory correction. The model also captures the differential effects on bias of the externally imposed forces. By overestimating an increased force under the assistive condition, the bias in the forward model accrues more rapidly and is balanced by the sensory feedback at a higher level. The converse applies to the resistive force. The pattern of variance propagation is also captured by the model. The variance of the state estimate derives from two sources of variance in the system: the first is the variability in the response of the arm to the motor commands and the second is the noise in the subsequent sensory feedback. Initially, when the hand is in view, the state estimate is assumed to be accurate. The accuracy of the prediction from the forward model component of the Kalman filter depends on the accuracy of the current state estimate (one of its inputs). Therefore, during the early part of the movement, when the current state estimate is accurate, the sensorimotor integration process weights heavily the contribution of the forward model to the final estimate. However, in the later stages of the movement, when the current state estimate is less accurate, the sensory feedback must be relied on to correct for inaccuracies in the forward model. In the Kalman filter, the relative weighting shifts from the forward model toward sensory feedback over the first second of movement and then remains approximately constant, resulting in the asymptote of the variance propagation. In accord with the experimental results, the model predicts no change in variance under the two force conditions.

We have shown that the Kalman filter is able to reproduce the propagation of the
bias and variance of estimated position of the hand as a function of both movement duration and external forces. The Kalman filter model suggests that the peaking and gradual decline in bias is a consequence of a trade-off between the inaccuracies accumulating in the internal simulation of the arm’s dynamics and the feedback of actual sensory information. Simple models that do not trade off the contributions of a forward model with sensory feedback, such as those based purely on sensory inflow or on motor outflow, are unable to reproduce the observed pattern of bias and variance propagation (13). The ability of the Kalman filter to parsimoniously model our data suggests that the processes embodied in the filter—namely, internal simulation through a forward model together with sensory correction—are likely to be embodied in the sensorimotor integration process. We feel that the results of this state estimation study provide evidence that a forward model is used by the CNS in maintaining its estimate of the hand location. Furthermore, the state estimation paradigm provides a framework to study the sensorimotor integration process in both normal and patient populations. The model predicts monotonically increasing bias and variance, if the afferent signal is eliminated, and undershoot rather than overshoot in bias propagation if the forward model is eliminated. These specific predictions can be tested in both patients with sensory neuropathies, who lack proprioceptive reaference, and patients with damage to the cerebellum, a proposed site for the forward model (3).

REFERENCES AND NOTES


8. The experimental setup consisted of a planar, virtual visual feedback system (described in D. M. Wolpert, Z. Ghahramani, M. I. Jordan, Exp. Brain Res. 103, 450 (1995)) in conjunction with a planar, two-degree-of-freedom manipulandum driven by two torque motors (described in R. Mayer, faycie, East, Massachusetts Institute of Technology [1989]). Each participant gripped a manipulandum on which his thumb was mounted. The manipulandum was used to accurately measure the position of the participant’s thumb and also, using the torque motors, to apply forces to the hand. The hand was constrained to move along a straight line passing transversely in front of the participant. The virtual visual feedback system was used to project computer-controlled images into the plane of the movement. Eight untrained male participants, who gave their informed consent, performed 300 trials each. Each trial started with the participant visually placing his thumb at a target square projected randomly on the virtual environment illuminated for 2 s, thereby allowing the participant to perceive visually his initial arm configuration. The light was then extinguished, leaving just the initial target. The participant was required to move his hand either to the left or right, as indicated by an arrow in the initial starting square. This movement was made in the absence of any visual feedback of the participant’s arm configuration. The participant was instructed to move until he heard a tone, at which point he stopped. The timing of the tone was controlled to produce a uniform distribution of path lengths from 0 to 30 cm. During this movement, the participant moved more rapidly at the null or constant assisive or resistive force field of 5 N generated by the torque motors. Although it is not possible to directly probe a participant’s internal representation of the state of his arm, we examined a function of this state: the estimated visual location of the thumb. The relation between the state of the arm and the visual coordinates of the hand is known as the kinematic transformation (J. Craig, Introduction to Robotics: Mechanics and Control (Addison-Wesley, Reading, MA, 1989)). Therefore, once at rest the participant indicated the visual estimate of the unseem thumb position using a trackball, held in his other hand, to move a cursor projected on a monitor and lee the movement along the line. The discrepancy between the actual and visual estimate of thumb location was recorded as a measure of the state estimation error. The bias and variance of the state estimates were ana-

9. While the Kalman filter is a recursive least square algorithm, the bias and variance of the state the bias and variance as a function of final position, movement dura-


11. Estimation based purely on motor outflow is also known as “dead reckoning.” This uses the rate of change of a variable, as estimated by a forward model, to update the current estimate. This term derives from its usage by sailors in navigation, who would estimate the position of their ship at sea on the basis of its previous position, time elapsed, and their estimated velocity over the ground. By effectively internally modeling the ship’s dy-

12. This setting is consistent with the independent data that participants tend to under-estimate in pointing tasks, which suggests an overestimation of distance traveled (U. Soechting and M. Flanders J. Neuro-

13. A model based purely on motor outflow (dead reck-

14. We thank P. Day for his assistance in reviewing the manuscript. This project was supported by grants from the McDonnell-Pew Foundation, ATR Human Information Processing Research Laboratories, Si-


16. The system dynamics, E = x(t) + w(t) + v(t), was defined as the initial state vector for each new trial and was the same for all participants. The system was used to simulate the behavior of a participant who had been given prior training in the task. The system was used to simulate the behavior of a participant who had been given prior training in the task.