Bayesian Models of Motor Control

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Motor control is fundamental to the nervous system: only through our movements do we interact with the world. Many models of motor control assume that of all the ways we could move, we typically choose one of the best. This implies that we can have a ‘notion’ of how bad one movement is in comparison to other possible movements. Within the framework of decision theory, this notion is formalized by a cost function that assigns a numerical value to every possible movement. The right movement decision seems simple: choose the action \( a^* \) that has the lowest associated cost. This decision process can be compactly described by the equation,

\[
a^* = \arg \min_a \text{cost}(a)
\]  

For example, several studies have proposed that people move their hand from one position to another in a fashion that is as ‘smooth’ as possible. Thus, the cost function penalizes movements that are not smooth. It was found that many properties of human reaching movements, such as the velocity profiles, can be well predicted by such cost functions.

This framework assumes that we can deterministically choose a movement and be sure of its outcome. Yet, most motor outcomes are affected by uncertainty. To illustrate, if we aim at the center of a dartboard, we are not certain to hit the bullseye with the dart (even if we are a seasoned champion). If we continue to aim at the center and throw many times, we will end up with a distribution of dart positions. This distribution, \( p(x|a) \), characterizes the likelihood of each outcome, the dart position \( x \), given that we chose action \( a \), the aiming point. This affects how we should choose the best action, the one that minimizes our likely cost:

\[
a^* = \arg \min_a \left( \sum_{\text{possible outcomes}} \text{cost} (\text{outcome}) \ p(\text{outcome}|a) \right)
\]  

In other words, we should choose the action that minimizes our expected cost. In the example of playing darts, the best aiming point is a point where we will receive high scores even if we make large mistakes. Indeed, both amateur and world-class players are known to adopt a strategy that is well predicted by this approach.

While playing darts, the errors largely stem from motor noise (Figure 1(a)). However, there are many sensory sources of uncertainty as well. For example, our visual system is noisy and the location of the dartboard relative to our body is thus uncertain (Figure 1(a)). Moreover, our proprioceptive system is noisy as well; the exact configuration of our body as we release the dart is uncertain (Figure 1(a)). These sources of uncertainty combine to produce uncertainty in the movement outcome given our movement decision.

The difficulty in treating these movement decisions is that the probability of an outcome given our action decision \( p(x|a) \) is generally difficult to compute. The problem is that computing this distribution requires the specification of information that is generally uncertain. This includes information about our body as well as the external world. Bayesian inference specifies how such pieces of information should be combined. It thus predicts how pieces of information should be integrated to allow for motor control that minimizes our cost.

Bayesian Integration

Combining uncertain information to produce a coherent and accurate estimate of the world is a central problem faced in motor control. A number of psychophysics studies have analyzed how people integrate multiple sources of uncertain information to make sensorimotor decisions.

Combining Prior Knowledge with New Evidence

As an example of how we integrate uncertain information to estimate the world, consider the game of tennis. When playing tennis, it is helpful to estimate where the ball will land. Vision does not provide perfect information about the ball’s trajectory or velocity, and we are thus uncertain where the ball will land. The visual system, although noisy, still provides us with an estimate, or likelihood, of where the ball will strike the court. This likelihood is the probability of having a particular sensory input for each possible location the ball may land (Figure 1(b)).

This knowledge may be combined with information obtained from experience: the locations where the ball may land are not uniformly distributed over the court. The locations are usually concentrated within the confines of the court and may be highly peaked near the baselines where it is most difficult to return the ball. This distribution of positions is called the prior (Figure 1(b)). Bayes’ rule defines how to combine the prior and the likelihood to make an optimal estimate of the location where the ball lands (Figure 1(b)).
Bayes’ rule states that the probability of the ball landing at position $x$ given our observation $o$ is the product of the prior probability of the ball at $x$, with the likelihood of the observation $o$ given the position $x$, divided by the probability of the observation:

$$p(x|o) = \frac{p(x)p(o|x)}{p(o)}$$  \[3\]

The distribution produced by eqn [3] is shown graphically Figure 1(c). We can also interpret Bayes’ rule as the ‘optimal’ means of combining a prior and a likelihood as it produces an estimate with the minimum uncertainty. A few studies have shown that when people combine prior and new information, their behavior is close to that predicted by Bayes’ rule. Peoples’ ability to integrate priors and likelihoods in a manner that is close to the optimal prediction by Bayes’ rule has been shown in many modalities.

A typical study will let people use a motor task to indicate their estimate of the location of a target. In every trial, this location will be drawn from a Gaussian probability distribution (the prior). One group of subjects experience a narrow target distribution and thus have a narrow prior. A different group of subjects will experience a wide target distribution, thus having a wide prior. Bayesian statistics predicts how subjects should combine the likelihood with the prior. These predictions are then compared to human performance.

Such paradigms have been applied to numerous estimation problems. Sensorimotor integration, force estimation, timing estimations, speed estimations, the interpretation of visual scenes, and even cognitive estimates are examples. These studies jointly demonstrate that people are very good at combining prior knowledge with new evidence in a way predicted by Bayesian statistics.

**Cue Combination**

In many cases, it is not prior knowledge that is combined with a likelihood but, rather, two different cues that are combined into a joint estimate. For example, we may see and feel an object at the same time. We can then use what we saw and what we felt to infer the properties of the object. Bayesian statistics allows us to also solve these problems and the posterior is simply the product of the likelihoods (Figure 1(d)). Some studies have found that people are also optimal at this combination.

As a typical study, we consider an analysis of how people combine visual and auditory information to estimate the position of a target. In such a study, the precision of visual and auditory perception is
measured for each subject (unimodal). Subsequently, the precision and accuracy of perception is measured when subjects can use both modalities (bimodal). The performance in the bimodal trials can be predicted from the unimodal trials using Bayesian statistics.

As with studies investigating prior–likelihood integration, such a paradigm has been applied to numerous cue combination problems. It has been applied to the combination of visual and auditory information as well as tactile and visual information. It has also been applied to several cases in which two pieces of knowledge from the same modality are combined. For example, texture and stereo disparity are both cues for estimating the depth of a visual object. In all tested cases, cues are combined by the subjects in a manner that is close to the optimum prescribed by Bayesian statistics.

Bayesian Integration over Time

The state of the world and our information about it are continually changing. We thus constantly need to integrate this new information with our current beliefs to inform our estimates of the world. This implies that Bayesian integration should take place in a continuous manner.

This approach is extensively taken in modern applications of control theory. Many of these applications are built on the idea of Kalman filtering, which is a method for using an error in our prediction of the world to continuously update our beliefs (Figure 2(a)). This technique, although not usually described as such, is equivalent to a sophisticated application of Bayesian statistics. At every time step, a Kalman filter combines its estimate of the world’s state (the prior) with a measured observation (the likelihood) to update the prediction of the world’s current state, represented by a posterior (Figure 2(b)). This formalism is well developed and used in a wide range of applications from aeronautics to humanoid robotics. Indeed, even the motor control problems of two applications as disparate as controlling a jet and controlling our bodies share many computational analogies. In both cases, continuously incoming information needs to be assessed to move precisely (albeit on different timescales). Only recently has this methodology of Kalman filtering been applied to make quantitative predictions of human movement behavior.

A number of studies have examined how subjects integrate information in a continuous fashion. These studies have compared the way in which subjects move with the predictions of optimal Bayesian models. They have found close agreement between the predictions of the optimal theory and the way movements are actually executed.

As an example of this problem, we consider a recent theory of motor adaptation. The properties of our muscles change continuously throughout our lives. Over several timescales, muscles change – fatigue over the course of hours, disease over the course of weeks, and aging over many years. This means that we must estimate the strength of our muscles if we are to move precisely. The error in our estimate of the strength of our muscles will translate into a movement error. We can use this error to obtain a likelihood function characterizing the strength of the muscles. According to Bayesian statistics, we need to combine the newly obtained information, our motor error, with our prior belief. We can thus infer a new and improved estimate (Figure 2(c)). Often, adaptation is probed using a target jump paradigm. In these paradigms, an experimental manipulation is used to change subjects’ perception of the strength of their limb. In these circumstances, Bayesian statistics predicts that

Figure 2  (a) Typical procedure for optimally estimating the world’s state in modern control theory. A model of the world, combined with a motor command, is used to estimate a predicted state, or prior distribution (green). Observations of the world dictate the likelihood of a particular observation given the current world state (red). A Kalman filter is used to make a Bayesian update of our belief in the world’s current state (blue). (b) This process of Bayesian inference repeats itself at each time step. (c) Motor adaptation can be framed as an analogous update procedure. Our prior belief of muscle strength (green) is integrated with our observed motor error (red) to update a belief of our muscle’s strength.
Bayesian Inference of Structure

We previously discussed how people combine two cues into a joint estimate using Bayes' rule. The application of these models implicitly assumed that we are certain that both cues have a common source: if we hear a tone while seeing a flash, we assume that both of the cues originate at the same position and have a common cause. This idea has been used very successfully for describing human behavior in cue combination experiments.

Although successful as implemented thus far, these probabilistic models have obvious shortcomings. For instance, we know from experience and experimental studies that if two cues are very dissimilar our perception of unity breaks down. If we see a flash far to our right while perceiving a tone far to our left, we perceive two independent events. We infer the structure of events; we estimate if two events have a common cause or if they just randomly co-occur. This implies that if two events are perceived as having a common cause, they should influence the perception of each other. On the other hand, if they are perceived as not having a common cause, the perception of each should be independent of the other. In some circumstances, the cues can create an illusion of a common cause, the so-called ventriloquist effect.

Traditional Bayesian models of psychophysical behavior are unable to explain this range of phenomena. Indeed, experiments that tested these models used cues that were close to coincident. For example, the position of a visual stimulus was close to the position of an auditory stimulus.

Other studies have tested subject performance in situations in which two cues are dissimilar from one another. A typical study will present a visual stimulus at a random position within the visual field and simultaneously present an auditory stimulus at a different random position. Subsequently, subjects are asked where they perceive the stimuli.

These studies have found that when two stimuli are near coincident, people tend to infer a common cause and use each cue to guide estimation of the other. With increasing disparity between the cues, subjects' belief in a common cause decreases (Figure 3). Traditional Bayesian models predict that in the case of Gaussian likelihoods the estimate of the value of one cue should be linearly influenced by the value of the other cue. In sharp contrast to these predictions, experiments have found nonlinear cue interactions. These interactions are well predicted if we assume that on each trial the subjects infer a common or distinct cause for both cues.

These effects are found in a wide range of experimental situations. They have been found in position estimation using visual and auditory stimuli, in the estimation of depth from several cues, and also in number estimation using visual, tactile, and auditory stimuli. Evidence suggests that subjects integrate not only priors and likelihoods but also the causal structure underlying a set of sensory stimuli.

The statistical problem that subjects solve in cue combination implicitly involves an inference about the causal structure of the stimuli. In these studies, people are uncertain about the identity and number of relevant variables; for example, did the flash of light cause the auditory tone, did the tone cause the flash, was there an unknown cause for them both, or were they simply coincidental? The problem faced by the nervous system is thus similar to cognitive problems that occur in the context of causal induction. Many experiments demonstrate that people interpret events in terms of cause and effect. The results presented here show that sensorimotor integration exhibits some of the factors that make human cognition difficult to understand. Carefully studying and analyzing seemingly simple problems such as cue combination may provide a fascinating way of studying the human cognitive system in a quantitative manner.

Future Directions for Bayesian Inference

The Bayesian models reviewed so far do well at predicting the results from many experimental studies of motor control. Whereas in theory Bayesian statistics' applicability is rarely limited, in practice there are many cases in which this technique is hindered.

Most of the previously discussed Bayesian models assume that noise sources are Gaussian and that the interactions between the subject and the world are linear. Recent approaches in Bayesian statistics allow the application of powerful framework well beyond these simple assumptions. For instance, the structure inference problem is a simple case of non-Gaussian...
probability distributions. The techniques that may be applied to such problems range from linearization techniques such as extended Kalman filters over variational techniques to particle-filtering methods. The specialized Bayesian literature deals extensively with such computational difficulties.

Bayesian inference allows us to estimate the present state of the world given all the sensory observations we have obtained from the past until now. If the problem we are faced with requires making only one decision at a single point in time (static problem), then decision theory (see eqn [2]) readily allows us to decide optimally. Yet, movement is fundamentally a sequential decision (dynamic) problem. Any motor command we produce in the present influences the situations in which we will find ourselves in the future. This implies that motor commands are not independent from each other but, rather, each command must be viewed in the context of all possible future situations it may direct us.

Optimal control theory is the systematic study of problems of this class. Often utilizing a Bayesian framework, it employs analytical and numerical techniques to solve the motor control problem. For the set of problems in which dynamics are linear, noise is Gaussian, and cost functions are quadratic, optimal control provides efficient solutions. Much research addresses ways of extending the approaches to more complicated problems. Typical applications involve the control of humanoid robots and the control of aircraft. The theory is complex and beyond the scope of this article. Advances in optimal control coupled with advances in Bayesian methods hold promise for allowing progressively more complicated movement behaviors to be analyzed and predicted.

**Discussion**

Much if not most of neuroscience is driven by postulates regarding the problems the nervous system is
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Bayesian models prescribe how the nervous system should behave, as opposed to neural modeling, which describes how the nervous system behaves. To clarify the distinction, models derived from meaningful descriptions of the problem to be solved should be considered normative or prescriptive. For example, some theories of movement assume that people try to move as smoothly as possible, and these models explain a large amount of experimental data. However, there is no explicit reason why smooth movements would be better than similar but less smooth movements. Perhaps more to the point, these models do not yield insight on why subjects move the way they do. In the case of smooth movements, research demonstrated that a different cost function, clearly tied to the movement problem, could also predict the data; optimizing movements for precision naturally leads to smooth movements—a cost function that is of obvious importance.

A different way of modeling the properties of the nervous system is the so-called ‘bottom-up’ approach. Numerous measured or inferred properties of neurons are used to run comprehensive computer simulations of neurons within expansive networks, the results of which are meant to mimic the actual nervous system. This approach relies on the accurate knowledge of many system parameters—a formidable requirement. Furthermore, in large, complex systems such as these, small deviations in parameters can result in gross and qualitative differences from the actual system being emulated—in this case the nervous system. Even in areas where bottom-up modeling is practical, such as action potential propagation in squid giant axons, normative models may contribute to an understanding of the system. It has been conjectured that the density of sodium channels is optimally adapted to maximize the speed of action potential conductance, very possibly the result of evolutionary pressures to minimize the flight response time. This is of obvious normative reasoning because fleeing fast from approaching predators can mean the difference between life and death. Normative modeling of low-level cellular properties is possible and in close analogy with the normative ‘top-down’ modeling of behaviors made by decision theory.

Bayesian integration offers a computational framework for combining various sensory information, from multiple modalities and different points in time, into a joint estimate of the world. Consistent with these ideas, unimodal brain regions are known to be affected by uncertainty. For example, primary visual cortex is influenced by the statistics of a stimulus. Multimodal regions that combine information are similarly influenced by probabilities. Prefrontal, temporal, and parietal cortices are likely to exhibit similar statistical principles. Crucial in the timing of motor behaviors and motor learning, the cerebellum’s function can also be explained in Bayesian terms. Interestingly, however, even cortical regions traditionally thought of as unimodal, such as primary visual and auditory cortices, have been shown to be responsive to multiple sensory modalities and receive projections from multiple sensory regions. Taken together, the functional and anatomical connectivity of the brain is consistent with the multimodal computations necessary for Bayesian inference. Considering how salient the problem of uncertainty is, numerous, if not all, brain regions can be expected to utilize Bayesian statistics to reduce uncertainty.

Bayesian statistics and normative modeling hold promise for many areas of neuroscience because they formalize the problems the nervous system needs to solve while addressing the inherent uncertainties. Normative models have few free parameters in comparison to neural models—radically simplifying their application. Moreover, normative modeling is synergistic with neural modeling; combining the two techniques will provide models that not only predict but also explain neural behavior. By quantitatively predicting behavior from these normative–neural models, we can develop a deeper understanding of the problems being solved by the nervous system. This will also allow us to ask better, more informed questions in future neuroscientific experiments.

See also: Bayesian Cortical Models; Computational Approaches to Motor Control; Motor Psychophysics; Sensorimotor Integration: Models.

Further Reading
