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Representations of uncertainty in sensorimotor control

Gergő Orbán and Daniel M Wolpert

Uncertainty is ubiquitous in our sensorimotor interactions, arising from factors such as sensory and motor noise and ambiguity about the environment. Setting it apart from previous theories, a quintessential property of the Bayesian framework for making inference about the state of world so as to select actions, is the requirement to represent the uncertainty associated with inferences in the form of probability distributions. In the context of sensorimotor control and learning, the Bayesian framework suggests that to respond optimally to environmental stimuli the central nervous system needs to construct estimates of the sensorimotor transformations, in the form of internal models, as well as represent the structure of the uncertainty in the inputs, outputs and in the transformations themselves. Here we review Bayesian inference and learning models that have been successful in demonstrating the sensitivity of the sensorimotor system to different forms of uncertainty as well as recent studies aimed at characterizing the representation of the uncertainty at different computational levels.

Address
Computational and Biological Learning Lab, Department of Engineering, University of Cambridge, Trumpington Street, Cambridge CB2 1PZ, UK

Corresponding author: Wolpert, Daniel M (wolpert@eng.cam.ac.uk)

When a batter takes a swing at a ball, inference, decision-making, and action planning go hand-in-hand to perform the movement. Uncertainty arises at all levels of this process [1]. Inference is uncertain, for example, because sensory inputs are noisy, delayed, and may require transformations to obtain relevant variables (e.g. depth estimation from binocular cues). In addition, the model of the environment is also uncertain, requiring the batter to estimate properties of the gusting wind, as well as how this will interact with the rotating ball. Finally, motor execution introduces other sources of uncertainty. For example, motor commands are themselves noisy and need to be anticipatory as they are issued long before they have an effect due to the long motor delays. Understanding and characterizing these different forms of uncertainty is necessary if the goal is to achieve optimal performance.

Bayesian framework

Uncertainty can arise from both random processes, such as noise reflecting unpredictable fluctuations on a signal, as well as from nonrandom processes, such as ambiguity as to the weight of a can one is about to pick up. Bayesian statistics formalize the optimal strategy under circumstances where noise and ambiguity are present. Both noise and ambiguity render our inferences about important variables of the environment (e.g. spin of the ball) uncertain, which is reflected in the inference. Crucially, the end result of Bayesian inference is not a single estimate of the value we are interested in. Instead it provides an estimate of the probability of each possible value (e.g. each possible spin of the ball) being correct, termed the posterior probability. Calculating such a posterior requires the representation of two different forms of information. First, the *a priori* probabilities of each setting of the variables are represented by the prior distribution (e.g. faster spinning balls may be less common than slower spinning balls). Second, the link between different settings of the variable and the sensory information needs to be known. This allows one to calculate how probable the sensory input is for different possible states of the world (termed the likelihood) — for example, a curved trajectory of the ball is more likely if the ball is spinning than if it is not. The posterior can then be estimated by multiplying the prior by the likelihood for each setting of the variable (and normalizing the result to sum to a probability of one over all possible settings). In recent years, evidence has been accumulating that both uncertainties arising in the sensory system and those resulting from the task being performed are optimally integrated in a way that is consistent with Bayesian processing [2–4]. These studies suggest that the sensorimotor system represents both the statistics of the task (prior) as well as the statistical relation between variables and sensory feedback (to calculate the likelihood) and combines these two sources of information in a Bayesian fashion.

In general, making a decision about the preference of alternative actions requires that the entire distribution of possible values is taken into account. The extension from making inferences about variables to choosing a single best estimate or optimal action is bridged by the concept of a loss function. The loss function specifies the penalty for taking a particular action if a particular value were true. If one knows the posterior and the loss function it is possible to determine which action will lead to the smallest average loss, and this can be considered as the optimal action. Several studies have imposed explicit loss functions in sensorimotor tasks and shown that the actions selected are close to optimal [5,6], although some people

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are willing to accept a higher average loss if it reduces (risk-averse) or increases (risk-seeking) the variance of their loss [7,8].

The application of Bayesian inference and decision theory to a dynamical system such as the human body has led to the framework of optimal feedback control (OFC) [9]. OFC proposes that the sensorimotor system sets up an optimal time-varying feedback controller to minimize a cost (loss) function. This framework has started to tie together previously disparate areas such as planning, on-line control, coordination, and the interaction of effort and noise (for reviews see [10–12]). An elegant aspect of OFC is that it avoids the need to specify hard constraints on task goals, in that it uses a single mixed cost function that is usually a combination of accuracy (positional, velocity, etc.) and effort. The relative importance of each of the components of this cost has been shown to be altered by task requirements or by instructions [13••]. Solving for the optimal feedback controller is possible for linear systems, and efficient approximations are now available for nonlinear systems [14]. The end result is a time varying feedback controller that uses an estimate of current state, obtained from noisy and delayed feedback as well as efference copy, to generate the motor commands. The feedback gains on state variables such as position, velocity, and muscle activation, typically have complex temporal profiles, which determine the way the movement evolves. Although OFC specifies the optimal command, motor noise will corrupt the command (Figure 1a) leading to performance variability. The framework explains a wide range of observations and has made a number of testable predictions, many of which have been verified (e.g. [13••,15•,16–21]).

Even before the motor system decides to act, a decision must be made, for example, choosing the target of the action. Such decision-making has a long history of study in the form of drift-diffusion models in which noisy evidence in favor of one target versus another is accumulated over time until a decision boundary is reached [22,23]. Such models can explain both the time to reach decisions and their accuracy as a function of stimulus quality. Drift diffusion models can be optimal in terms of making the fastest decisions (on average) for a given level of accuracy [24]. Because our sensory apparatus is attached to the motor apparatus, the initiation of an action often removes the sensory input stream that led to the action. For example, when we initiate a saccadic eye movement we terminate any visual input which led to the decision to move. However, as there are substantial delays in the sensorimotor system it will always be the case in these situations that having initiated movement there are a few tenths of a second of sensory information which were not used to initiate the decision but could still be in the processing pipeline to guide the action. A recent study shows that this information is processed and can

even lead to subjects changing their mind mid-movement, usually to correct an error but also sometimes to spoil a good start [25•]. The pattern of changes was well accounted for by a modified drift-diffusion model in which integration continues after the initial decision and the decision reversed if a new change-of-mind bound is crossed.

Inference and learning

Crucially, Bayesian inference assumes the existence of internal models that describe how *states* of the environment (including our body) give rise to observed patterns of sensory stimuli and how *parameters* of the environment affect the resulting stimuli. For example, the state is a set of variables that characterize the moment-to-moment variation in task-relevant variables such as the position and velocity of the hand (Figure 1b). In contrast, the *parameters* reflect properties of the environment that change on a slower time-scale, for instance the weight of a can (Figure 1c). Finally, the *structure* represents the form of the equations of motion and the relevant inputs and outputs. The model defines which parameters, such as mass or moment of inertia, are relevant in determining the behavior of a can or a power tool upon acting on them, and the structure can represent the dynamics of cans as opposed to the dynamics of a power tool (Figure 1d). Inference involves learning the correct structure, its parameters, and estimating the evolving state. An important consequence of Bayesian inference at these three levels is that there are clear interactions. For example, as states and parameters both require inference, any uncertainty in parameters will also affect subjective uncertainty of inferred states [26]. In the following sections we discuss the forms of uncertainties that arise at the levels of states and parameters.

State uncertainty during inference

Uncertainty in the state of the environment and of our body is an important feature of sensorimotor control (Figure 1b). The central nervous system seems to have knowledge of its own sensory [2] and motor uncertainty [6], as well as how these uncertainties evolve over time [27,28] and is close to optimal in using this information in both estimation and control. A major challenge in everyday tasks is that actions are performed in an environment in which evidence is continuously accumulated and the reliability of different sources of information can change, therefore the uncertainty associated with predictions and inferences must also change. In such situations, motor plans can be modified on-line when changes occur in the reliability of the sensory inferences [29] or in the reliability of the predictions of sensory feedback [21].

Parameter uncertainty and learning

When learning a novel task, parameters that characterize the task are unknown but subjects already have priors over these parameters (Figure 1c). During the early stages

Figure 1
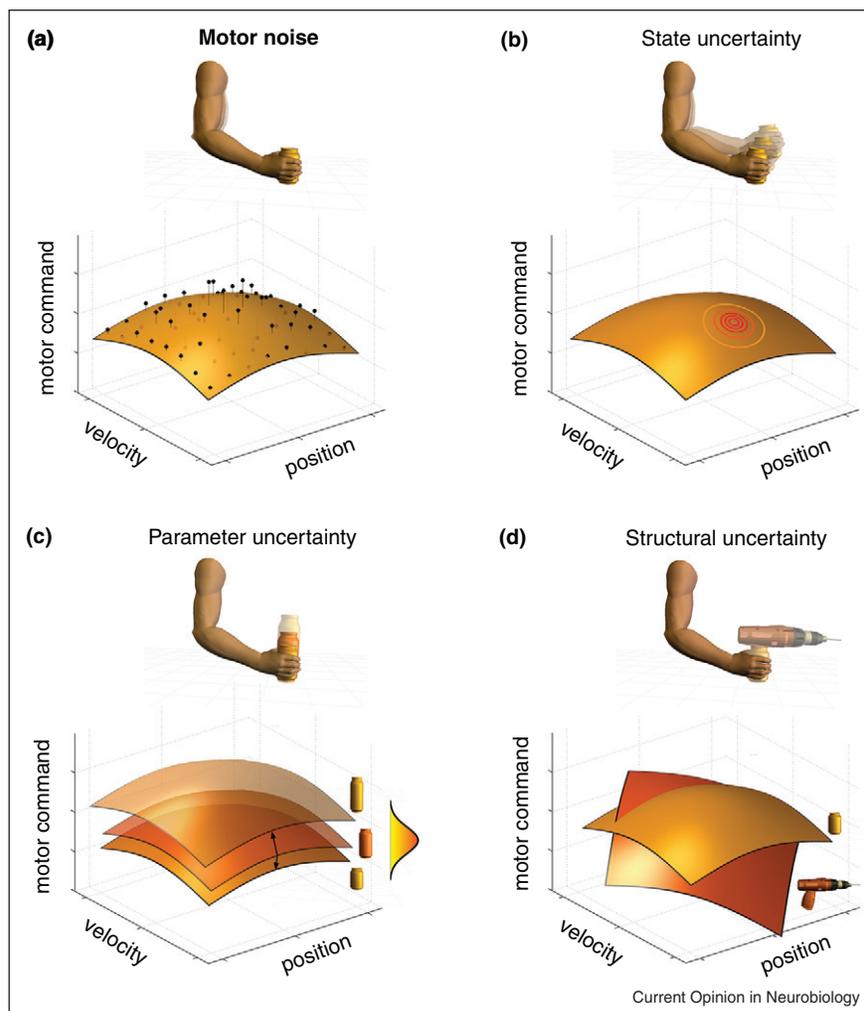
Schematic of a feedback controller and different forms of sensorimotor uncertainty. Given a task such as lifting a can, a controller may specify the motor command (yellow surface) as a function of state variables, the hand position and velocity, at a given point in time. **(a)** Motor noise will introduce random deviations (black dots) from the optimal command (orange surface), typically with larger deviations for larger motor commands. **(b)** State uncertainty. As sensory inputs from proprioception and vision are noisy, there is uncertainty when inferring the state, and Bayes rule results in a posterior probability distribution over possible states (contour lines with posterior probability increasing from gold to red). **(c)** Parameter uncertainty. If the settings of the dynamics of the body or the characteristics of the task are unknown this introduces parameter uncertainty. For example, for different masses of a can, the desired motor commands will change. For the simple task of lifting a can, its mass may simply scale the desired motor command (surfaces represent the command for cans of three different weights). Similar to state uncertainty, all possible parameter settings need to be considered. The final command may then be a weighed sum of the motor commands for each mass, with the weighting reflecting the respective posterior probabilities of that parameter (inset shows a weighting across motor commands surfaces). **(d)** Structural uncertainty occurs when there is uncertainty as to the equations of motion themselves. For example the dynamics of a power tool are different from those of a can giving strikingly different relations between states and motor commands (golden and bronze surfaces), and these different structures need to be identified and learned. The set of relevant parameters will depend on identifying the structures.

of learning there is likely to be high uncertainty over the parameter estimates and even after extensive learning, although the estimates may improve, uncertainty always remains. The way that subjects update their internal models in the face of errors, particularly at the beginning of learning, can reveal the priors over the parameters of the internal model. For instance, when subjects are exposed to a novel force field that depends only on the position or only on the speed of the hand, the initial adaptation is biased toward an interpretation that the force field depends on both position and speed [30]. Only through extensive training does the model reflect only position or speed-dependent forces. The interpretation of these results is that there is a strong prior that forces experienced by the hand will depend on both position and velocity in a correlated manner. Supporting this view is that forces which depend on both position and velocity in a correlated manner are easiest to learn, whereas those

that depend on position and velocity in an anti-correlated manner are hardest to learn, and those that depend on either position or velocity alone are of intermediate difficulty.

The structure of errors can be informative as to the uncertainty in the internal models controlling action. For example, in saccadic adaptation experiments [31], even when the average error across trials is the same, reliable errors result in a high level of adaptation, whereas more variable errors cause no adaptation [32]. This result highlights that the reliability of the internal model also has an effect on planning motor actions in that visual errors do not simply drive adaptation according to their magnitude, but adaptation depends on the reliability of the errors, consistent with Bayesian model learning. Similarly, the errors can be informative about the parameter settings of a task. For example, a recent study has examined how the errors could be used to estimate a varying parameter, that is the magnitude of a visuomotor rotation (between the hand and its displayed position) that was drawn randomly from a set of possible rotation for each movement [21]. In this situation the OFC not only has to generate appropriate time-varying gains but also needs to determine the parameter of the internal model, that is the current visuomotor rotation. The OFC model was extended to perform this inference. To be able to account for the experimental data it was necessary to use the model uncertainty, as reflected in the ability of the model to predict the incoming sensory data, to decrease the feedback gains in the presence of high uncertainty.

Uncertainty in the internal model may also be reflected in the nervous system's use of impedance (stiffness) control to change the dynamic properties of the body. During the early stages of dynamic (force-field) learning, the stiffness of the arm is increased through co-contraction. This reduces the positional effect of a perturbation but at the cost of increased effort. As the internal model is learned and used to directly compensate for the perturbation, the impedance of the arm reduces [33,34]. Examining impedance control under circumstances where task variables fluctuate shows that impedance decreases in parallel with the adaptation of the internal model [35]. Because of sensorimotor noise and time delays, even a perfect internal model may not be sufficient for control. For example, when using a knife to cut through an apple, deviations from the top of the apple can lead to the knife slipping. However, as the slip can be to the left or the right, and this is only sensed with a time-delay, using an internal models to compensate for the slip may be too late. In such situations it has been shown that the stiffness of the arm can be increased in the direction of the instability so as to reduce deviations only in the task-relevant direction [36,37]. These results indicate that uncertainty in both states and parameters of the internal models are reflected by controlling arm impedance by the

nervous system. A recent study has made a promising start toward integrating impedance control within the OFC framework by formulating impedance control as the optimal response in the face of uncertainty about the dynamics of the body and environment [38•].

Structural learning

While the majority of sensorimotor tasks are phrased as learning parameters (e.g. the mass of a can, Figure 1c), many tasks have also have uncertainty in the structure (e.g. whether we are holding a can or a drill, Figure 1d). Again, within the Bayesian framework if we can assign probabilities to different possible structural models, we can choose the action that has the lowest loss averaged across the possible models. Equivalent problems arise in human cognitive learning, where the structure underlying observed data needs to be inferred: while in cognitive learning causal or similarity relationships need to be inferred from observations, in motor learning dynamic relationships need to be inferred from movement errors. Recently, powerful techniques have been developed that match some important features of human capabilities in tasks that require structure learning [39,40]. Bayesian model learning in humans has also found support in a range of phenomena including causal learning in adults [41] and infants [42]; and in learning the structure of novel visual stimuli [43,44].

In sensorimotor control there is evidence (e.g. the learning to learn phenomenon) that provides indirect support to the idea that structural learning is a crucial component of human learning (for a review see [45]). A recent set of studies have directly examined structural learning showing that learning in a sensorimotor task can be best described by Bayesian model learning [46•,47]. Also, human performance has been shown to reflect some key aspects of model learning, including the facilitation of learning tasks with a statistical structure shared with previously trained models; and decreased interference between tasks corresponding to different internal models. These studies provide strong evidence that representations of model uncertainty and Bayesian model learning are part of the computational repertoire used by the nervous system during motor learning.

Neural representation of uncertainty

Relating neural activity to various components of sensorimotor control has seen considerable progress in recent years (e.g. [48]). However, identifying the neural substrate for the representation and manipulation of sensorimotor uncertainty is a far harder problem and is likely to need substantial input from theories of neural computation. Several models have recently been developed to reproduce computations that have been supported by behavioral studies, such as state-estimation [49] and decision-making [22]. For example, a neurally inspired model has been developed to perform state-estimation by

implementing a Kalman-filter in a network that can be mapped onto cortical circuits, under the assumption that the uncertainty is predefined and Gaussian [50]. In addition, neural models have been developed that are capable of representing and using uncertainty in decision-making [51•]. Currently it is unclear how these models can be generalized to represent more complex forms of uncertainty and to tasks where the number of state variables is increased.

A recent study suggested that the prior distribution over visual scenes is represented in the distribution of spontaneous activity in visual cortical neurons in the absence of the visual input, that is in the dark [52••]. In the presence of a visual input, the distribution of evoked activity patterns in these same neurons then represent the posterior probability distribution that results from inference about the visual scene. Importantly, this result highlights that response variability (as reflected in the distribution of evoked activity patterns) might reflect uncertainty in inference. The difference between spontaneous (prior) and evoked activity (posterior) in visual cortex may have correlates in premotor cortex where activity pre-movement reflects a set of possible actions and activity during movement is then narrowed to one particular movement [53••]. The link between neural response variability and posterior uncertainty may be a general principle of neural processing. This is supported by studies which show that when a stimulus is presented the variance of firing rate drops significantly irrespective of the task being performed and the brain area being recorded [54], consistent with the prediction of a broad class of probabilistic models where a wide prior distribution shrinks into a posterior upon stimulus presentation [26].

Most studies examining the neural representation of uncertainty have focussed on state uncertainty, and are yet to address the representation of parameter and structural uncertainties, which are likely to require further theoretical advancements. Importantly, a model of the neuromodulatory system indicates that norepinephrine might signal unexpected uncertainty (that is errors larger than expected) [55]. As pointed out above, reliability of errors may be an important indicator of model uncertainty, therefore norepinephrine may provide the nervous system with a signal to rate the quality of uncertainty, and thus to represent model uncertainty.

Conclusions

Normative models — that is those based on the principle of optimality — of sensorimotor control have been immensely successful in explaining various aspects of motor control both in humans and in other animals. Optimal behavior is not necessarily ubiquitous in every task under every condition [56]. There are two reasons, however, to formulate perception, decision-making, and action in terms of normative principles: first, it is striking how many phenomena fits comfortably within this framework; second, establishing optimality criteria helps to identify the proxies and approximations applied by the nervous system to achieve efficient performance. Neural implementations that can represent different forms of uncertainty including state, parameter, and model uncertainty remain a challenge to computational theories, but progresses in this direction are promising.

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