THE MODULAR ORGANIZATION OF MOTOR CONTROL: WHAT FROGS CAN TEACH US ABOUT ADAPTIVE LEARNING

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Abstract. Investigations of motor control in the spinaized frog have suggested the presence, within the spinal cord, of a number of discrete control modules that may act, either individually or in combination, to generate a variety of motor behaviors. The experimental findings indicate that the simultaneous activation of two modules leads to the vectorial summation of their output forces. These findings have led us to consider the output generated by the spinal cord as a system of vector–valued basis functions. In this context, the execution of complex motor behaviors and the adaptation to novel environments may be investigated as forms of function approximation.

Key Words. Motor control, Bio control, Function approximation, Impedance control, Adaptation

1. INTRODUCTION

Recent evidence obtained by focal microstimulation of the frog's spinal cord has revealed that the lumbar grey matter contains a number of circuits that are organized to coordinate the activation of multiple muscles (Bizzi et al. 1991, Mussa-Ivaldi and Giszter, 1992). As a consequence, the mechanical effect of activating a small region in the lumbar grey matter is a pattern of forces that may be measured at the ankle and that converge toward an equilibrium point in space. In this article we explore some of the implications of these findings with respect to the task of generating a variety of motor behaviors and of adapting the learned behaviors to changing mechanical environments.

2. THE MODULAR ORGANIZATION OF THE FROG'S SPINAL CORD

We begin by discussing some recent experiments which were directed at identifying the organization of motor output in the frog's spinal cord. (Bizzi *et al.*, 1991; Giszter *et al.*, 1993). In these experiments, Bizzi, Giszter and Mussa–Ivaldi stimulated with a microelectrode the gray matter of the lumbar cord and measured isometric forces at the ankle with the frog's leg held in a variety of postures. Each stimulus consisted in a train of current impulses which lasted typically 300 milliseconds. The impulses had a duration of one millisecond and a frequency of 40 Hz. The peak amplitude ranged between 1 and 6 microamperes.

The analysis of the mechanical responses was restricted to the horizontal plane. Ankle locations were specified as pairs of Cartesian coordinates with respect to the hip joint. The ankle was placed at a number of locations (9 to 16), which formed a regular grid over the leg's workspace. At each location, the force vector, F, elicited by the stimulation of the same spinal-cord locus and with the same current parameters was recorded. The measured force vector varied as a function of the workspace location, x . The changes in force through the workspace may be attributed to a number of factors: the neural activation of muscles, as well as their lengths, moment arms and visco-elastic properties.

The data collected in this microstimulation experiment constitute a set of samples of a time-varying force field, $F(x,t)$, obtained at a number of tested sites. F(x, t) denotes the force vector at the location, r, after a latency, t, from the onset of the stimulus. In most instances, the spatial distribution of the forces induced by the stimulation was structured in a well defined pattern: the flow of force vectors converged towards a single equilibrium point. The area of the spinal cord from which such convergent fields were observed was quite broad. Force fields converging to different equilibrium points have been observed by placing the stimulating electrode in different sites of the spinal cord. These experiments indicated that there are at least four spinal regions from which four distinct convergent fields are elicited. Within each region, the stimulation of the premotor layers of the spinal gray matter generates a similar pattern of force vectors.

In all likelihood, the convergent force fields derive at least in part from the activation of the spinal interneurons. The branches of these interneurons make synaptic connections with different motoneurons[1] Remarkably, when the electrode was placed within a motoneuron pool, the stimulation induced a radically different type of field. The force vectors were arranged in a parallel or divergent pattern instead of converging to an equilibrium point. This result indicates that the convergence of the field is likely due to a critical balance of different muscles. Balance that is lost when the electrical stimulus activates only the motoneurons connected to a single muscle or to a group of synergistic muscles.

In summary, these microstimulation experiments suggested that the interneurons in the spinal cord may be organized in a relatively small number of modules. Each module is connected to a balanced set of motoneuron pools. Thus, each module organizes the mechanical behavior of a group of spring-like muscles into an end-point field that converges to a single equilibrium position. We are led then to ask whether and how the central nervous system may generate not just a few fields but a full repertoire of them by combining the outputs of a few modules. This question has been addressed by stimulating two separate spinal sites, first independently and then simultaneously (Bizzi *et al.*, 1991; Mussa-Ivaldi *et al.*, 1994). Remarkably, in the large majority of the cases (87.8%) the simultaneous stimulation of two sites resulted in a force field proportional to the vector sum of the fields obtained by the stimulation delivered at each point. This finding indicates that the central nervous system may generate a repertoire of fields by a simple superposition mechanism.

3. ENDPOINT SUMMATION AND KINEMATIC REDUNDANCY

The finding of vector summation has been particularly surprising when the frog's leg was connected to the force sensor in a *kinematically redundant* configuration (Mussa-Ivaldi *et al.*, 1994). In this case, the foot was attached to the sensor through a gimbal mechanism which allowed the leg to assume a variety of configurations while the center of the foot was held rigidly at a location in the plane. Theoretical considerations are sufficient to establish that the endpoint forces of a kinematically redundant limb need not to combine according to vector summation, even in the simple case of direct muscle activation (Gandolfo and Mussa-Ivaldi, 1993).

The redundancy of a limb is established by the imbalance between the limb's degrees of freedom and the number of end-point coordinates. For example, in our experiment the configuration of the frog's leg was specified by six joint angles: three at the hip, one at the knee and two at the ankle. We indicate these angles collectively by the array $q = (q_1, q_2, \ldots, q_6)$. At the same time, the center of the foot was constrained by the gimbal to remain on the horizontal plane. Thus, the position of the foot was determined by a two–dimensional array: $x = (x_1, x_2)$. With such an imbalance between degrees of freedom and end point coordinates, the mapping from q to x cannot be inverted to derive uniquely the leg configuration corresponding to any given foot location.

The generalized force in the leg's configuration space is a 6–dimensional torque vector, $\tau = (\tau_1, \tau_2, \ldots, \tau_6)$. The activation of a viscoelastic muscle, m, is expected to give rise to a field of generalized forces in configuration space, that is a mapping, ϕ, from q to τ: $\tau = \phi(q)$. As far as one is dealing with configuration space– the space of all independent degrees of freedom– and with a set of independent actuators, one can prove that the mapping $\phi(q)$ obeys the rule of vectorial summation (Gandolfo and Mussa–Ivaldi, 1993): given two distinct muscles, m and n, with torque fields $\phi_m(q)$ and $\phi_n(q)$, their simultaneous action gives rise to the field

$$\phi_\Sigma(q) = \phi_m(q) + \phi_n(q). \tag{1}$$

It is crucial to stress that in the above expression the three fields, ϕ_Σ, ϕ_m and ϕ_n are evaluated at the same configuration, q. In contrast, with three different configurations, q_a, q_b and q_c it is possible that

$$\phi_\Sigma(q_a) \neq \phi_m(q_b) + \phi_n(q_c). \tag{2}$$

even when Equation (1) is satisfied.

Let us now consider the field of forces generated at the endpoint of the redundant arm by the activation of two independent actuators. Each one of these fields may be regarded as the outcome of an experiment in which a muscle is activated and the end–point force vector $F = (F_1, F_2)$ is measured at a number of locations in the x_1, x_2

[1] Motoneurons constitute the final output stage of the spinal cord. They are organized in clusters, or "pools", of cells which innervate the same muscle.

plane. Let us indicate by $F_m(x)$, $F_n(x)$ and $F_\Sigma(x)$ the endpoint force fields obtained by activating, respectively, muscle m, muscle n and both muscles simultaneously. If one assumes that Equation (1) is true, one can inquire whether $F_\Sigma(x) = F_m(x) + F_n(x)$.

The answer is no. Because of the kinematic redundancy, the same hand location in the above expression will eventually correspond to three different joint configurations, q_m, q_n and q_Σ. Therefore, in spite of the fact that we are looking at the same endpoint location, we are now in the case described by Equation (2) rather than (1)

The above considerations establish that the endpoint fields of a redundant limb need not combine according to vectorial summation, even in the simple case in which these fields are induced by direct muscle stimulation. However, we cannot rule out vector summation in particular cases nor are we able yet to establish how non-linear the behavior of a limb is expected to be given the limb's biomechanical structure. Remarkably, the experimental results of Mussa–Ivaldi et al. (1994) have indicated that endpoint field summation is the predominant outcome in the presence of kinematic redundancy. This finding is important as it suggests that *the neural controller of a redundant mechanical system may neglect the details of the system's kinematics and focus exclusively at the "end point" that is at the site of interaction between the system and its environment.* This is one of the main aspects of what is now known as "impedance control" (Hogan, 1985).

4. FIELD APPROXIMATION

The findings described in the previous sections lead to a formal analysis of motor control based on the framework of function approximation (see also (Sanner and Slotine, 1992)). Let us consider a simplified system consisting of a set of K independent control modules acting in parallel upon the muscles of a multi-joint limb. Each control module establishes the viscoelastic properties of a group of muscles. As a result, each module generates at the interface between the limb and the environment a force-field

$$F_i = \Phi_i(x, u_i). \tag{3}$$

where u_i indicates the controller's command variable. The findings of the microstimulation experiments suggest that the net force field generated by the whole ensemble of controllers is:

$$F(x, u_1, \ldots, u_K) = \sum_{i=1}^{K} \Phi^i(x, u_i). \tag{4}$$

We may define the *repertoire* of a control network as the set of all possible net fields with all possible values of the control variables. If we denote by $\mathcal{U}_i$ the set of the admissible values for the command variable u_i, the repertoire of the control networks is the set:

$$X = \left\{ \sum_{i=1}^{K} \Phi^i(x, u_i) \mid u_i \in \mathcal{U}_i \right\}$$

Vector fields provide not only a description of the control processes but also a framework for specifying the planning of a desired behavior. In robotics some researchers have proposed to specify the planning of complex tasks by force fields defined over a manipulator's workspace. For example, Kathib (Kathib, 1986) used potential fields to represent the planning of reaching motions within obstacle-ridden environments. Kathib (1986) and Hogan (1984) suggested to implement the planned potential functions by a set of controllers operating in parallel. According to this view, each controller derives the forces induced by a target or by an obstacle by directly computing the gradient of the corresponding potential field. Thus, the field specified by the planner is faithfully implemented by the controllers.

Here, we present a different approach in which both planning and execution are directly represented as vector fields instead of scalar potential fields. A vectorial representation is indeed more general than a scalar representation. It is always possible to derive the former from the latter, whereas a vector field may not be reducible to a potential function. Second, we may reasonably assume that a vertebrate's motor control system has a repertoire, X, generated by the vector combination of independent modules. This repertoire is limited by the pre-defined properties of the controllers and of the actuators. In other words we cannot assume that any goal may be accurately mapped into a corresponding motor output. Instead, the spinal microstimulation experiments suggest that control primitives are established a-priori by the connections between muscles and neural circuits. Following this view, the execution of an arbitrary motor plan is equivalent to a field-approximation problem: given a planned field, $P(x)$, the problem is to find a field, $F(x) \in X$, which minimizes some norm

$$\| P(x) - F(x) \|^2$$

suitably defined over the limb's state space (see also the section on motor control in Poggio, 1990).

The field-approximation problem assumes a more tractable form if a planned behavior is specified by a finite set of M force vectors, $\{P^1, P^2, \ldots, P^M\}$, defined at M points, $\{x^1, x^2, \ldots, x^M\}$, rather than by a continuous field, $P(x)$. We consider these vectors as samples (or "examples") of a field to be filled in (or "completed") by an appropriate choice of control parameters.

For the sake of clarity we may further simplify our discussion by using a factored form for the the output function (3) implemented by each control module:

$$\Phi_i(x, u_i) = u_i \phi^i(x). \tag{5}$$

We call this form *linear tuning*: the control variable, u_i plays the role of a scaling factor applied to a (nonlinear) output field. In this case, the repertoire of the control network is the linear span:

$$X = \left\{ \sum_{i=1}^{K} u_i \phi^i(x) \mid u_i \in \mathcal{U}_i \right\}$$

and we may apply the methods of linear algebra as outlined in Mussa-Ivaldi (1992) for approximating an arbitrary pattern of vectors. Given a set of M pattern vectors, $P^1, \ldots, P^M$, specified at M distinct locations, $x^1, \ldots, x^M$, the approximation goal is to find a set of control parameters such that

$$\sum_{i=1}^{K} u_i \phi^i(x^j) \sim P^j$$

for $j = 1, \ldots, M$. In an N-dimensional vector space, this goal is expanded into a system of MN linear equations (one per data component) in K unknowns. This system of equations can be compactly written as:

$$\Phi u = \hat{P} \tag{6}$$

where we have introduced the (unknown) control vector

$$u = (u_1, u_2, \ldots, u_K),$$

the matrix

$$\begin{bmatrix} \phi_1^1(x^1) & \phi_1^2(x^1) & \ldots & \phi_1^K(x^1) \\ \phi_1^1(x^2) & \phi_1^2(x^2) & \ldots & \phi_1^K(x^2) \\ & \ldots & & \\ \phi_1^1(x^M) & \phi_1^2(x^M) & \ldots & \phi_1^K(x^M) \\ & \ldots & & \\ & \ldots & & \\ \phi_N^1(x^1) & \phi_N^2(x^1) & \ldots & \phi_N^K(x^1) \\ \phi_N^1(x^2) & \phi_N^2(x^2) & \ldots & \phi_N^K(x^2) \\ & \ldots & & \\ \phi_N^1(x^M) & \phi_N^2(x^M) & \ldots & \phi_N^K(x^M) \end{bmatrix},$$

and the "pattern vector"

$$\hat{P} = (P_1^1, P_1^2, \ldots, P_1^M, P_2^1, P_2^2, \ldots, P_2^M, \ldots, P_N^1, P_N^2, \ldots, P_N^M).$$

The approximation problem (6) can be solved for any set of pattern vectors if the output fields, $\phi^i(x)$, are linearly independent. In this case, the output fields– which we call *basis fields* – form a basis for a K-dimensional functional space. It is possible to derive basis fields from scalar basis functions as detailed in (Mussa-Ivaldi, 1992)[2]. Following this approach, a general representation of a continuous field is obtained by combining K_I irrotational basis fields and K_S solenoidal basis fields:

$$F(x) = \sum_{i=1}^{K_I} c_i \varphi^i(x) + \sum_{i=1}^{K_S} d_i \psi^i(x).$$

An irrotational basis field, $\varphi^i(x)$, has zero curl and is the gradient of some scalar basis function, $g_i(x)$, that is

$$\varphi^i(x) = \nabla g_i(x) \quad \text{and} \quad \mathrm{curl}(\varphi^i) = 0$$

A solenoidal basis field, $\psi^i(x)$, has zero divergence. In the Euclidean metric, an irrotational basis field is obtained from a basis function, $g_i(x)$, by applying the operator $A\nabla$, where A is an antisymmetric[3] matrix:

$$\psi^i(x) = A\nabla g_i(x) \quad \text{and} \quad \mathrm{div}(\psi^i) = 0.$$

This statement can be demonstrated for $x \in \Re^N$, with $N \geq 2$. In particular, with N = 2 and N = 3 an antisymmetric matrix, A, corresponds to a 90^o rotation operator.

The set of control coefficients, c_i and d_i, obtained from the approximation of a field feature can be regarded as a *representation* of the corresponding planning goal within the repertoire of the controller network.

5. ADAPTIVE CONTROL

The presence of a set of independent control modules provides a powerful framework for the representation of motor learning. We may distinguish between two broad classes of motor learning: *skill learning* and *adaptive learning*. The first type of learning refers to the acquisition of new patterns of control that lead to the execution of novel behaviors. This happens for example, when we learn

[2] See also (Wahba, 1982) for a similar generalization of splines to the approximation of vector fields on the sphere.

[3] A matrix, $A = [a_{i,j}]$ is said to be antisymmetric if $a_{i,j} = -a_{j,i}$ $(a_{i,i} = 0)$.

to play tennis, or to drive a car. In contrast, adaptive learning is the process by which a repertoire of previously acquired skills is transported across different environments. To put it in more formal terms, consider the following differential equation that describes the behavior of a broad class of dynamical systems:

$$D(x, \dot{x}, \ddot{x}) = C(x, \dot{x}, t) \tag{7}$$

The term, $D(\cdot)$ on the left—hand side is a non–linear time–independent second–order differential expression that captures the dynamics of a plant at the interface with the environment. For example, the controlled system may be an arm in which case x indicates the position of the hand and $D(\cdot)$ is the force generated at the hand in response to an externally imposed displacement. The term $C(\cdot)$ on the right–hand side of (7) is the time– and state–dependent force generated by a controller upon the system described by $D(\cdot)$. Equation (7) is a second–order ordinary differential equation which defines a unique trajectory, $x(t)$ for any given initial condition, $x_0 = x(t_0)$, $\dot{x}_0 = \dot{x}(t_0)$. In this context, learning new skills corresponds to establishing a repertoire of controllers, $C_i(x, \dot{x}, t)$, that generate a corresponding repertoire of trajectories, $x_i(t)$. The task of adaptive learning can be instead described as follows. Suppose that a new load is attached to the controlled system. This load may be represented as an additional dynamical term, $E(x, \dot{x}, \ddot{x})$. With the controller of Equation (7), the differential equation describing the system with the load is:

$$D(x, \dot{x}, \ddot{x}) + E(x, \dot{x}, \ddot{x}) = C(x, \dot{x}, t). \tag{8}$$

Generally, this equation admits a new solution, $x^*(t)$, given the same initial conditions, $(x_0, \dot{x}_0)$. The purpose of adaptive learning is to generate a correction of the old controller so as to restore the behavior of the system as it was generated by Equation (7) before the onset of the load. A possible way to represent this correction is by means of a new controller, C', expressed as the old one, C, plus an additive term, D:

$$C'(x, \dot{x}, t) = C(x, \dot{x}, t) + D(x, \dot{x}, t).$$

In this case, it is not difficult to see that a sufficient condition for restoring the old controller is that, along the original trajectory $x(t)$, the following differential equation be satisfied:

$$E(x, \dot{x}, \ddot{x}) = D(x, \dot{x}, t). \tag{9}$$

If this is the case, the equation

$$D(x, \dot{x}, \ddot{x}) + E(x, \dot{x}, \ddot{x}) = C'(x, \dot{x}, t)$$

is reduced to the original equation (7) for the system without load. We must stress however, that this approach to load compensation is by no means unique. In fact, a strategy based upon the increase of the controller's impedance about the desired trajectory, $x(t)$, would be equally adequate to restore the original behavior (Shadmehr and Mussa–Ivaldi, 1994).

The approach described by Equation (9) is equivalent to state that adaptation is achieved by constructing an internal model (the controller field D) of the environment (the load field, E). Recent experiments of Shadmehr and Mussa–Ivaldi (1994) have indeed suggested that the construction of such an internal model may be the process through which human subjects achieve the adaptation of multi–joint arm movement to external loads. In these experiments, subjects were asked to execute reaching movements of the hand in the horizontal plane while holding the handle of a robot manipulandum. During the initial part of each experiment, the manipulandum acted as a low–impedance passive device (the motors were turned off) and the subjects were asked to move their hand toward a set of targets located at different location of the horizontal plane. Under these circumstances, the hand movements were characterized by smooth straight–line hand trajectories, as described by several authors (Morasso, 1981; Flash and Hogan, 1985). In a second part of the experiment, the robot manipulandum was programmed to generate a force field, that is a function that mapped the instantaneous hand velocity into a corresponding force applied to the subject. Since the force field significantly changed the dynamics of the task, subjects' initial movements in the force field were grossly distorted as compared to their movements in free space. However, with practice, hand trajectories in the force field converged to a smooth and straight path, very similar to that observed in free space. In order to investigate the mechanism underlying this adaptation, Shadmehr and Mussa–Ivaldi (1994) observed the response to sudden removal of the field after a training phase. The resulting trajectories were approximately mirror images of those which were observed when the subjects were initially exposed to the field. This suggested that the arm controller had indeed composed an internal model of the applied field. A model that, like the field D in Equation (9) the nervous system used to predict and compensate the forces imposed by the environment.

The construction of an internal model is quite consistent with the field–approximation framework described in the previous section (Sanner and Slotine, 1992). Indeed, let us suppose that a set of modules or "pattern generators" is implemented– for example– by the neural circuits within a subject's spinal cord and let us suppose that each pattern generator when active induces a field $\phi_i(x, \dot{x}, t|c_i)$ of endpoint forces. In this expression, the variable, c_i is an "activation variable" representing a tuning effect of descending commands. Using this representation, the adaptive controller described by Equation (9) can be written as

$$E(x, \dot{x}, y(t)) \sim \sum_i \phi_i(x, \dot{x}, t|c_i) \tag{10}$$

where $y(t) = \ddot{x}(t)$ and the sum is extended over a particular set of spinal modules. The above expression describes a field approximation problem whose goal is to derive a set of control variables, c_i, that minimize some norm

$$\| E - \sum_i \phi_i \|^2$$

defined over the space of endpoint trajectories.

6. CONCLUSION

The microstimulation of the frog's spinal cord has provided us with important evidence suggesting that the output stages of the vertebrate motor system is organized into a small set of independent control elements. Each control element coordinates the activations of a group of viscoelastic muscles and the observable consequence of these activations is a field of forces acting upon the controlled limb.

The modular nature of these control elements is expressed by the observation that their simultaneous activation leads to the vectorial summation of the corresponding fields. Remarkably, this summation property is preserved when the forces are measured at the endpoint of a kinematically redundant limb. We are led by these findings to conclude that the force fields induced by the muscle spring–like properties at the interface between a controlled limb and its environment may constitute a "vocabulary" of simple control functions that are combined to construct more complex behaviors. From this standpoint, our findings are consistent with the general framework of impedance control (Hogan, 1985).

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