Topical Review

Computational principles of sensorimotor control that minimize uncertainty and variability

Paul M. Bays[1] and Daniel M. Wolpert[2]

[1]*Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK*
[2]*Department of Engineering, University of Cambridge, Trumpington Street, Cambridge CB2 1PZ, UK*

Sensory and motor noise limits the precision with which we can sense the world and act upon it. Recent research has begun to reveal computational principles by which the central nervous system reduces the sensory uncertainty and movement variability arising from this internal noise. Here we review the role of optimal estimation and sensory filtering in extracting the sensory information required for motor planning, and the role of optimal control, motor adaptation and impedance control in the specification of the motor output signal.

Corresponding author P. M. Bays: Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK.   Email: p.bays@ion.ucl.ac.uk

From a computational perspective, the task of motor control is to use sensory inputs, which inform us about the current state of our body and environment, to generate motor commands that will accomplish a particular goal. However, in computing this sensorimotor transformation, the motor system faces substantial challenges. First, the sensory signals that form the input can be both inaccurate and variable ('noisy'), leading to uncertainty in the estimate of the state. Second, the motor output command is itself corrupted by noise during its transmission to the musculature, introducing variability into the movement. Finally, the environment in which the motor system operates is variable, changing as we interact with objects around us, with the result that the sensorimotor transformation must be frequently updated. Here we provide an overview of some of the computational principles which allow human motor control to be dexterous despite these apparent obstacles.

We begin by reviewing two ways in which the CNS can minimize uncertainty in the sensory input: firstly, by combining multiple sensory signals with prior knowledge to refine sensory estimates; and secondly, by predictive filtering of the sensory input to remove less informative components of the signal. Next, we review how the motor system can select actions so as to minimize the negative consequences of noise in the motor output. Finally, we review how motor adaptation and impedance control can be employed in parallel to minimize movement errors caused by variability in the environment.

Sensory noise and optimal integration

Accurate motor control requires precise knowledge of the state of the body, such as the angular positions and velocities of the joints. However, the sensory organs that provide this information have limited resolution, and the sensory signals they transmit are corrupted by neuronal noise, with the result that sensory estimates of state variables are imprecise. State information is often available in more than one sensory modality. In estimating the current position of the hand, for example, the CNS may have access to both visual and proprioceptive information about its location. Combining these two sources of information can result in a more precise position estimate than could be obtained from either source alone. Specifically, given a visual estimate of location, V, and a proprioceptive estimate of location, P, a single location estimate can be obtained by calculating a weighted average $w_\mathrm{p}P + w_\mathrm{v}V$. If the visual and proprioceptive estimates are both independently corrupted by Gaussian noise with variance σ_V^2 and σ_P^2, respectively, the optimal estimate of location is obtained by weighting each source in proportion to its precision (the inverse of its variance): $w_\mathrm{P} = \sigma_\mathrm{V}^2/(\sigma_\mathrm{P}^2 + \sigma_\mathrm{V}^2)$ and $w_\mathrm{V} = \sigma_\mathrm{P}^2/(\sigma_\mathrm{P}^2 + \sigma_\mathrm{V}^2)$ (Clark & Yuille, 1990; Ghahramani *et al.* 1997).

Experimentally, the precision of vision and proprioception can be measured by asking subjects to align their left hand under a table with either a visual target or a proprioceptive target (their unseen right hand). This approach reveals proprioceptive localization to be better in depth and visual localization better in azimuth (van

Beers *et al.* 1998), as illustrated in Fig. 1*A*. The optimal integration hypothesis therefore predicts that the estimate of depth should rely more on proprioceptive input and the estimate of azimuth should rely more on vision (Fig. 1*B*). This model has been confirmed by experimental studies of hand localization in which subjects point to combined visual and proprioceptive targets (van Beers *et al.* 1996, 1999, 2002). Optimal integration has also been demonstrated in estimating properties of objects, for example in combining visual and haptic input to estimate size (Ernst & Banks, 2002), and in integrating visual texture and motion cues to estimate depth (Jacobs, 1999).

Even when only one source of state feedback is available, the motor system will generally have prior knowledge that certain states of the body are more likely than others (for example that the arms spend more time in front of the body than behind it). According to the theory of Bayesian inference, the imperfect estimate of the state obtained from sensory input can be improved by taking into account the prior probabilities of different configurations.

In the Bayesian framework, the strength of a belief is represented by a real number between zero and one, which reflects the probability that we assign to our belief, e.g. $P(A)$. Bayes's rule specifies how to optimally update our beliefs as new information becomes available:

$$\overbrace{P(\text{state}|\text{sensory input})}^{\text{Posterior}} = \frac{\overbrace{P(\text{sensory input}|\text{state})}^{\text{Likelihood}}\ \overbrace{P(\text{state})}^{\text{Prior}}}{P(\text{sensory input})}$$

Here, $P(\text{state})$ reflects our *prior* belief in a particular state of the world before the sensory input is received. In order to integrate the new sensory information with this prior belief, Bayes's rule states that one should calculate the *likelihood* of the state: the probability of the sensory input given the hypothesized state, $P(\text{sensory input}|\text{state})$. This reflects how probable it is that we would receive, for example, the current proprioceptive input given a particular arm configuration. By multiplying the prior by the likelihood and normalizing (scaling so that the sum of the probabilities over all possible states sum to one) we can estimate the probability of the state given the sensory input, termed the *posterior* of the state. This posterior now becomes our new prior belief and can be further updated based on new sensory input. As when combining multiple sensory inputs, this method effectively weights the two sources of information, the prior and the likelihood, according to their precision (Cox, 1946; Bernado & Smith, 1994).
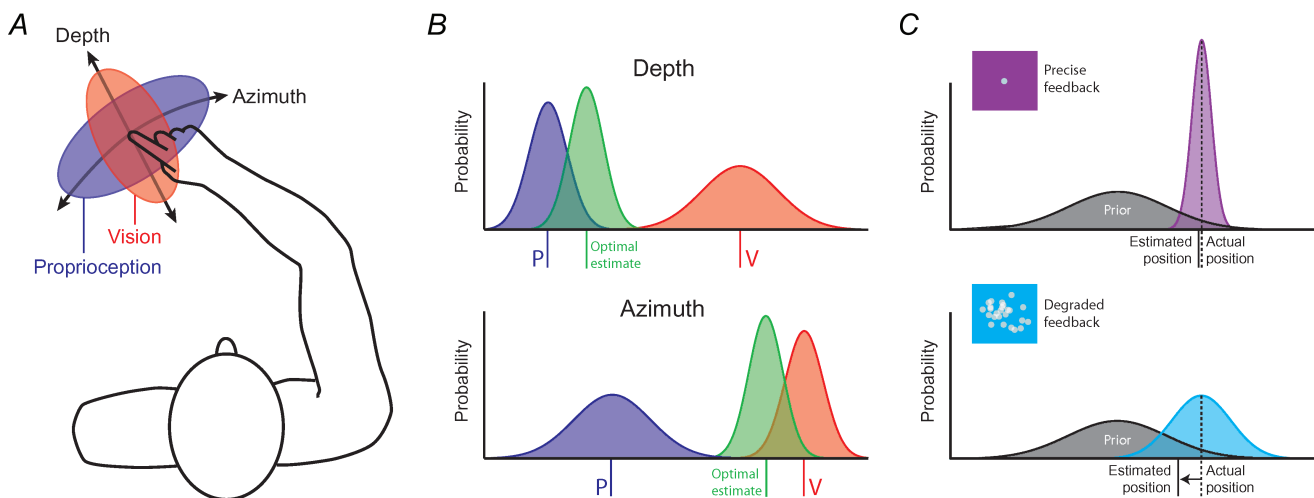

Figure 1. Optimal integration in the estimation of hand position
A, ellipses illustrate the precision of visual (red) and proprioceptive (blue) estimates of hand position in the horizontal plane. The narrower an ellipse in a certain direction, the more precise the estimate. (Adapted with permission from Van Beers *et al.* 2002.) *B*, the uncertainty in the sensory input can be represented as a probability distribution of possible locations. In depth (top), the proprioceptive estimate of position (blue) has a lower variance than the visual estimate (red). When there is a discrepancy between visual and proprioceptive estimates, the optimal combined estimate is obtained by weighting each source by the inverse of its variance. This combined estimate (green) has lower variance than either input alone. In azimuth (bottom), the relative precision of vision and proprioception is reversed, with the result that the optimal estimate now relies more on vision than proprioception. *C*, an estimate of position obtained from visual input alone can be improved by combining it with knowledge of a prior distribution of probable positions. The extent to which this prior distribution (grey) influences the optimal position estimate depends on the variance in the visual input. When visual feedback is very precise (top), the prior distribution has little effect, but when the variance of the visual estimate is increased (bottom), the optimal estimate becomes biased towards the mean of the prior distribution.

Bayesian inference has recently been demonstrated in a study in which subjects made online corrections to a reaching movement based on momentary visual feedback of hand position (Kording & Wolpert, 2004*a*). This visual feedback, presented midway through the movement, was displaced laterally by a distance that varied from trial to trial. The range of displacements experienced over the course of many trials formed a prior probability distribution. According to the Bayesian model, this prior distribution can be combined with the feedback on a given trial to provide an optimal estimate of the position error. For movements in which very precise visual feedback was given, this prior distribution of displacements had little influence on the estimate of hand position, which was based almost entirely on the visual feedback from the current trial (Fig. 1*C*, top). However, when the visual feedback was artificially degraded, the state estimate became increasingly biased towards the mean of the prior distribution, as predicted by a Bayesian model (Fig. 1*C*, bottom). This suggests that the CNS internally represents both the prior statistics of the environment and the uncertainty in its sensors, and can combine these two sources of information in an optimal fashion.

Several computational schemes have been proposed by which a population of neurons could represent uncertainty and thereby compute in a Bayesian manner (Knill & Pouget, 2004). One proposal is that each neuron in a population codes for a particular value of an estimated parameter, such as hand position, and the activity across the population explicitly represents the probability of the different values using a convolution code (Zemel *et al.* 1998). Alternatively, in a gain encoding scheme the peak activity of a population reflects the estimate and the firing rate indicates the uncertainty, increasing with decreasing variance in the estimate (Pouget *et al.* 2003). However, there is currently little direct evidence for either of these models.

Reafference as 'noise' and sensory filtering

We have discussed how sensory input is corrupted by neuronal noise, and how the resulting uncertainty can be minimized by the CNS. From the point of view of generating estimates about the outside world, sensory input is further corrupted by reafference: changes to the sensory input that result solely from our own actions (Sperry, 1950; Von Holst & Mittelstaedt, 1950; Von Holst, 1954). A number of filtering mechanisms have been proposed that attenuate or remove this self-generated input from the incoming sensory stream, thereby enhancing the processing of external events.

An example of sensory filtering that has been widely investigated is the reduction in tactile sensitivity observed during movement of a digit or limb (Angel & Malenka,

1982; Chapman *et al.* 1987; Milne *et al.* 1988). A possible neural mechanism for this movement-related gating has been identified in primates by Seki *et al.* (2003). They observed reduced activation of spinal interneurons by primary tactile afferents in the superficial radial nerve during an active wrist movement. The most likely mechanism was identified as presynaptic inhibition of the primary afferents (Eccles *et al.* 1961; Miller, 1998) resulting from a central command signal. The theory that sensory gating is triggered by descending signals from motor planning areas is supported by a recent study by Voss *et al.* (2006). Pulses of transcranial magnetic stimulation (TMS) over primary motor cortex were used to delay planned finger movements at the motor output stage. Sensory suppression of cutaneous stimuli was observed at the intended time of movement, despite this being substantially prior to the actual onset of the movement.

While movement-related gating filters out sensations resulting from voluntary movement, it also removes externally generated sensations that are unrelated to the movement. Von Holst (1954) and Sperry (1950) proposed a more specific mechanism of sensory filtering that leaves external input intact. According to this model, self-generated sensations are predicted based on an 'efference copy' of the motor command. By subtracting this prediction from the incoming sensory stream, the self-generated component can be removed. Modern formulations of this theory (illustrated in Fig. 2*A*) include a forward model: an internal representation of the environment that is used to transform the efference copy signal into a sensory prediction (Jordan & Rumelhart, 1992; Wolpert & Miall, 1996; Davidson & Wolpert, 2005).

This kind of predictive cancellation has been observed in the electrosensory systems of electric fish (Bell, 2001). Electric fish possess both electroreceptors for sensing current and electric organs driven by motor commands for discharging current. To prevent the discharge of a fish's own electric organs interfering with its ability to sense its surroundings, the self-generated component is removed from the output of electrosensory cells by an adaptive predictive mechanism. Bell (1981, 1982, 1986) blocked the electric organs of mormyrid fish with curare, and then delivered an artificial electrical stimulus every time the fish generated a discharge motor command. At first, the artificial stimuli produced substantial activation in neurons receiving electrosensory input, but these responses were greatly attenuated after a few minutes of consistent pairing of the stimulus with the motor command. When the artificial stimuli were subsequently stopped, a negative image of the expected activation was observed in response to each motor command: a clear indication of predictive cancellation as proposed by Sperry and Von Holst.

Sensory cancellation has also been observed in the primate vestibular system. A subclass of neurons

within the vestibular nucleus receives input from the semicircular canals, and projects to spinal motor neurons that innervate muscles in the neck. These 'vestibular-only' neurons mediate a reflex which generates compensatory muscle responses in response to head motion, stabilizing the head in space. While beneficial at rest, this reflex would be inappropriate during active head movements, and these neurons receive a cancellation signal that attenuates responses to active movements (McCrea *et al.* 1999; Roy & Cullen, 2001, 2004).

In humans, a cancellation mechanism may be responsible for the attenuation of tactile sensations that occur as a result of one body part touching another (Shergill *et al.* 2003). If subjects are instructed to reproduce an externally applied pressure on one finger by pressing with a finger of the other hand, they consistently overestimate the force required (Fig. 2*B*, blue circles). This effect is not observed when subjects reproduce the force indirectly, by controlling the pressure on the finger via a joystick (Fig. 2*B*, blue squares). This implies that the sensation in the passive finger is perceived as substantially weaker when it is directly self-generated than when it is externally applied. Unlike a gating process, this attenuation has been shown to depend on a spatially and temporally precise prediction of the self-generated sensory input (Blakemore *et al.* 1999*a*; Bays *et al.* 2005, 2006).

The type of mechanism illustrated in Fig. 2*A* may also underlie our ability to distinguish between our own actions and external events. Sensory feedback from our own actions should closely match the feedback predicted on the basis of efference copy, whereas external influences can be identified by large discrepancies between predicted and actual feedback. Many of the symptoms of schizophrenia, such as auditory hallucinations and delusions of control, appear to involve patients incorrectly identifying their own actions as having an external source. This has led to the suggestion that schizophrenia results in part from a deficit in predicting the sensory consequences of one's actions (Feinberg, 1978; Frith, 1992; Frith *et al.* 2000). Consistent with this theory, patients with schizophrenia show less attenuation of self-generated sensation than controls (Blakemore *et al.* 2000; Shergill *et al.* 2005), performing substantially better on the force reproduction task than healthy subjects (red circles, Fig. 2*B*).

Converging evidence from theoretical, neuro-physiological, and functional imaging studies suggests a role for the cerebellum in sensory filtering. In electric fish, the neurons identified as sites of attenuation are found in the electrosensory lobes, regions with a strong anatomical similarity to the cerebellum. These neurons receive projections carrying both proprioceptive input and central input related to the motor command.
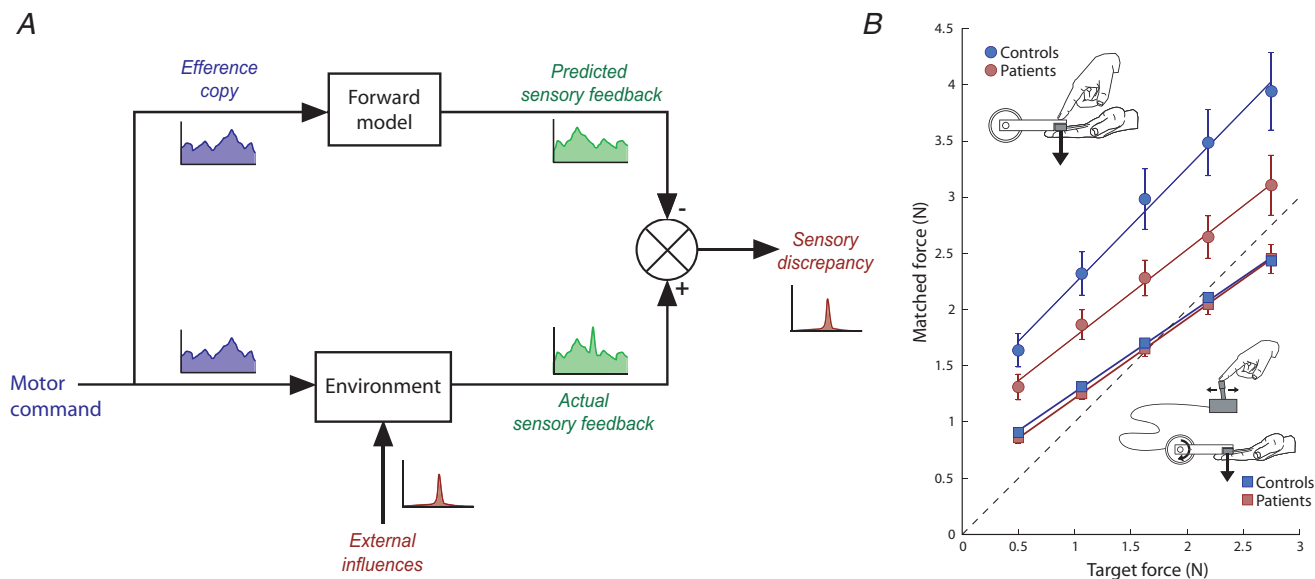

Figure 2. Predictive filtering of self-generated sensation
A, schematic representation of a sensory cancellation mechanism. On the basis of efference copy, a forward model predicts the sensory feedback that will result from a planned action. Subtracting this prediction from the actual sensory input reveals an estimate of the sensory feedback due to external influences. *B*, performance of healthy subjects (blue) and schizophrenic patients (red) on a force-matching task. Subjects were instructed to reproduce a target force, applied to the left index finger by a torque motor, either directly by pressing with the right index finger (circles) or indirectly by controlling the torque motor output with a joystick (squares). Average matching force is shown as a function of target force. Error bars indicate ± 1 s.e.m. across subjects. Dashed line represents perfect performance. Adapted with permission from Shergill *et al.* (2005).

Adaptation of the predictive cancellation signal has been shown to result from plasticity at these synapses (Bell *et al.* 1993). Similarly, the primate 'vestibular-only' neurons described above are thought to receive projections from the nodulus-uvula region of the cerebellum (Xiong & Matsushita, 2000).

In humans, functional imaging studies support a role for the cerebellum in tactile attenuation (Blakemore *et al.* 1998, 1999*b*). Activity in the right anterior cerebellar cortex is reduced when a tactile stimulus is self- rather than externally generated. This may reflect the generation of a predictive cancellation signal in cerebellar areas ipsilateral to the active hand. These studies revealed a significant correlation between activation in the cerebellum and the somatosensory cortex, but only for self-generated stimuli. This is again consistent with modulation of the input to sensory areas by a signal originating in the cerebellum.

The involvement of cerebellar areas in sensory attenuation is consistent with proposals that the cerebellum is a component of the forward model system that predicts the consequences of planned actions (Ito, 1970; Miall *et al.* 1993; Wolpert & Kawato, 1998). The physiological structure of the cerebellum makes it a strong candidate for learning and maintaining internal models. Purkinje cells, the only output neurons from the cerebellar cortex, receive synaptic inputs from parallel fibres and climbing fibres. Parallel fibres originate in granule cells which transmit input from association areas of the cerebral cortex. Parallel fibres may make as many as 200 000 synapses on a single Purkinje cell (Ito, 1984), and it has been proposed that the complex transformation from parallel fibre input to Purkinje cell output may implement an internal model. To implement a forward model, this theory proposes that parallel fibre inputs carry an efference copy of the motor command, and the Purkinje cell output signals predicted sensory feedback (Miall *et al.* 1993).

Motor noise and optimal control

In addition to the problems of interpreting noisy sensory input, the motor system must also contend with neuronal noise in the motor output. Over the normal force range of movement, the total noise affecting the activation of each muscle is not constant, but increases approximately linearly with the amplitude of the motor command signal (Schmidt *et al.* 1979; Meyer *et al.* 1988). This signal-dependent noise results directly from the physiology of the motor pool, in which motor-units are recruited in order of increasing twitch amplitude (Jones *et al.* 2002; Hamilton *et al.* 2004). Each activated motor-unit has some variance in its firing rate, and the total variance is the sum of the individual variances of all the recruited units. The effect of this noise is to make movements variable.

It is naturally desirable for planned movements to be carried out accurately, and it has been suggested that movement variability is minimized by taking advantage of the redundancy in the motor system (Harris & Wolpert, 1998). Any motor task can in theory be achieved by an infinite number of possible trajectories, movement durations, and levels of muscle cocontraction. Despite this redundancy, human movement patterns are highly stereotyped (Bahill *et al.* 1975; Morasso, 1981; Lacquaniti *et al.* 1983). This consistency is characteristic of a computational approach known as optimal control, in which a 'cost' is specified as a function of the movement, and the motor output with the lowest cost selected (Bryson & Ho, 1975; Harris, 1998).

Costs have been proposed that can reproduce a range of empirical data, e.g. arm movement data can be modelled by minimizing the jerkiness of the hand (Flash & Hogan, 1985) or minimizing the rate of change of torques at the joints (Uno *et al.* 1989). However, the issue of movement variability has generally been overlooked. Recently, stochastic optimal control models have been developed which explicitly take account of the noise in the motor command. For example, optimal control models that minimize endpoint variability under signal-dependent noise accurately reproduce the observed temporal profiles of both arm reaching movements and saccadic eye movements (Harris & Wolpert, 1998), and predict the way in which feedback is used to correct movements online (Todorov & Jordan, 2002). The choice of endpoint variability as a cost has several advantages over previous proposals: it is easy to compute from sensory feedback, as the CNS needs only to monitor errors at the end of a movement rather than integrating a quantity such as jerk or torque change over the movement, and unlike these other measures, endpoint variability has obvious behavioural relevance.

Although minimizing variability can account for a range of movement data there are other factors that can also be included in the overall cost, such as movement duration and energy. The relative weighting of different components within the cost may well vary across different tasks and types of movement. For example, successful models of walking have been developed based on minimizing energy (Srinivasan & Ruina, 2006), while it is possible to model the saccadic main sequence, the relation between saccadic amplitude and duration, by minimizing a cost which combines both movement duration and eye movement variability (Harris & Wolpert, 2006).

Whichever parameter is chosen to determine the cost, almost all optimal control models assume a cost function that minimizes the square of that parameter. To take the example of endpoint error, this means that a 2 cm error carries four times the cost of a 1 cm error. However, as illustrated in Fig. 3*A*, alternative cost functions can be hypothesized, such as a cost proportional to the absolute error, or a function that punishes all non-zero errors equally. The form of the cost function has recently been

investigated in a study by Kording & Wolpert (2004*b*). Subjects attempted to align their hand with a target under an experimentally imposed visual error. The statistical distribution of this visual error was asymmetric, with the result that the optimal alignment of the hand with the target depended on the cost function. For example, it can be shown that to minimize the absolute error, the median of the distribution must be aligned with the target, whereas to minimize the squared error, the mean of the distribution should be aligned (Fig. 3*B*). The results of this study reveal a cost function that is proportional to the squared error for small errors, but increases more slowly than the squared error for larger errors (Fig. 3*C*). Models that assume a squared error are therefore good approximations, but the motor system is less influenced by outliers than these models predict.

Variability in the environment, motor adaptation, and impedance control

Optimal control models generally define an optimal trajectory but not how that trajectory should be achieved. The muscle activations required to generate a given limb movement depend on the dynamics of the limb and the environment in which it moves. One of the biggest challenges facing the motor system is coping with

variability in these dynamics. Changes can occur over long time periods due to developmental changes in the length of limb segments and the size and strength of muscles, but also on much shorter time scales as a result of interactions with the environment, such as when manipulating a tool.

A computational approach that is well-suited to dealing with such changes is the inverse model, an internal representation of the dynamic environment that is used to compute motor command signals to produce a desired movement (Kawato *et al.* 1987; Wada & Kawato, 1993; Jordan, 1995). When the dynamics change, for instance when we pick up an object, the inverse model no longer captures the dynamic properties of the system, resulting in inaccurate movements. However, these movement errors can be transformed into a training signal that may be used to adapt the inverse model until it correctly represents the new dynamic environment (Kawato *et al.* 1987; Jordan & Rumelhart, 1992).

Experimentally, this kind of motor adaptation has been studied by applying state-dependent forces to the arm during reaching movements, either via a robotic manipulandum held in the hand (Shadmehr & Mussa-Ivaldi, 1994), or by rotating the subject and thus inducing Coriolis force in the moving arm (Lackner & Dizio, 1994). On initial exposure these force fields cause large deviations in arm trajectory, followed by corrective
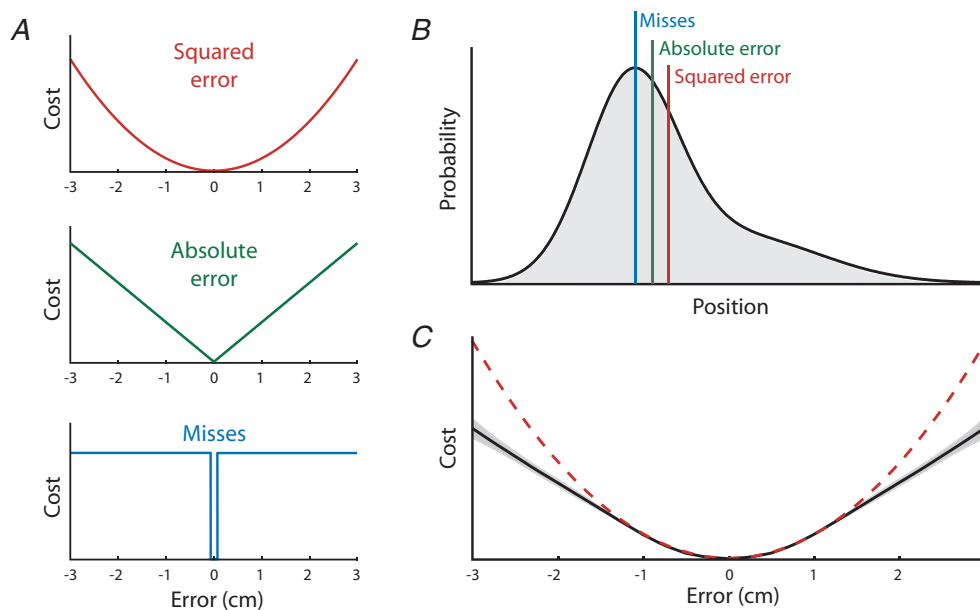

Figure 3. Cost functions for optimal control
A, optimal control models attempt to minimize a specified 'cost', such as the error in position at the end of a movement. Cost functions are shown that minimize different features of position error: the squared error (top), the absolute error (middle), or the number of misses (i.e. non-zero errors, bottom). *B*, one of the asymmetric probability distributions of position used in Kording & Wolpert (2004*b*). Vertical lines indicate the point in the distribution that should be aligned with the target in order to minimize each of the cost functions shown in *A*. *C*, the continuous black line indicates the cost function inferred from the results of Kording & Wolpert (2004*b*); the grey area represents ± 1 s.e.m. across subjects. The squared error is shown for comparison (red dashed line). Adapted with permission from Kording & Wolpert (2004*b*).

movements to reach the target (Fig. 4*A*, top). However, with practice hand paths gradually become straighter and approach the pre-exposure trajectory (Fig. 4*A*, bottom), implying that the motor system has integrated the external forces into its internal model of dynamics. If the force is unexpectedly absent on a movement, a large deviation of the hand path is observed in the opposite direction to the earlier errors, confirming that the motor system is actively compensating for the expected external force.

Neuronal correlates of motor adaptation have been observed in primary motor cortex (M1). In primates, adaptation to a novel force field at the hand is accompanied by changes in preferred direction of neurons in the arm area of M1 (Gandolfo *et al.* 2000). Following adaptation, the shift in preferred direction at the population level matches the shift in muscle activity required to compensate for the force field (Li *et al.* 2001). These neuronal changes outlast the exposure to the perturbation, consistent with our ability to recall previously learned dynamics even after a gap of several months (Brashers-Krug *et al.* 1996; Gandolfo *et al.* 1996).

In humans, several imaging studies support cerebellar involvement in acquiring new inverse models (Imamizu *et al.* 2000; Nezafat *et al.* 2001). From a theoretical standpoint, the aspects of the cerebellum's structure and connectivity that make it a candidate for maintaining forward models also make it an ideal neural basis for inverse models. According to one model, parallel fibre inputs to the cerebellum signal desired movement goals, and the Purkinje cell output signals the error in the current motor output, with the inverse model implemented by the parallel fibre-Purkinje cell synapses (Kawato, 1999). The efficacy of these synapses appears to be modulated by input from climbing fibres, originating in the inferior olive, via long-term depression (Marr, 1969; Albus, 1971; Fujita, 1982; Ito, 2001). Electrophysiological studies in primates

have observed increased climbing fibre activity during initial movements under a novel load or changed visual feedback (Gilbert & Thach, 1977; Ojakangas & Ebner, 1992). These and other studies (e.g. Gellman *et al.* 1985; Andersson & Armstrong, 1987) suggest that climbing fibre inputs signal discrepancies between expected and actual sensory input. Climbing fibre input may therefore act as a training signal which, via plasticity of the parallel fibre-Purkinje cell synapses, adapts the inverse model to minimize errors in prediction.

The cerebellar architecture appears to be highly modular (Oscarsson, 1979; Bower & Woolston, 1983), so it is possible that the cerebellum implements many forward and inverse models simultaneously (Wolpert & Kawato, 1998; Wolpert *et al.* 1998; Haruno *et al.* 2001). In an fMRI study in which subjects learned to switch between two different sensorimotor transformations, cerebellar activation became localized in different areas under the two different transformations (Imamizu *et al.* 2003). This may reflect the acquisition of distinct internal models implemented in spatially segregated regions of the cerebellum's modular architecture.

While adaptation of the inverse model is a viable strategy when the dynamics of the environment vary predictably, we often engage in tasks in which this is not the case. For example, when drilling into a wall with an electric drill, the aim is to keep the drill bit perpendicular to the wall. However, small deviations in the angle of the drill bit to the wall produce forces that tend to destabilize the posture (Rancourt & Hogan, 2001). As these small deviations may result from motor output noise alone, it is not possible for the motor system to predict the forces that will act on the hand. In this situation stability can be improved by cocontracting the muscles in the arm, increasing the stiffness ('impedance') at the hand and so reducing the effect of the destabilizing forces. This impedance control

Figure 4. Motor adaptation and impedance control during reaching movements
A, typical hand trajectories for out-and-back movements to targets (red) on first exposure to a velocity-dependent force field (top) and after 20 movement blocks (sets of 8 targets) in the field (bottom). Arrows (green) indicate the direction of force during outward movement. The increase in movement accuracy with training results from a strategy of motor adaptation, in which appropriate forces are generated to counteract the predictable force field. *B*, hand trajectories on first exposure to a divergent force field (top left), and after 100 movements in the field (top right). In this unpredictable force field, increased movement accuracy reflects a strategy of impedance control. Stiffness ellipses (bottom) indicate restoring force to a step displacement of the hand in different directions, before and after training. The increase in stiffness is tuned to the direction of maximum instability, perpendicular to the direction of motion (black arrow). Adapted with permission from Burdet *et al.* (2001).
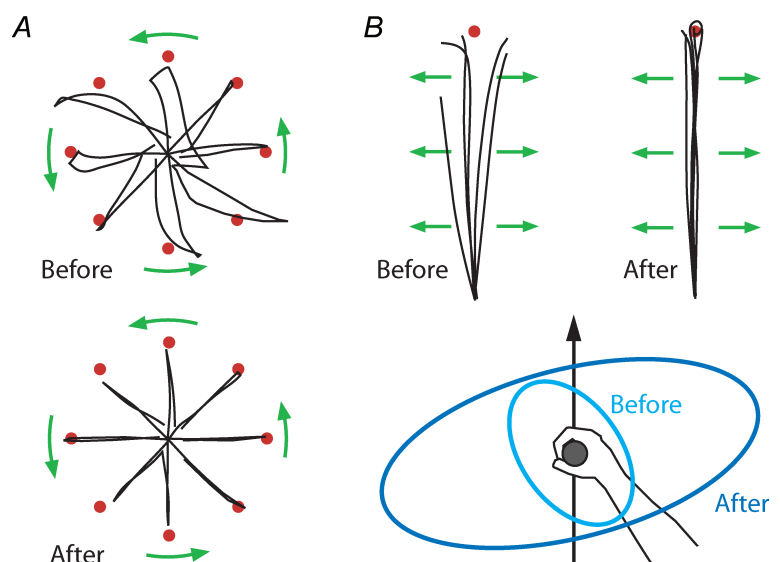
strategy was investigated by Burdet *et al.* (2001) by asking subjects to make reaching movements in a destabilizing force field generated by a robotic manipulandum (Fig. 4*B*, top). Deviations of the hand from a straight line resulted in forces on the hand in the same direction, creating an unstable dynamic environment. After initial errors, subjects responded by cocontracting muscles in the arm in such a way as to increase stiffness only in the direction perpendicular to motion, i.e. in the direction of the external force (Fig. 4*B*, bottom). Compared to stiffening equally in all directions, this task-specific control strategy not only decreases metabolic cost, but may also increase movement accuracy, as motor output noise increases with muscle activation.

Impedance control can be a valuable strategy even when faced with a predictable dynamic environment. In the initial stages of exposure to a novel force field, subjects respond by cocontracting arm muscles to increase stiffness; as adaptation progresses, high stiffness becomes unnecessary and levels of cocontraction systematically decrease (Thoroughman & Shadmehr, 1999; Wang *et al.* 2001). Even when dealing with a known dynamic environment, such as when manipulating a familiar object, uncertainty in state estimation means that compensation based on an inverse model will always be imperfect. The motor system's response to such uncertainty has been investigated using force fields that vary in strength from movement to movement. If the field strength on each movement is drawn from a Gaussian distribution, subjects learn to compensate for the mean force experienced over the previous few trials, while increasing stiffness to counteract the effects of variability about the mean (Scheidt *et al.* 2001; Takahashi *et al.* 2001). The two control strategies of motor adaptation and impedance control are therefore employed in parallel to minimize the effects of uncertainty and variability in the dynamic environment.

Conclusions

In this brief review we have introduced some of the computational principles revealed by the experimental study of motor control. Recent approaches have begun to emphasize that noise in sensory inputs and motor outputs as well as uncertainty about the environment are crucial in determining neural processing. Two broad classes of computational approach have emerged as pre-eminent. First, the principle of optimality has been shown to play a role both in minimizing uncertainty in sensory estimation, through optimal integration and Bayesian inference, and in minimizing variability in motor output, through optimal control. Second, internal models are implicated both in filtering sensory inputs, using sensory predictions generated by the forward model, and in minimizing movement errors due to variability

in the environment, through adaptation of the inverse model.

While great advances have been made in our understanding of these topics at a computational level, our knowledge of the underlying neurophysiology is much less complete. In particular, we currently have very little idea how the algorithms underlying optimal integration and optimal control are realized at the neuronal level. It is to be hoped that future research will reveal a unifying framework in which both the computational and physiological bases of sensorimotor control can be understood.

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