# Motor Control in the Brain

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**Abstract**

There has been much progress in the development of a model of motor control in the brain in the last decade; from the improved method for mathematically extracting the predicted movement direction from a population of neurons to the application of optimal control theory to motor control models, much work has been done to further our understanding of this area. In this paper recent literature is reviewed and the direction of future research is examined.

## 1 Introduction

In the last decade there has been a push from investigating the coordinate system used in the brain, which has been the focus of research since the 1970s, back toward using reductionist experiment techniques and developing more encompassing models of motor control in the brain[28]. Optimal control theory applied to motor control in the brain has also recently started being explored as a framework for models. This has lead to research into the underlying biology of the implementations of internal models of movement and reinforcement learning reward systems in the brain[32]. In addition to this, with the discovery of motor primitives[24], which are often referred to as the 'building blocks of movement', many of the ideas about neural activity carried out in the motor cortex need be reworked. The analysis techniques employed by researchers have been improved and of course the computing power available has increased enormously, and these developments have in turn opened the door to the need for further mathematical technique developments for accurate movement analysis and prediction. There have been numerous robotics implementations of motor control/learning systems[12][10][3] exploring theories and models with an "understand by building" approach and also very excitingly a movement toward developing artificial limbs controlled through neural activity, devices known as neural prosthetics[28]. We review these topics here.

**Outline** The remainder of this article is organized as follows. In Section 2 through Section 5 we discuss the analysis techniques, ideas, and the underlying biology of the various parts of new models being developed today. In Section 6 we look at two different model types, the Optimal Feedback Control model proposed by[32] and the MOSAIC model brought forth in [21]. Section 7 looks at some of the work being done by Andrew Schwartz and others[28] in the development of neural prosthetics. Finally, in Section 8 we look at the directions that future research is headed and make concluding remarks in Section 9.

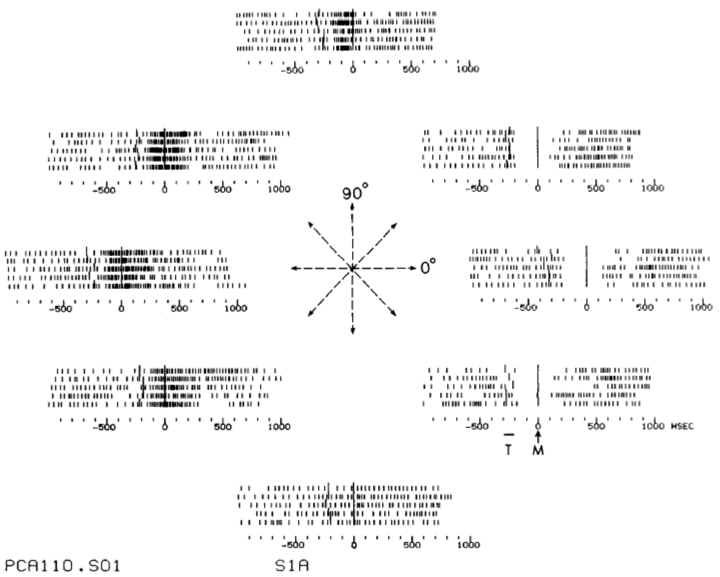

Figure 1: Activity of a neuron of M1 in response to center-out arm movements in 8 different directions in 2D space. The preferred direction of this cell is to the top left.

## 2 PVD vs OLD

Much of the work done in motor control in the brain is based on what is known as population vector decoding. This began when Apostolos Georgopoulos discovered that different neurons in the motor cortex respond differently to limb movements in a certain direction[6]. The direction to which they responded was termed the 'preferred direction' (Figure 1) of a neuron and it was found that by taking the vector sum of the discharge of a population of neurons weighted with a scalar it was possible to accurately predict limb movement direction in a 2D space[7]. This process is called finding the population vector decoding (PVD) of an ensemble of neurons.

Since the first work in PVD numerous other parameters of limb control aside from movement direction have been associated with the neural discharge of the motor cortex, including arm position[18], target position[1], overall trajectory[11], distance to target[5], acceleration[4], and many more, calling into question what exactly is being calculated by the motor cortex. Many have argued that the encoding of higher-level limb movement parameters discredits the possibility of a low-level muscle control, however Emanuel Todorov presented a model in 2000 that gives rise to these higher level phenomena through low-level muscle control, arguing that the assumption that muscle activation is identical to endpoint force lead to confusion in previous studies. In his model he accounts for muscle length and rate of change as well as muscle force activation. This provides compensation for the position and velocity dynamics of the arm and gives rise to a correlation between endpoint kinematics and neuron firing while in fact coding only for low-level muscle control parameters.

While the majority of research looking at PVDs focuses on correlations between unimanual contralateral and activity in the motor cortex, there is research from Steinberg et al.[31] examining the correlation between

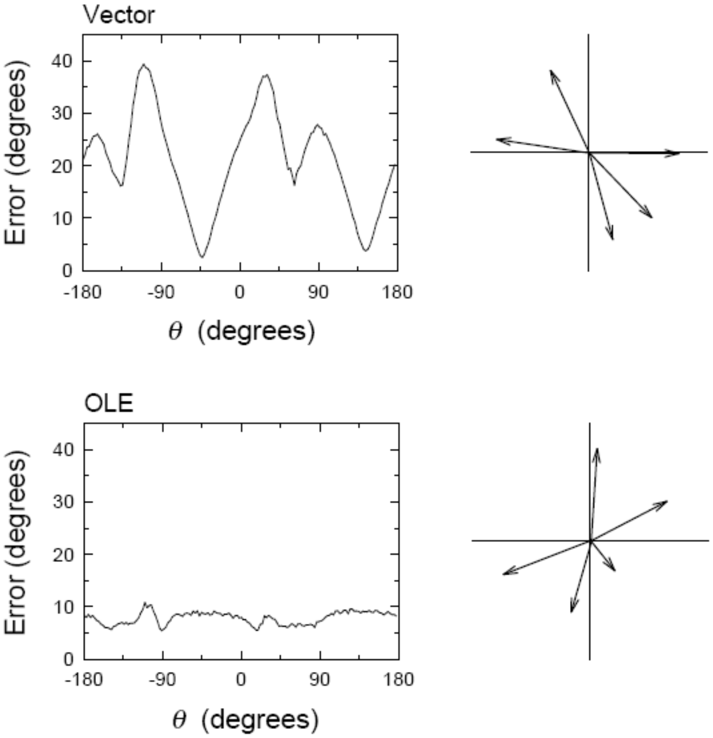

Figure 2: The vector and OLE reconstructions of the direction of a two-dimensional vector using five neurons with random preferred direction vectors, taken from [27].

neurons and bimanual movements that shows that neurons encode bimanual movement PDs as well. The study examined the directional tuning of a group of cells for unimanual left arm, unimanual right arm, bimanual parallel, and bimanual opposite movements. It was found that roughly 60% of the cells examined were tuned to more than one direction. In addition to this it was also found that cells strongest response was not always to the contralateral effector, suggesting that the interaction between the two hemispheres and the standard assumption that the motor cortex controls activity stricly on the contralateral side of the body needs to be further examined.

In 1994 Salinas and Abbott brought forth a new method for calculating the population vector, called optimal linear decoding (OLD)[27]. OLD is a more accurate and efficient method that also corrects for the bias and nonorthogonality of the preferred directions of cells when the sample size is small and lacking uniform distribution (Figure 2). In addition to this, while only the direction of movement is captured by the PVD, the OLD captures both the direction of movement as well as the magnitude. Clearly this is also desirable and for all of these reasons in today's research the original PVD algorithm has been replaced by the OLD and variations thereof. One of these was brought about in the paper by Steinberg et al.[31] mentioned above. By measuring the neuron's tuning during four different movement patterns they were able to create a best fit preferred direction (BFPD) from the four tunings for each cell and take the population vector of a group of cells using the BFPDs. They found that the cells' tuning was better represented by the BFPD which was created using information from unimanual and bimanual movements over the standard contralateral unimanual movement PD tunings, and that in fact the BFPDs represented their tunings almost

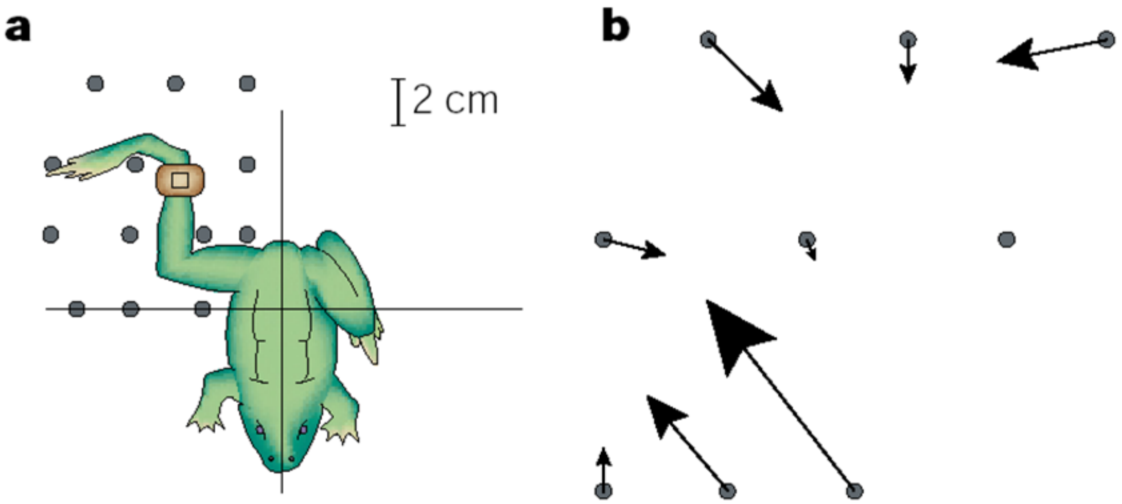

Figure 3: (a) The tested leg locations for microstimulation of the spine and (b) the peak force vectors recorded from each of the nine locations show in (a), taken from[23].

optimally. Georgopoulos et al. also made use of the OLD method in their research on the neural coding of finger and wrist movements in 1999 and found that the OLD algorithm outperformed the PVD at all sample sizes tested[8].

## 3 Motor Primitives

Motor primitives are a very interesting and promising area in motor control research. As mentioned above, motor primitives can be thought of as the building blocks of movement; much like words are to language. Motor primitives were discovered in a now well-cited study performed on the spinal cords of frogs where microstimulation was applied to certain points in the spine known to cause movement in a group of muscles in the leg. It was observed that when current was applied and the leg was moved to different positions on the 2D plane the degree of force with which the leg moved varied even as the electrical stimulation was held constant. As this was charted out it was discovered that for a particular spinal stimulation site the movement effected on the leg muscles caused the leg to be drawn toward an equilibrium point (Figure 3) creating force field. This field did not remain constant though, following the initial stimulation the field changed continuously through time. A natural effect of this is that the point of equilibrium does not remain constant, but moves throughout the field defining a trajectory. The movement effected then is caused by a smooth temporal shifting of the equilibrium position throughout the force field. Formally, these force fields are defined as nonlinear functions of limb position, velocity, and time that usher an effector toward an equilibrium point with a bell shaped velocity profile and are titled ‘motor primitives’.

Of noted interest is that it was found when two spinal sites are stimulated simultaneously the resulting force field is a vector summation of the induced force fields (Figure 4). With little imagination it can be seen that the fact that motor primitives can be strung together serially or in parallel with each other can allow

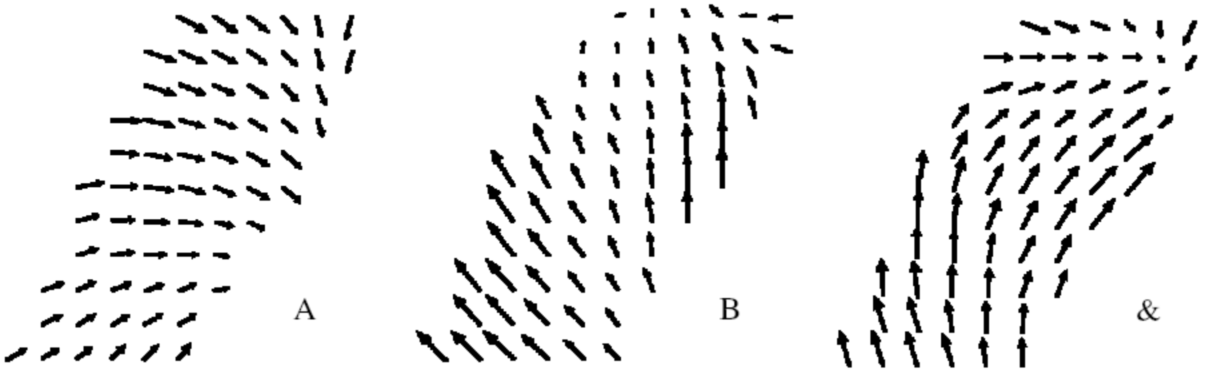

Figure 4: The fields A and B were obtained as responses from to different spinal sites to microstimulation. The & is the result of stimulating both sites at the same time, resulting in a statististically significant similarity to the vector summation of the two (more than 0.9); taken from[23].

for the basic actions that they represent to be brought together through a weighted summation to create any number of complex actions; a generative ability similar to that of language.

The vector summation of force fields presents a simple method for implementing complex action that allows a number of the nonlinearities of neuron population-muscle interaction to be ignored. It is apparent that having such a powerful tool at its disposal would be of great benefit to any system attempting fluid motion under as many degrees of freedom as the human body operates, and that any models of motor control in the brain must consider them when dealing with motor action execution. In [23] Mussa-Ivaldi and Bizzi explore the idea of motor primitives and methods of transforming a planned limb movement into a set of motor commands that carry out the action. The idea is that a group of neurons represent a basic movement 'module', and that motor learning consists of tuning these neurons and then combining them in serial or parallel with other modules to produce any one of a vast number of motor behaviours in a straight-forward manner.

As modelers interested in accurately modeling the motor control system in the brain it would be of great benefit to know the set of motor primitives being used by the body, known as the primitive behaviour repertoire. Since the technique of microstimulation of a spinalized subject used to examine the frogs' primitive set is not apt to be a suitable method for defining the motor primitives of a human and manual estimation techniques are subject to design and implementation errors, it is necessary that another avenue be explored. Jenkins and Mataric do exactly this in their 2003 paper[14]. Using a stream of data from a motion capture system they used an extension of Isomaps to extract a spatio-temporal structure and perform dimension reduction to isolate primitives forming a vocabulary. They found that although their implementation utilized inelegant procedures, they were successfully able to derive plausible primitive sets capable of being used to synthesize new human motion using an automated approach with a fraction of the time, effort, and training involved in the manual approach.

# 4 Central Pattern Generators

CPGs are neural networks capable of producing rhythmic output without any guiding sensory or central input. Their existence first confirmed in the well renowned study by Graham-Brown[9]. In this study, Graham-Brown found that stimulation of certain points in the spine was capable of producing a rhythmic stepping movement in cats without any descending commands from the cortex.

At a biological level, CPGs are neural networks composed of heterogeneous, rhythm producing subnetworks. Many types of neurons are found in these networks, but the most important ones are the bursting, bistable, and inhibitory neurons. Bursting neurons are capable of firing endogenously as well as in the presence of neurotransmitters, acting to provide the timing for the network. Their properties, such as cycle period and burst duration determine the overall temporal properties of the CPG. Bistable neurons are capable of generating sustained periods of depolarization and can be controlled with depolarizing and hyper polarizing pulses. The inhibitory neurons are central to controlling the timing of the neurons that fire in post inhibitory rebound.

CPG networks produce their rhythmic activity through one of two general subnetwork types: pacemaker-driven networks or networks with emergent rhythms. Both of these networks are intuitively named. Pacemaker-driven networks achieve a steady alternating oscillatory pattern and are most often found in CPG networks involved in functions which are constantly active, such as controlling heartbeat. Networks with emergent rhythms have their temporal patterns defined by the synaptic couplings between neurons that are not intrinsic oscillators[25]. A commonly cited example of such networks are the CPGs that control swimming locomotion in lampreys by inducing a wave motion through the body and propelling it through the water. Each segment of the lamprey is controlled by a CPG that causes left-right alternation; keeping segments in time with each other to achieve a proper overall pattern involves descending input with commands for coordination. This system for motor action execution is also highly adaptable as it not only allows for the lamprey to easily deal with variable current and densities, but also compensates for body growth and development throughout the course of the lamprey's life. This is a good example of how it is possible for a relatively simple system composed of individual CPGs controlling separate motor primitives to be used to generate highly complex and varying behaviour. Mussa-Ivaldi and Solla examine this network in detail in [25] while discussing ideas about how a CPG might be able to take advantage of the organization of the spine to enact complex patterned movement.

In the same paper, Mussa-Ivaldi and Solla go on to describe the different potential architectures appropriate for the various components of a system containing CPG controlled movements carried out through motor primitive activation. These include attractor neural networks as characterized by a Lyapunov function that describes the equilibrium point and gradient of a force field, a mixture of expert networks to represent movements generated through a combination of several force field primitives, and a two-layered feed-forward network as described by Jordan in his 1989 paper "Action" to capture the action of the control signal. Depending on the goals/focus of the simulation different architectures and combinations thereof will be appropriate.

# 5 Internal Models in the Brain

Internal models are in essence cause and effect mappings of motor actions to changes in the environment maintained by the brain. There are two kinds of internal models, forward and inverse. A forward model is one that predicts what will happen as the result of a motor action, and an inverse model is one used to

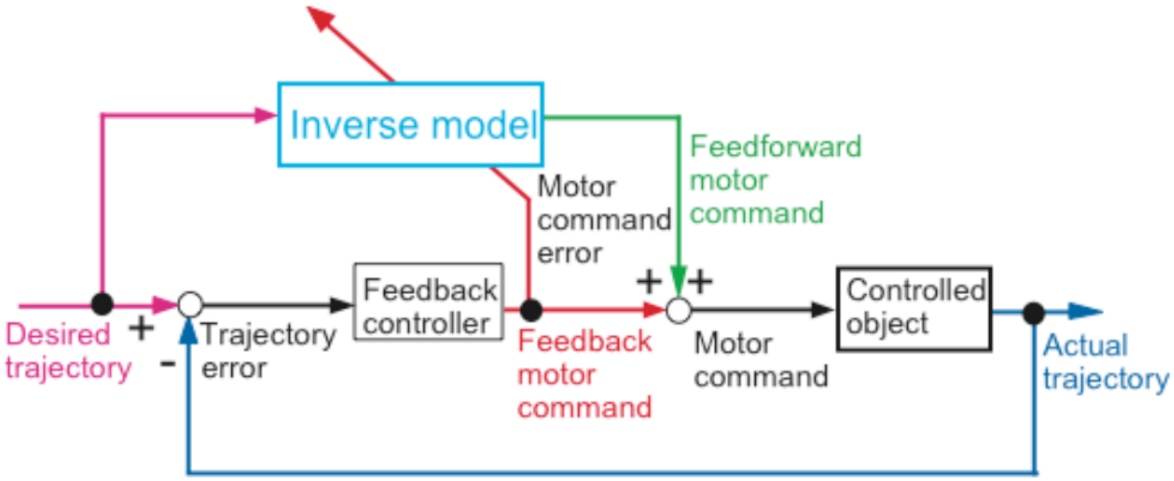

Figure 5: General Feedback-Error-Learning model as proposed by Kawato, taken from [16]

find the appropriate motor action to cause a desired change in the environment. Both are heavily subject to adaptation and refinement through experience and are critical to motor action planning, execution, and learning. There is a growing body of evidence suggesting that the brain maintains multiple consolidated internal models allowing humans to easily function and switch between numerous different environments with different dynamics [19]. This is explored through studies involving dynamic perturbation of reaching movement, involving active self-recalibration, as is the case when the torso is twisting and the arm makes a reaching movement to a target, and adaptive tool-usage, where the body's movement dynamics are changed by the use of a tool.

Many researchers [13] [20] [34] have brought forth evidence suggesting that the cerebellum is a major component of the forward modeling system, and it is also well observed that it's biological structure makes it well designed for learning and storing internal models. Bays and Wolpert have suggested that the highly modular structure of the cerebellum could indicate that both the forward and inverse models are employed simultaneously [2]. Kawato notes that due to the highly uniform landscape of the cerebellum across different regions and functions, much unlike the cerebral cortex, it is also likely that a theory that can explain even only a small part of the cerebellum's operations is likely to have principles that extend to all the other regions [21]. Following this statement, Kawato et al. have proposed a model for a feedback-error-learning system that would allow the body to acquire an inverse model in the cerebellum under a supervised learning scheme (Figure 5) [16]. The system works as follows: The desired trajectory is fed into the inverse model which transforms it into an appropriate motor command, at the same time a crude feedback command is generated to correct the error between the desired trajectory and the trajectory generated from the inverse model. This summation of the of the inverse model motor command and the feedback command are sent to the controlled object, and the feedback command is used as an error signal to train the inverse model. The stability and convergence of this model was recently mathematically proven [26] and has been successfully applied to several robotics demonstrations [22].

There is experimental proof supporting this model of a feedback-error-learning system in the cerebellum from neurophysiological studies performed on monkey cerebellums during ocular-following responses [15]. The corresponding neural parts of the system involve the retina, accessory optic system and brain stem for the feedback circuit, and the cerebral and cerebellar cortical pathways as well as the cerebellum for the feed forward pathway and inverse dynamics model. The error signal in this system is computed as the movement of the image on the retina (retinal slip), since the goal is tracking, even though it is not explicitly computed through some neural mechanism as it is in the system described in Figure 5. It has been shown, however, that the system is encoding more than twice as much information about the motor error in the brain than it is calculating sensory error information, making it highly likely that the error signal is in fact based on motor error and not retinal slip [33] [2].

In work done looking at noise reduction in a system Bays and Wolpert state that one of the components underlying current noise-inclusive models of motor control is inverse model adaptation. They discuss the idea of removing the self-generated component from sensory information by using an efference copy of the motor command that is fed through the system and subtracted from the incoming sensory stream. This predictive cancellation of sensory input has been seen in electrical fish and also explains why we can't tickle ourselves. It is believed that sensory filtering occurs in the cerebellum, as experiments on fish and primates as well as functional imaging studies on humans show activity occurring here during studies designed to elicit sensory filtering from the brain.

Looking back again at the vector summation of force fields, it can be seen that they provide a simple method for implementing complex action that allows a number of the nonlinearities of neuron population-muscle interaction to be ignored. Applying this to internal models, Mussa-Ivaldi et al. use the definition of motor primitives as force fields to define an internal model of limb dynamics as another force field that relates the forces generated by a muscular apparatus to the state of motion of a limb, greatly simplifying the concept over other proposed implementations of the internal model of limb dynamics. In this case, motor learning would simply consist of tuning a group of neurons that activate a particular spinal site activating a force field appropriately [23], and it becomes quite obvious again how motor primitives can be of great use to the overall system.

Armed with an inverse model based on motor primitive implementation and an OLD giving a predicted direction and magnitude estimations, it seems natural that a test of these systems and their accuracy would involve feeding the predicted direction and magnitude estimations to the inverse model and compare the resulting weighted summation of motor primitives against results collected from a live subject. Indeed there are many obstacles to before this kind of testing can be achieved, such as replicating the prioperceptive input and other information being fed into the cerebellum or isolating it from such input for testing, and again proper identification of motor primitives can be a difficult task in and of itself. Clearly though overcoming these obstacles and being able to perform such a test of one's model would allow for a much greater assurance of correctness than is available to us now. Kawato also states the need for complete control over neural input in his paper [21] and even goes so far as to define a new framework for a discipline called manipulative neuroscience based on the idea of manipulation of all the inputs to the system for testing and prediction purposes.

## 6 Optimal Feedback Control Model / MOSAIC

Optimal control theory is a discipline of mathematics that focuses on controlling a system while minimizing a cost function of some kind. Optimal feedback control is a subset of this field which considers optimizing cost functions based on the current state of the system. It is natural to think the motor control system of the body would operate as an optimal feedback control system, minimizing a cost of some nature (ie energy, distance traveled, shakiness, endpoint error). Todorov and Jordan formalized this idea recently in their

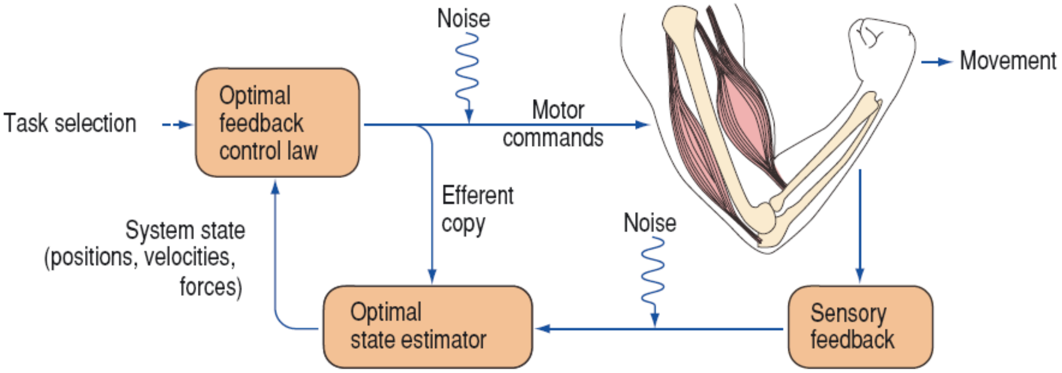

Figure 6: Optimal feedback controllers operate by combining efferent copies of motor commands with sensory feedback and correcting errors that influence the behavioural goal, taken from [30]

2002 paper [32] showing that optimal feedback control theory quite possibly has much more to offer than other conceptual frameworks that have been the focus in the past such as the servo-controlled that focus on feedback based control and the and sensorimotor transformations focused on identifying the coordinate frames that motor control in the brain operates under.

Optimal feedback control system have many potential costs to measure optimality by, but it is not clear what that cost should be for motor control systems. In a large number of models the square of end point variability, movement duration, or energy costs are used, and while this can lead to a good approximation, it is also a biologically inaccurate one as well. Studies conducted on humans show that for small errors the cost is proportional to the squared error but it increases less quickly for larger errors [2]. In [29] Steve Scott supports the propositions from Todorov and Jordan in [32] and argues that global task errors should be used as the cost function. The idea behind global task errors being that of the many parameters of the system, only only those that influence the goal are monitored/corrected, a technique known as the minimum intervention principle. It is likely that the human body does this, as it allows for the controlled degrees of freedom to be reduced to only a few dimensions, making the problem significantly more manageable from a computational perspective.

One of the basic features of biological systems is the noise inherent in all communications between its components. Notably, when a subject performs a simple reaching task several times there is variability between each execution, however the subject will remain successful. A simple example would be during a reaching task where the goal is to touch a large circle within arms length, as long as the subject's hand finishes its trajectory inside of the circle the controller would not correct the motor action, even though the hand may not land in the same spot every time. Optimal feedback controllers can replicate this trial-to-trial variability with successful outcome through the minimum intervention principle. A critical part of optimal feedback controllers are internal models, used for motor planning and execution before sensory feedback is available. This allows for the system to react faster than is possible for a feedback based system, such as those operating under a servo-controller. Once sensory feedback is available the optimal feedback controller will use this information to correct any error affecting behavioral goals, minimizing the cost function (Figure 6). It is likely that the brain uses movement errors to correct its inverse models until they accurately reflect the operating environment. During these motor activities it has been shown that the cerebellum is highly active; however on a more in depth there is little known about how the underlying optimal integration and

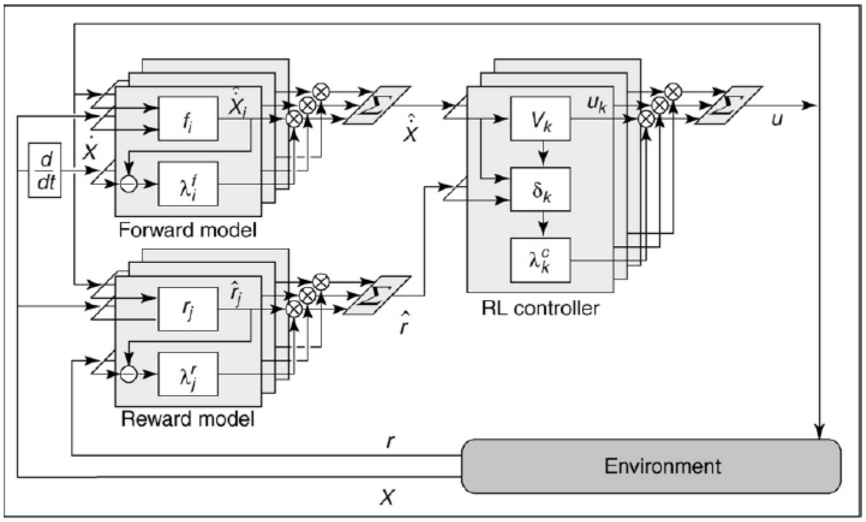

Figure 7: The architectural organization of the MOSAIC system. It is worth noting that the architecture does not select just one forward or reward model or RL controller, but instead it is possible that it will utilize many of them, blending their weighted outputs, taken from [17]

control algorithms necessary for optimal feedback control are implemented in the brain [2].

Initially, the idea of applying reinforcement learning in the brain was confronted with a difficult theoretical issues: Plain reinforcement learning is much to slow to be a plausible mechanism actually be implemented in the brain. However, Kawato et al. have remodeled the algorithm, introducing into it a hierarchy that allows for a quickly obtained optimal estimate at the higher levels which is then used to constrain the workspace of the lower levels and achieve a finer-grain accurate solution in a plausible amount of time [17]. Most studies investigating this possibility however hard code higher level representations, which is the same as assuming that all of the necessary parameters at the higher levels are genetically predetermined. As an alternative, Kawato et al. propose a modular selection and identification control (MOSAIC) system which allows for the logical subdivision of the reinforcement learning problem into several smaller subproblems.

The MOSAIC system is compromised of three sets of expert networks with the ability to self organize. These three networks maintain internal forward models, approximate actual rewards and use reinforcement learning controllers for computing the optimal control motor commands (Figure 7). Here the error signal for the internal forward models is taken as the forward model's predicted system dynamics compared to the actual resulting system dynamics. The other two networks used the difference between predicted reward and actual reward values as error signals. These signals are then also used to weight the outputs from each of the experts and to regulate the learning rate of the expert networks. Kawato et al. state that this system setup allows for modularity to emerge without ad hoc tuning by researchers or an assumption of genetic predetermination [17].

Constructing an optimal control feedback system with the reinforcement learning controlled by a MOSAIC system which has been implemented using motor primitives as a base for the internal models we can start to see how the research of the last decade in motor control can start to be tied together to weave a new model of the functioning of motor control in the brain. No doubt there are many difficult obstacles to overcome before a system resemblant of this could be constructed involving implementation and interface issues between the components, but nonetheless it is still very exciting to see even an outline of a more complete model of motor control in the brain emerging.

## 7 Neural Prosthetics

Research into neural prosthetics is a new field, and there are many different disciplines underlying its advancement. Basing their research heavily on work started by Georgopoulos et al. looking into predicting the movement direction intended by the subject based on a population vector analysis of an area of the motor cortex, Andrew Schwartz et al. have been developing an interaction system between monkeys and a robotic arm controlled by the neural discharge of an ensemble of neurons in the monkey's brain.

This process involves first surgically attaching micro electrodes in the monkey's brain that allow the activity of a group of neurons to be recorded. After recovery the monkey is trained to move a mouse cursor in VR via the neural discharge of the monitored ensemble. If the algorithm used to extract the intended movement of the monkey perfectly extracted motor commands then the monkey would be unable to tell the difference between control of the VR cursor and its arm and continue moving its arm throughout the task. However, this is not at all the case and it is noted that there is a great deal of work to be done on intended movement extraction techniques before this will occur. The monkey does succeed in controlling the VR cursor reasonably well though and hit most of the targets.

The next step involved restraining the monkey's arm entirely and training it to continue to operate the VR cursor without any arm movement. Notably, after the animal adjusted to this task there was no EMG sent down its arm while operating the VR cursor. Also, it was observed that the preferred direction of the recorded units would change as well with the switch from hand to brain control.

When moving from VR cursor control to the control of an actual robotic arm, there was some difficulty with the monkey being afraid of the large piece of machinery near it. This was overcome however and using pieces of food as motivation, the monkey was trained to use the robotic arm in an object retrieval reaching task. Schwartz states that where the current neural prosthetic implementation lacks control more specific than general reaching, future research will hopefully lead to identifying motor cortical activities that can be used to control more features of a neural prosthesis, such as the wrist, fingers, and finer-grain force control [28].

## 8 Future Work

Clearly there is boatloads of future work in the research of motor control in the brain. Throughout this paper there have been several avenues of future work mentioned, one of these was the development of a system that allows for the OLD of an appropriate population of neurons to be used as input for an inverse model predicting a weighted summation of motor primitives that can then be compared against actual motor primitives being used by a subject, recognized by a program capable of analyzing streaming video input and determining the base set of motor primitives at play. Another was to look at combining an optimal feedback controller system with a MOSAIC reinforcement learning system implemented with motor primitives used to define the internal models.

In addition to these there is a need for the development of better mathematical analysis techniques for deriving sets of motor primitives [14], and little is known about the biological implementation of the algorithms underlying optimal integration and control at the neuronal level [2]. These are both areas where developments could lead to breakthroughs not only in neuroscience but also other disciplines as well.

Looking at neural prosthetics, there has been work done by Georgopoulos that successfully captures the fine grained movement of the wrist and fingers to a high degree of accuracy [8] that could potentially be integrated into the current system. Although the focus is motor control in the brain, perhaps it would be beneficial to delve into recording signals from the CPGs in the spine of subjects for control of prosthetic limbs; it is known that all motor command signals go through the gray matter in the spine, this could help to shed light on what is not being recorded from the activity in the motor cortex necessary for accurate motor command recreation. On the idea of motor primitives, if they can be accurately identified it seems logical that having the same primitives implemented in the robotic arm would go a long ways toward making its control intuitive.

Obviously these are all very difficult problems and there are many variables involved and obstacles that need to be overcome before any of this would be possible, all the same there is a great deal of exciting future work ahead for research into motor control in the brain that we can look forward to.

## 9 Conclusions

In this paper I have several of the topics in much of the recent literature in motor control. I started by examining the original population vector encoding algorithms and the algorithms for movement prediction that were developed from that, following this motor primitives and their implications were discussed as well as central pattern generators and their role in simplifying complex rhythmic actions. Inverse models in the brain were examined followed by a look at optimal feedback control theory applied to motor control and the MOSAIC system for reinforcement learning. I ended this paper by discussing the exciting work in the field of neural prosthetics and areas for future work.

In conclusion, this is a very exciting time to be involved in the research of motor control in the brain and I greatly look forward to unraveling this mystery further.

## References

[1] G. E. Alexander and M. D. Crutcher. Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. *J. Neurophysiol.*, 41:164–178, 1990.

[2] P. Bays and D. Wolpert. Computational principles of sensorimotor control that minimize uncertainty and variability. *J Physiol*, 572.8:387–396, 2007.

[3] G. End, J. Morimoto, T. Matsubara, J. Nakanishi, and G. Cheng. Learning cpg sensory feedback with policy gradient for biped locomotion for a full body humanoid. *AAAI-05 Proceedings*, pages 1237–1273, 2005.

[4] D. Flament and J. Hore. Relations of motor cortex neural discharge to kinematics of passive and active elbow movements in the monkey. *J. Neurophysiol.*, 60:1268–1284, 1988.

[5] Q.-G. Fu, D. Flament, J. D. Coltz, and T. J. Ebner. Temporal encoding of movement kinematics in the discharge of primate primary motor and premotor neurons. *J. Neurophsiol.*, 73:863–854, 1995.

[6] A. Georgopoulos, R. Caminiti, J. Kalaska, and J. Massey. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci*, 2:1527–1537, 1982.

[7] A. Georgopoulos, R. Caminiti, J. Kalaska, and J. Massey. Spatial coding of movement: A hypothesis concerning the coding of movement direction by motor cortical primitives. *Exp. Brain Res. Suppl.*, 7:327–336, 1983.

[8] A. Georgopoulos, G. Pellizzer, A. Poliakov, and M. Schieber. Neural coding of finger and wrist movements. *J. of Computational Neuroscience*, 6:279–288, 1998.

[9] T. Graham-Brown. The intrinsic factors in the act of progression in the mammal. *Proc R Soc Lond B Biol Sci*, 84:308–319, 1911.

[10] J. Hale and F. Pollick. 'sticky hands': learning and generalisation for cooperative physical interactions with a humanoid robot. *'IEEE Transactions on Systems, Man, and Cybernetics*, 35:512–521, 2005.

[11] S. Hocherman and S. P. Wise. Effects of hand movement path on motor cortical activity in awake, behaving rhesus monkeys. *Exp. Brain Res.*, 83:285–302, 1991.

[12] A. Ijspeert, J. Nakanishi, and S. Schaal. Movement imitation with nonlinear dynamical systems in humanoid robots. *ICRA2002 Proceedings*, pages 1398–1403, 2002.

[13] M. Ito. Neurophysiological aspects of the cerebellar motor control system. *Int. J. Neurol.*, 7:162–176, 1970.

[14] O. Jenkins and M. Mataric. Automated derivation of behavior vocabularies for autonomous humanoid motion. *AAMAS*, pages 225–232, 2003.

[15] K. Kawano. Ocular tracking: behavior and neurophsyiology. *Current Opinion in Neurobiology*, 9:467–473, 1999.

[16] M. Kawato, K. Furukawa, and R. Suzuki. A hierarchical neural-network model for control and learning of voluntary movement. *Biological Cybernetics*, 57:169–185, 1987.

[17] M. Kawato and K. Samejima. Efficient reinforcement learning: Computational theories, neuroscience and robotics. *Current Opinion in Neurobiology*, 17:205–212, 2007.

[18] R. E. Kettner, A. B. Schwartz, and A. P. Georgopoulos. Primate motor cortex and free arm movements to visual targets in three-dimensional space iii. positional gradients and population coding of movement direction from various movement origins. *J. Neurosci*, 8:2938–2947, 1988.

[19] J. Lackner and P. DiZio. Motor control and learning in altered dynamic environments. *Current Opinion in Neurobiology*, 15:653–659, 2005.

[20] R. Miall and D. Wolpert. Forward model for physiological motor control. *Neural Net*, 9:'1265–1279.

[21] K. Mitsuo. From 'understanding the brain by creating the brain' towards manipulative neuroscience. *Philisophical transactions of the Royal Scoiety of London: Biological Sciences*, 363(1500):2201–2214, 2008.

[22] H. Miyamoto, M. Kawato, T. Setoyama, and R. Suzuki. Feedback-error-learning neural network for trajectory control of a robotic manipulator. *Neural Networks*, 1:251–265, 1988.

[23] F. Mussa-Ivaldi and E. Bizzi. Motor learning through the combination of primitives. *Phil Trans R Soc Lond*, 355:1755–1769, 2000.

[24] F. Mussa-Ivaldi, S. Giszter, and E. Bizzi. Linear combinations of primitives in vertebrate motor control. *Proc Natl Acad Sci USA*, 91:7534–7538, 1994.

[25] F. Mussa-Ivaldi and S. Solla. Neural primitives for motion control. *IEEE Journal of Oceanic Engineering*, 29:640–651, 2004.

[26] J. Nakanishi and S. Schaal. Feedback error learning and nonlinear learning adaptive control. *Neural Networks*, 17:1453–1465, 2004.

[27] E. Salinas and L. Abbot. Vector reconstruction from firing rates. *J. Comp. Neurosci.*, 1:89–107, 1994.

[28] A. Schwartz. Useful signals from the motor cortex. *J Physiol*, 597.3:581–601, 2007.

[29] S. Scott. Optimal feedback control and the neural basis of volitional motor control. *Nature Publishing Group*, 5:534–546, 2004.

[30] S. Scott. Inconvenient truths about neural processing in primary motor cortex. *Physiology in Press*, 2008.

[31] O. Steinberg, O. Donchin, A. Gribova, S. C. de Oliveira, H. Bergman, and E. Vaadia. Neuronal populations in primary motor cortex encode bimanual arm movements. *European Journal of Neuroscience*, 15:1371–1380, 2002.

[32] E. Todorov and M. I. Jordan. Optimal feedback control as a theory of motor coordination. *Nature Neurosci*, 5:1226–1235, 2002.

[33] B. Winkelman and M. Frens. Motor coding in floccular climbing fibers. 95:2342–2351, 2006.

[34] D. Wolpert, R. Miall, and M. Kawato. Internal models in the cerebellum. *Trends Cogn Sci*, 2:338–347, 1998.