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# Computational motor control in humans and robots
## Stefan Schaal and Nicolas Schweighofer

Computational models can provide useful guidance in the design of behavioral and neurophysiological experiments and in the interpretation of complex, high dimensional biological data. Because many problems faced by the primate brain in the control of movement have parallels in robotic motor control, models and algorithms from robotics research provide useful inspiration, baseline performance, and sometimes direct analogs for neuroscience.

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## Introduction
The theory of motor control was largely developed in classical engineering fields such as cybernetics [1], optimal control [2], and control theory [3,4]. These fields have addressed many crucial issues, such as negative feedback and feedforward control, stochastic control, control of over-actuated and under-actuated systems, state estimation, movement planning with optimization criteria, adaptive control, reinforcement learning, and many more. From the viewpoint of computational neuroscience, an interesting question is in how far the insights, methods and models developed in engineering sciences also apply to motor control in biological organisms. The answer to this question is not always clear. On one hand, the distributed processing in the nervous system often does not enable us to classify control strategies according to the crisp definitions and 'box charts' of engineering domains. On the other hand, evolution has probably come up with a variety of control strategies that have not yet found parallels in engineering. Nevertheless, in certain instances, most researchers agree that strategies of biological motor control resemble methods of control theory, as in the example of time-delayed systems, in which feedforward control with predictive state estimation is a common concept. An extended discussion of such issues can be found in an excellent recent textbook on computational motor control [5•].

The view taken here is that methods from engineering science can be useful in various ways. First, they can simply function as an inspiration of what possible approaches and theories exist for a given problem (e.g. [6–8]). Second, they can offer a baseline of what behavioral performance can be achieved using the best theory available that is suitable for the motor system at hand, irrespective of whether this theory is biologically plausible or not. If a more biologically faithful model demonstrates a different level of performance, it might be explained by the differences of this model from the baseline-engineering model. And third, of course, some engineering approaches might be directly applicable to models of biological control, as, for instance, in oculomotor control [9,10].

In this review, we focus on recent research in computational motor control, with a view towards parallels between computational modeling and theories in artificial intelligence and robotics, in particular robotics with anthropomorphic or humanoid robots. We structured this review according to the control diagram in Figure 1, which is commonly used in robotics and can also function as an abstract guideline for research in biological motor control [11]. This diagram distinguishes between five major stages of motor control: first, the higher level processing and decision making, which defines the intent of the motor system; second, the motor planning stage; third, the potential need and problem of coordinate transformations; fourth, the final conversion of plans to motor commands; and fifth, the preprocessing of sensory information such that it is suitable for control. Of course, the separation of the stages in Figure 1 might not be present in some control algorithms and in biological systems, but, as will be seen below, a conceptual differentiation of these stages will be useful for our discussion.

## The brain as a mixture model
The motor command generation stage in Figure 1, which is usually associated with some of the main motor area in the primate brain such as the primary motor cortices and the cerebellum, has been the focus of a large amount of neurophysiological and computational research. It is now relatively well established that the central nervous system makes use of the computational principle of internal models, which are mechanisms that can mimic the input–output characteristics of the motor apparatus (forward models), or their inverse (inverse models) [11,12]. Research in this area has started to focus on how multiple

**Figure 1**
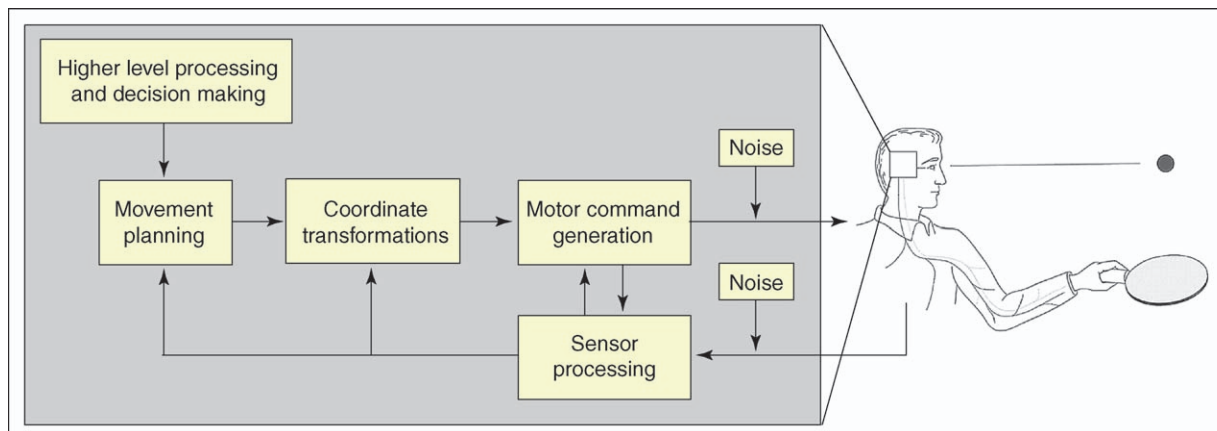


Sketch of a generic motor control diagram, typically used in robotics research, that can also function as a discussion guideline for biological motor control.

tasks are controlled with internal models, for example, objects with different weight or inertial properties. This topic is discussed in the literature as multiple model learning, contextual model switching, or mixture models.

The main principle of the 'mixture of experts', a neural architecture [13] developed in machine learning, and its newer derivatives developed specifically for motor control [14,15], is the 'divide and conquer' principle: multiple specialized simple internal models can outperform a single large-scale internal model that tries to accomplish everything by itself. This strategy is especially useful for ill-posed problems. Holding two objects of different weight with the same arm posture, for instance, requires different motor commands. A single neural network would only learn the average motor command of both objects, and thus perform poorly on both of them, whereas a mixture of experts can learn the exact inverse by switching object specifically.

How are the multiple models encoded in the CNS? Recent imaging and neurophysiological studies support the existence of multiple internal models [16–19] in separate neural substrates. Alternatively, if neurons that form the internal model multiplicatively code contextual (such as a color cue associated with a movement) and non-contextual information (such as the state of the arm), then a single network, that is, the same neural substrate, could encode several internal models, each accessed by different contextual cues [20,21[•]].

## The brain as a stochastic optimal controller
Because noise, as sketched in Figure 1, is predominant in the nervous system, it is bound to affect motor control. On the efferent side, in motor neurons for instance, the standard deviation of noise is between 10% and 25% of the mean activity of a motor neuron [22]. What strategies

does the central nervous system use to minimize the effects of noise on movements? A first solution is to generate smooth movements. Harris and Wolpert [23] proposed a signal-dependent noise theory according to which the goal of motor planning is to minimize the effects of noise on target errors. The commonly observed relative straightness of arm movements and the smooth bell shape velocity profile thus result from the minimization of the consequence of noise on the motor output. Second, redundancy due to the number of overcomplete muscles reduces variability [23], and the resolution of redundancy on the muscular level is well modeled by the theory of signal dependent noise [24]. Third, redundancy due to the large number of contributing neurons further reduces variability. Hamilton *et al*. [25[•]] showed that using the proximal joints during movements might help to decrease end-point variability because the larger muscles of these proximal joints have more motor units, which result in reducing variability. The redundancy of cortical neurons might additionally play a part in reducing the effect of noise on movements: the reduced number of surviving (noisy) neurons in stroke patients might cause greater end-point variability [26[•]].

Noise in motor control can, in theory, arise from sensory (i.e. target localization), planning, execution, or muscular origins. Van Beers *et al*. [27[•]] showed that the variability observed in hand position after reaching movements is not explained by sensory or planning noise, but rather by noise in movement execution. Jones *et al*. [28] ruled out the possibility of large muscular noise by showing that variability in thumb force production mostly arises from the noisy discharges of motoneurons. Todorov and Jordan [23] suggested a complete theory of stochastic optimal feedback control, which addresses motor planning, motor execution and redundancy resolution and that can account for a large body of experimental data. Note,

however, that the computational complexity of learning stochastic optimal control is still daunting in nonlinear motor systems, even in theory. Furthermore, signal dependent noise-based theories might need some revisions as co-contraction actually reduces the movement variability in single joint elbow movements [29], despite injecting theoretically more noise due to higher muscle contraction levels.

## Generalization and error-based learning

A crucial component of the theory of motor command generation regarding internal models is how internal models are learned, stored in short- and long-term memory, and how they generalize to new tasks. To quantify such issues, Shadmehr and co-workers [30] developed a novel approach to derive the extent of learning generalization from trial-to-trial changes in behavior in human experiments using a manipulandum that can exert force fields on the hand during movements. It was shown that the spatial generalization of learning, for example, the extrapolation of a learned force field to areas of the workspace of the hand where the field had not been experienced before, can be modeled in terms of spatially localized basis functions, that is, spatially tuned receptive fields, similar to that used in modern statistical learning approaches [31]. These basis functions, which are combined to form the internal model of the force field, were bimodal, as was found in the spatially preferred directions of firing in cerebellar Purkinje cells [30,32]. Detailed changes in trial-to-trial performance could be predicted from an error-based learning rule, that is, a gradient descent supervised learning method.

A recent study by Franklin *et al.* [33] broadened the scope of force field studies in demonstrating how error-based learning can also adjust the level of co-contraction for reaching movement in an unstable force field, essentially addressing the question of how the brain could learn impedance control (i.e. the adjustment of compliance in a task-specific way). The authors propose a computational model that can learn appropriate patterns of muscle activation to compensate for both perturbing forces and instabilities, in addition to predicting the evolution of movements observed in humans. At the core of the model is an intriguing asymmetric learning rule that has higher learning gains for agonistic muscles than for antagonistic muscles, and also a decay term to reduce co-contraction if only small movement errors are experienced.

Models of motor learning usually assume a quadratic error function in which the mean squared error is minimized over repeated trials; humans, however, seem to use an error function that is quadratic for small errors, but significantly less than quadratic for large errors, making it robust to outliers [34]. Furthermore, supervised learning of internal models with neural networks requires that neurons receive two inputs: one that carries the input

signal, and the other the movement error, such that the synaptic strength for the inputs to the neuron can be modified. The cerebellar Purkinje cells have such architecture, with the inputs from the inferior olive carrying the error signal [35]. Because the inferior olive neurons have a very low firing rate, the interference effect of the error signals on the Purkinje cell outputs is minimized. Schweighofer *et al.* [36[••]] recently proposed that moderate electrical coupling between inferior olive neurons can induce a 'chaotic resonance', which maximizes the transmission of the error signals in spite of these low firing rates, and thus might facilitate learning of internal models in the cerebellum.

Motor skill learning is sometimes hard or even impossible [37]. For arm movements, it is, for instance, impossible to learn two opposite force fields sequentially: learning of the second field can wipe out learning of the first one. Random scheduling of the two fields together with contextual cues, however, enables learning of both fields [38]. Besides random scheduling, another approach to learn complex tasks is to use a developmental method in which movements of increasing difficulty are attempted as learning progresses [39,40].

## Operational space control and redundancy resolution

As sketched in Figure 1, before reaching the motor command generation stage, information flow from motor planning requires a stage of coordinate transformations to transform external or task coordinates to the internal coordinates of the motor system, for example, a Cartesian space to muscle or joint space conversion. Given that in most motor tasks the number of degrees of freedom (DOFs) of the internal space significantly exceeds the number of DOFs in external space, it is necessary to resolve how to employ the excess of DOFs in internal space. This problem is called the degree-of-freedom problem [41] or the problem of redundancy resolution.

Earlier studies in computational motor control hypothesized specific organizational principles that could help to circumvent the problem of redundancy resolution, for example, in the form of freezing certain DOFs or slaving them together so that the simplified system had no redundant DOFs anymore [42]. These approaches, however, could not quite explain the behavioral findings that, on average over repeated trials, the variability in internal coordinates often exceeds the variability in task space coordinates. For example, in point-to-point reaching movement with the unconstrained arm, the variability of joint angular trajectories is significantly larger than the variability of end-effector coordinates [23]. Interestingly, recent trends in research on task control and redundancy resolution in biological movement have moved increasingly closer to ideas of 'operational space control' and 'inverse kinematics' control as suggested in the 1980s in

robotics [43,44]. The key idea of operational space control is that a desired movement in task space, for example, bringing a cup of coffee to the mouth, can be transformed with the help of the Jacobian of the kinematics of the movement system into a desired movement in internal space, and that stable controllers can be formulated for such an approach. However, given the excess of DOFs in internal space, only a fraction of the internal DOFs is properly constrained, and the unconstrained DOFs can be used to fulfill subordinate criteria, for example, energy efficiency, avoidance of joint limits, and so on. This unconstrained part of the internal space was termed the 'uncontrolled manifold' [42], and is referred to as null-space in the engineering literature. From the viewpoint of task achievement, it is not necessary to suppress the inherent noise in biological motor control for the unconstrained internal DOFs, such that they tend to exhibit higher variability in repeated trials [23].

Relating redundancy resolution and task space control to the formal framework of operational space control enables us to examine several established task-space control theories in the framework of biological motor control. For instance, which variables are transformed from task space to internal space? Possible candidates are positions, velocities, accelerations and forces [45], and some recent behavioral results with a force manipulandum indicate that there seems to be no positional control in internal space for an externally defined reaching task [46•]. Another important issue is which principles are used to constrain the uncontrolled manifold, and solutions could include no control, avoidance of joint limits [47], task specific optimization [48], minimal intervention [49] and hierarchical task control [50••].

## Motor primitives in the brain
What units of action does the brain use for the generation of complex movement in the movement planning stage in Figure 1? From a computational point of view, it seems impossible that the low level motor commands for complex motor acts, for example, a tennis serve, could be learned from pure trial and error learning with unsupervised learning methods such as reinforcement learning [51]. Thus, there might be a 'language' of more abstract building blocks in motor control, that is, motor primitives (a.k.a. schemas, basis behaviors, macros, or options). It is important to note that such a 'building block' architecture is distinct from the mixture model approach described above, which was a theory of modules for movement execution. For instance, different load conditions might be addressed by the mixture model approaches above, but usually it is assumed that a movement plan has already been generated and that only the conversion from planning variables (e.g. desired positions and velocities of the limb) to motor commands needs to be performed.

Several interesting developments in research on motor primitives are worthwhile highlighting. One active area of investigation focuses on movement generation with submovements (or discrete strokes). From investigating the kinematics of arm movements in monkeys [52] and humans [53], Fishbach and Novak et al. argue that even complex movements with multiple velocity peaks can be decomposed into elementary strokes that form the basis of an intermittent stroke-based movement planning mechanism. In a similar vein, Rohrer et al. [54] observed that in reaching movements of recovering patients with brain lesions, the number of submovements decreased during recovery until smooth movement performance was regained, again arguing in favor of a stroke-based composition of complex movement. Sosnik et al. [55] demonstrated that practice of a novel stroke-based movement sequence can lead to the formation of new and more complex motor primitives, characterized by the co-articulation of previously distinct strokes.

That movement generation based on discrete strokes might not be sufficient to account for the full spectrum of motor behaviors was demonstrated in a functional magnetic resonance imaging (fMRI) experiment that compared the cortical activations between discrete and rhythmic movements in humans [56••]. This investigation found a distinct set of premotor and parietal activations in discrete movement (Figure 2) that led to the conclusion that rhythmic movements seem to be gener-

**Figure 2**



Discrete–rhythmic
Rhythmic–discrete
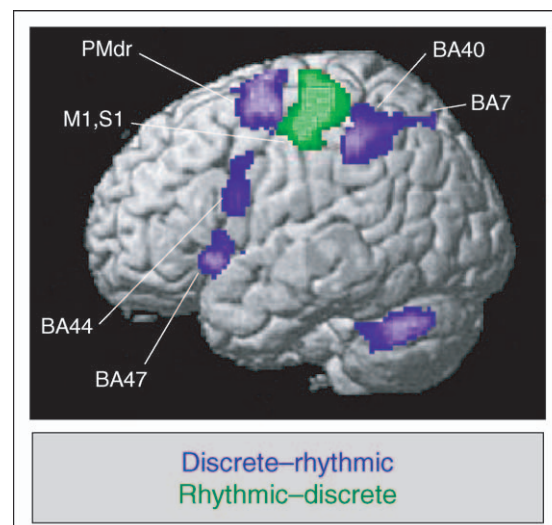
Differences of cortical activity between rhythmic and discrete movement, as reported in an fMRI experiment [56••]. The blue regions show brain areas that were more strongly activated during a discrete flexion-extension wrist movement than during a rhythmic wrist movement. The green regions demonstrate brain areas with larger activation during rhythmic wrist movement. Because discrete movement activated many more brain areas than rhythmic movement, it was concluded that rhythmic movement could not be composed of discrete strokes. Adapted from [56••].

ated by separate cortical mechanisms in primates. Interestingly, however, the study left open the possibility that discrete movements might actually be generated by a modulated rhythmic movement circuit. A modeling study [57•] formalized the idea of separate discrete and rhythmic movement primitives in the framework of learnable nonlinear dynamic systems. This framework highlighted the fact that complex desired trajectories, and their timing, can be generated by simple neural networks in real-time without the need to store desired trajectories in memory, or to have an explicit clocking mechanism [58,59]. Thus, for the first time, a computational bridge was formed between ideas of dynamic systems theory for motor control [60,61] and optimization approaches to the neural control of movement [12]. Moreover, the simple parameterization of goal-directed movement in this dynamic systems approach relates to experimental studies demonstrating goal directed movement through microstimulation of cortical [62] and spinal [63] circuits.

## The Bayesian brain in motor control

Because Bayesian decision theory enables optimal integration of prior knowledge and sensed noisy information from multiple sources, the concept of Bayesian inference is particularly useful when uncertainty about variables needs to be incorporated into decision-making. A remarkable result of modern statistical learning theory [31,64] is that many artificial and biological neural networks can be interpreted as Bayes optimal signal processing systems, despite possessing neither explicit knowledge of Bayes rule nor knowledge of the probability distributions of the involved variables. In the wake of the successes of Bayesian methods in visual perception [65,66], several research groups have started to investigate Bayes optimal processing in motor control, especially focusing on issues of

sensory processing, as indicated by the corresponding box in Figure 1.

By manipulating the bias and the reliability (i.e. noise) of visual feedback in a point-to-point reaching task in a virtual environment, Körding and Wolpert [67••] demonstrated that human subjects do, indeed, behave in a Bayes optimal way. First, subjects learned to adjust their movement strategy to minimize the pointing error in an altered visual environment with deterministic but shifted feedback, similar to the situation that has been previously reported in prism-adaptation experiments [68,69]. Second, subjects performed reaching movements with noisy feedback about their performance, in which different levels of noise were added to the feedback signal. Surprisingly, the reaching performance of the subjects could be explained only by a model of Bayesian integration of the learned prior from the first stage of the experiment and the feedback noise level applied in the second stage of the experiment. A related experiment demonstrated that Bayes optimal processing can also be achieved if the feedback signal is a sensed force signal [70], that is, it is not the visual modality of feedback that is important.

Sober and Sabes [71•] highlighted, however, some points of caution about the Bayesian view of signal processing. These authors demonstrated that in a point-to-point reaching task, proprioceptive and visual information could be combined in a task-dependent manner, that is, not solely based on the level of noise in the individual signals, but also based on what signals are the most useful for the task achievement. One could argue, however, that these results could be reconciled with the Bayesian view by considering Bayesian signal processing together with a task dependent loss function, which is a standard element

**Figure 3**
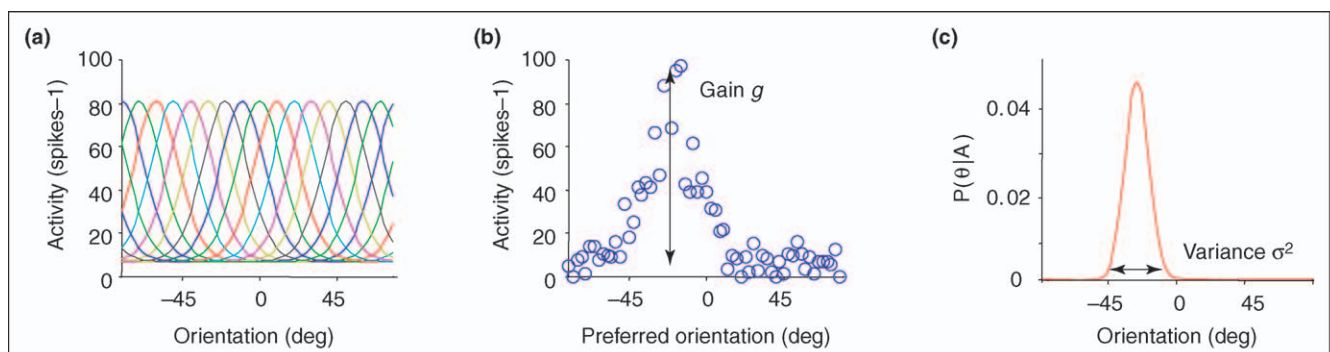


Simulations of Bayesian inference with gain encoding for the directional orientation of a reaching movement. **(a)** A population of idealized Gaussian directional tuning curves for 16 simulated cells, equally spaced over a range of reaching orientations; each color corresponds to the tuning curve of one cell. **(b)** Response of 64 simulated cells with Gaussian tuning curves similar to the ones shown in (a), in response to a movement direction of $-20°$. Each dot corresponds to the activity of one cell. The cells have been ranked according to their preferred direction and the responses have been corrupted by independent Poisson noise. **(c)** The posterior distribution over directional orientation obtained from applying a Bayesian decoder to the noisy hills shown in (b). With independent Poisson noise, the peak of the distribution coincides with the peak of the noisy hill, and the width of the distribution (i.e. the variance) is inversely proportional the gain of the noisy hill. Thus, the gain of the noisy hill represents the uncertainty in the population read-out. Adapted from [72••].

of Bayesian decision theory — future experiments are needed to clarify such issues. Finally, an intriguing model of how Bayesian signal processing could take place in neural population codes was recently suggested by Pouget et al. [72$^{\bullet\bullet}$,73]. The model demonstrates how Poisson noise in neural firing and a gain coding mechanism can be exploited to propagate uncertainty in neural processing — exactly what is needed for Bayesian inference (Figure 3).

## Conclusions and future directions

This review has highlighted recent research directions in computational neuroscience for motor control in which the computational foundations have strong overlap with theories in robotics and artificial intelligence. Points of discussion have included motor control with internal models and in the face of noise, motor learning, coordinate transformation, task space control, movement planning with motor primitives and probabilistic inference in sensorimotor control. Note that although Figure 1 also includes a box about higher level processing and decision making, as an input to the movement planning box, there has been very little computational motor control research in this area. Several interesting lines of research, however, point towards modeling decision making in terms of the intent of action: first, in the field of machine learning, inverse reinforcement learning [74] enables us to derive an intended cost function from observation. Second, in the field of brain–machine interfaces, there are efforts to read-out neural data to interpret on-going or future behavior [75]. And third, in research on the reciprocal interaction between action observation and action generation, eye-movement patterns seem to indicate whether purposeful action is performed or not [76$^{\bullet\bullet}$].

Two interesting trends in motor control research appear from the present review. First, there has been a growing acceptance of complex computational models of brain information processing. This trend seems to have been spurred by the wide recognition of the internal model theory, and by the need of systems-level computational models to interpret large-scale brain recordings as, for instance, obtained in neural prosthetics [77]. Second, there have been several model-based experiments, in which complex models function as a guide to the experiment design and subsequent data analysis (e.g. [78,79]). Although, as mentioned in the introduction, the models and algorithms of more engineering oriented sciences might not always be a perfect match for the information processing in the central nervous system, they do often provide solid foundations that can help us to ground the vast amount of neuroscientific data that is collected today, and they can be replicated, revised, and falsified more easily than purely data driven research.

## Acknowledgements

## References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Wiener N: *Cybernetics*. J. Wiley; 1948.

2. Bellman R: *Dynamic programming*. Princeton University Press; 1957.

3. Narendra KS, Annaswamy AM: *Stable adaptive systems*. Dover Publications; 2005.

4. Slotine JJE, Li W: *Applied Nonlinear Control*. Prentice Hall; 1991.

5. Shadmehr R, Wise SP: *The Computational Neurobiology of*
• *Reaching and Pointing: A Foundation for Motor Learning*. MIT Press; 2005.
This book is currently the most comprehensive and modern summary of computational motor control for arm movements, with many tutorials that enable less computationally trained readers to quickly understand the topics of state-of-the-art research.

6. Stein RB, Ogusztöreli MN, Capaday C: **What is optimized in muscular movements?** In *Human Muscle Power*. Edited by Jones NL, McCartney N, McComas AJ: Human Kinetics Publisher; 1986:131-150.

7. Miall RC, Weir DJ, Wolpert DM, Stein JF: **Is the cerebellum a Smith predictor?** *J Mot Behav* 1993, **25**:203-216.

8. Mehta B, Schaal S: **Forward models in visuomotor control**. *J Neurophysiol* 2002, **88**:942-953.

9. Robinson DA: **The use of control systems analysis in the neurophysiology of eye movements**. *Annu Rev Neurosci* 1981, **4**:463-503.

10. Lisberger SG: **The neural basis for motor learning in the vestibulo-ocular reflex in monkeys**. *Trends Neurosci* 1988, **11**:147-152.

11. Sabes PN: **The planning and control of reaching movements**. *Curr Opin Neurobiol* 2000, **10**:740-746.

12. Kawato M: **Internal models for motor control and trajectory planning**. *Curr Opin Neurobiol* 1999, **9**:718-727.

13. Jacobs RA, Jordan MI, Nowlan SJ, Hinton GE: **Adaptive mixtures of local experts**. *Neural Comput* 1991, **3**:79-87.

14. Wolpert DM, Kawato M: **Multiple paired forward and inverse models for motor control**. *Neural Netw* 1998, **11**:1317-1329.

15. Doya K, Samejima K, Katagiri K, Kawato M: **Multiple model-based reinforcement learning**. *Neural Comput* 2002, **14**:1347-1369.

16. Imamizu H, Kuroda T, Miyauchi S, Yoshioka T, Kawato M: **Modular organization of internal models of tools in the human cerebellum**. *Proc Natl Acad Sci USA* 2003, **100**:5461-5466.

17. Paz R, Boraud T, Natan C, Bergman H, Vaadia E: **Preparatory activity in motor cortex reflects learning of local visuomotor skills**. *Nat Neurosci* 2003, **6**:882-890.

18. Imamizu H, Kuroda T, Yoshioka T, Kawato M: **Functional magnetic resonance imaging examination of two modular architectures for switching multiple internal models**. *J Neurosci* 2004, **24**:1173.

19. Kurtzer I, Herter TM, Scott SH: **Random change in cortical load representation suggests distinct control of posture and movement**. *Nat Neurosci* 2005, **8**:498-504.

20. Salinas E: **Fast remapping of sensory stimuli onto motor actions on the basis of contextual modulation**. *J Neurosci* 2004, **24**:1113-1118.

21. Wainscott SK, Donchin O, Shadmehr R: **Internal models and**
• **contextual cues: Encoding serial order and direction of movement**. *J Neurophysiol* 2005, **93**:786-800.
The authors developed a reaching task in which forces on the hand depended both on the direction of the movement and on the order of the movement in a pre-defined sequence (a contextual cue). It is demonstrated that the contextual cue multiplicatively modulated the basis functions that form the inverse dynamics internal model.

22. Harris CM, Wolpert DM: **Signal-dependent noise determines motor planning**. *Nature* 1998, **394**:780-784.

23. Todorov E, Jordan MI: **Optimal feedback control as a theory of motor coordination**. *Nat Neurosci* 2002, **5**:1226-1235.

24. Haruno M, Wolpert DM: **Optimal control of redundant muscles in step-tracking wrist movements**. *Journal of Neurophysiology* 2005, Epub ahead of print.

25. Hamilton AFD, Jones KE, Wolpert DM: **The scaling of motor**
• **noise with muscle strength and motor unit number in humans**. *Exp Brain Res* 2004, **157**:417-430.
The authors showed experimentally that using proximal joints during movements might help to decrease end-point variability. Furthermore, simulations demonstrated that the reduced noise in larger muscles is due to the fact that larger muscles have more motor units: thus, neuronal redundancy reduces variability.

26. Reinkensmeyer DJ, Iobbi MG, Kahn LE, Kamper DG, Takahashi
• CD: **Modeling reaching impairment after stroke using a population vector model of movement control that incorporates neural firing-rate variability**. *Neural Comput* 2003, **15**:2619-2642.
The authors studied, both in simulation and experimentally with stroke patients, the effect of cortical neuron noise on the variability of reaching movement direction. Simulation results showed that the number of neurons controlling hand direction (via directional tuning) correlated with end-point errors. Further, experimental results demonstrated that stroke severity also correlated with directional variability. Thus, hypothesizing that stroke severity correlates with lesion size (which is far from being always true — see, Winstein *et al.* CSM abstract, J. Neurol. Phys. Ther. 2004 vol 28 4), it was concluded that the reduced number of surviving neurons in more affected patients causes greater end-point variability.

27. van Beers RJ, Haggard P, Wolpert DM: **The role of execution**
• **noise in movement variability**. *J Neurophysiol* 2004, **91**:1050.
To find out how different types of noise could best explain the variability of behavioral data, the authors fit the noise parameters in a model of arm reaching to data of human end-point reaching data. Their results show that most of the end-point variability could be explained by movement execution noise, with a combination of noise in the magnitude and noise in the duration of the motor output.

28. Jones KE, Hamilton AF, Wolpert DM: **Sources of signal-dependent noise during isometric force production**. *J Neurophysiol* 2002, **88**:1533-1544.

29. Osu R, Kamimura N, Iwasaki H, Nakano E, Harris CM, Wada Y, Kawato M: **Optimal impedance control for task achievement in the presence of signal-dependent noise**. *J Neurophysiol* 2004, **92**:1199.

30. Franklin DW, Burdet E, Tee KP, Osu R, Kawato M, Milner TE: **Feedback drives the learning of feedforward motor commands for subsequent movements (abstract)**. *Society for Neuroscience Abstracts* 2004, 871.9.

31. Bishop CM: *Neural Networks for Pattern Recognition*. Oxford University Press; 1995.

32. Thoroughman KA, Shadmehr R: **Learning of action through adaptive combination of motor primitives**. *Nature* 2000, **407**:742-747.

33. Donchin O, Francis JT, Shadmehr R: **Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control**. *J Neurosci* 2003, **23**:9032-9045.

34. Körding KP, Wolpert DM: **The loss function of sensorimotor learning**. *Proc Natl Acad Sci USA* 2004, **101**:9839-9842.

35. Schweighofer N, Spoelstra J, Arbib MA, Kawato M: **Role of the cerebellum in reaching movements in humans. II. A neural model of the intermediate cerebellum**. *Eur J Neurosci* 1998, **10**:95-105.

36. Schweighofer N, Doya K, Fukai H, Chiron JV, Furukawa T,
•• Kawato M: **Chaos may enhance information transmission in the inferior olive**. *Proc Natl Acad Sci USA* 2004, **101**:4655-4660.
The authors developed a realistic inferior olive network model and showed that moderate electrical coupling between cells produced chaotic firing, which maximized the input–output mutual information. This 'chaotic resonance' enables rich error signals to reach the Purkinje cells, even at low inferior olive neuron firing rates, and might enable efficient cerebellar learning.

37. Sanger TD: **Failure of motor learning for large initial errors**. *Neural Comput* 2004, **16**:1873-1886.

38. Osu R, Hirai S, Yoshioka T, Kawato M: **Random presentation enables subjects to adapt to two opposing forces on the hand**. *Nat Neurosci* 2004, **7**:111-112.

39. Sanger TD: **Neural network learning control of robot manipulators using gradually increasing task difficulty**. *IEEE Trans Rob Autom* 1994, **10**:323-333.

40. Ivanchenko V, Jacobs RA: **A developmental approach AIDS motor learning**. *Neural Comput* 2003, **15**:2051-2065.

41. Bernstein NA: *The Control and Regulation of Movements*. Pergamon Press; 1967.

42. Scholz JP, Schoner G: **The uncontrolled manifold concept: identifying control variables for a functional task**. *Exp Brain Res* 1999, **126**:289-306.

43. Khatib O: **A united approach to motion and force control of robot manipulators: The operational space formulation**. *International Journal of Robotics Research* 1987, **31**:43-53.

44. Nakamura Y, Hanafusa H: **Inverse kinematics solutions with singularity robustness for robot manipulator control**. *J Dyn Syst Meas Control* 1986, **108**:163-171.

45. Nakanishi J, Cory R, Mistry M, Peters J, Schaal S: **Comparative experiments on task space control with redundancy resolution**. In *IEEE International Conference on Intelligent Robots and Systems (IROS 2005)*: 2005.

46. Mistry M, Mohajerian P, Schaal S: **Arm movement experiments**
• **with joint space force fields using an exoskeleton robot**. In *IEEE Ninth International Conference on Rehabilitation Robotics*; *Chicago, Illinois, June 28-July 1*: 2005.
By using an exoskeleton robot manipulandum, the authors perturbed the elbow joint of subjects with a force field during point-to-point reaching movements with the unconstrained arm. Subjects learned to compensate for this force field and return after training to the same endpoint trajectories as before training. Interestingly, however, joint space trajectories did not return to the original performance. These results indicate that for reaching tasks, no position reference trajectory was generated in joint space. Rather, the biological controller behaved like a velocity-based or acceleration-based operational space controller with flexible resolution of redundancy in the null space of the task.

47. Cruse H, Wischmeyer E, Bruwer M, Brockfeld P, Dress A: **On the cost functions for the control of the human arm movement**. *Biol Cybern* 1990, **62**:519-528.

48. Ohta K, Svinin MM, Luo ZW, Hosoe S, Laboissiere R: **Optimal trajectory formation of constrained human arm reaching movements**. *Biol Cybern* 2004, **91**:23-36.

49. Bruyninckx H, Khatib O: **Gauss' principle and the dynamics of redundant and constrained manipulators**. In *Proceedings of the 2000 IEEE International Conference on Robotics & Automation; San Francisco, CA, April 2000*: 2000:2563-2568.

50. Khatib O, Sentis L, Park J, Warrent J: **Whole-body dynamic**
•• **behavior and control of human-like robots**. *International Journal of Humanoid Robotics* 2004, **1**:1-15.
Based on more than a decade of research on task-level control in redundant control systems, the authors develop a comprehensive control approach of how multiple tasks can be executed in a hierarchy of priorities, for example, as in bringing a cup to the mouth while maintaining postural balance and avoiding obstacles. This task–space control approach is among the most elegant and computationally clean approaches in humanoid robotics.

51. Schaal S: **Is imitation learning the route to humanoid robots?** *Trends Cogn Sci* 1999, **3**:233-242.

52. Fishbach A, Roy SA, Bastianen C, Miller LE, Houk JC: **Kinematic properties of on-line error corrections in the monkey**. *Exp Brain Res* 2005, **164**:442-457.

53. Novak KE, Miller LE, Houk JC: **The use of overlapping submovements in the control of rapid hand movements**. *Exp Brain Res* 2002, **144**:351-364.

54. Rohrer B, Fasoli S, Krebs HI, Volpe B, Frontera WR, Stein J, Hogan N: **Submovements grow larger, fewer, and more blended during stroke recovery**. *Motor Control* 2004, **8**:472-483.

55. Sosnik R, Hauptmann B, Karni A, Flash T: **When practice leads to co-articulation: the evolution of geometrically defined movement primitives**. *Experimental Brain Research* 2004, **156**:422-438.

56. Schaal S, Sternad D, Osu R, Kawato M: **Rhythmic movement is**
•• **not discrete**. *Nat Neurosci* 2004, **7**:1136-1143.
Subjects performed rhythmic and discrete wrist movements in a 4T fMRI scanner. The results demonstrated that rhythmic movement only activated rather few brain regions that can be classified as ipsilateral primary motor areas. Discrete movement, by contrast, activated a large number of additional brain areas, in particular premotor and parietal regions. Given that discrete movement activated much more brain circuitry than rhythmic movement, the study provided strong evidence that rhythmic movement does not seem to be composed of discrete strokes, because otherwise the same or more brain areas should be active during rhythmic movement than during discrete movement.

57. Ijspeert A, Nakanishi J, Schaal S: **Learning attractor landscapes**
• **for learning motor primitives**. In *Advances in Neural Information Processing Systems 15.* Edited by Becker S, Thrun S, Obermayer K: MIT Press; 2003:1547-1554.
The authors model discrete and rhythmic movement with nonlinear differential equations that form stable point and limit cycle attractors, respectively. The novel finding of this modeling approach was that such equations can be trivially learned with optimization methods, such that even rather complex movements such as a tennis forehand can be represented by such differential equations. Thus, this modeling approach created one of the first computational bridges between dynamic systems models to motor control and optimization theories.

58. Ivry RB, Spencer RM: **The neural representation of time**. *Curr Opin Neurobiol* 2004, **14**:225-232.

59. Lewis PA, Miall RC: **Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging**. *Curr Opin Neurobiol* 2003, **13**:250-255.

60. Kugler PN, Turvey MT: *Information, Natural Law, and The Self-Assembly of Rhythmic Movement*. Erlbaum; 1987.

61. Kelso JAS: *Dynamic Patterns: The Self-Organization of Brain and Behavior.* MIT Press; 1995.

62. Graziano MS, Taylor CS, Moore T: **Probing cortical function with electrical stimulation**. *Nat Neurosci* 2002, **5**:921.

63. Tresch MC, Saltiel P, d'Avella A, Bizzi E: **Coordination and localization in spinal motor systems**. *Brain Res Brain Res Rev* 2002, **40**:66-79.

64. MacKay DJC: *Information Theory, Inference, and Learning Algorithms*. Cambridge University Press; 2003.

65. Kersten D, Yuille A: **Bayesian models of object perception**. *Curr Opin Neurobiol* 2003, **13**:150-158.

66. Weiss Y, Simoncelli EP, Adelson EH: **Motion illusions as optimal percepts**. *Nat Neurosci* 2002, **5**:598-604.

67. Körding KP, Wolpert DM: **Bayesian integration in sensorimotor**
•• **learning**. *Nature* 2004, **427**:244-247.
In a very elegant experimental design, the authors investigated the bias and variance of end-point errors in a point-to-point reaching task in a virtual environment with noisy feedback. Initially, subjects learned to compensate for a random virtual displacement of the feedback of their hand relative to the target, which introduced a 1cm displacement prior in

their behavior. In a second experimental condition, subjects midway through the movement received noisy feedback of their finger position relative to the target. The question was how subjects would integrate this noisy feedback with the learned bias from the initial experimental condition. Interestingly, only information integration according to Bayes rule was able to account for the results.

68. Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT: **Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation**. *Brain* 1996, **119**:1183-1198.

69. Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT: **Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations**. *Brain* 1996, **119**:1199-1211.

70. Körding KP, Ku SP, Wolpert DM: **Bayesian integration in force estimation**. *J Neurophysiol* 2004, **92**:3161-3165.

71. Sober SJ, Sabes PN: **Flexible strategies for sensory integration**
• **during motor planning**. *Nat Neurosci* 2005, **8**:490.
The authors demonstrate in a reaching task in a virtual environment that the relative weighting of visual and proprioceptive feedback depends both on the sensory modality of the target and on the information content of the visual feedback, and that these factors affect different stages of motor planning in different ways. This weighting seems to be chosen such that the errors arising from the transformation of sensory signals between coordinate frames are minimized.

72. Knill DC, Pouget A: **The Bayesian brain: the role of uncertainty in**
•• **neural coding and computation**. *Trends Neurosci* 2004, **27**:712.
The authors demonstrate that the high variability in the responses of cortical neurons can be used to generate probabilistic population codes that represent Gaussian and non Gaussian probability distributions. Moreover, these codes reduce a broad class of Bayesian inference, such as decision making and cue integration, to simple linear operations. This result holds both for realistic neuronal variability and for tuning curves of arbitrary shape and provides a biologically plausible mechanism for Bayesian inference in the brain.

73. Saunders JA, Knill DC: **Humans use continuous visual feedback from the hand to control both the direction and distance of pointing movements**. *Exp Brain Res* 2005, **162**:458.

74. Ng AY, Russell S: **Algorithms for inverse reinforcement learning**. In *Proceedings of the Seventeenth International Conference on Machine Learning*. Morgan Kauffmann; 2000:663-670.

75. Andersen RA, Musallam S, Pesaran B: **Selecting the signals for a brain-machine interface**. *Curr Opin Neurobiol* 2004, **14**:720-726.

76. Flanagan JR, Johansson RS: **Action plans used in action**
•• **observation**. *Nature* 2003, **424**:769-771.
The authors demonstrate that in a block stacking task, the pattern of eye movements is approximately the same when the subjects perform the task themselves, or when the subjects are watching the same task as performed by a teacher, that is, eye movements anticipate the movement of the hand. Strikingly, such eye movement patterns change drastically when the subjects cannot observe the teacher's movement, that is, eye movements become purely reactive and much more random. The results indicate that eye movements provide information about the higher level motor program that steers purposeful action.

77. Andersen RA, Burdick JW, Musallam S, Pesaran B, Cham JG: **Cognitive neural prosthetics**. *Trends Cogn Sci* 2004, **8**:486-493.

78. Haruno M, Kuroda T, Doya K, Toyama K, Kimura M, Samejima K, Imamizu H, Kawato M: **A neural correlate of reward-based behavioral learning in caudate nucleus: a functional magnetic resonance imaging study of a stochastic decision task**. *J Neurosci* 2004, **24**:1660-1665.

79. Tanaka SC, Doya K, Okada G, Ueda K, Okamoto Y, Yamawaki S: **Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops**. *Nat Neurosci* 2004, **7**:887-893.