

NEURAL PRIMITIVES FOR MOTION CONTROL

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Abstract—The neural control of movement requires the ability to deal with changes, both in the environment and in the parameters that characterize the mechanical structure of the organism. Here we discuss the three types of coordinate representations that sensory and motor systems use to generate and control movements, and argue that the intrinsic redundancy of the musculoskeletal system can be exploited to implement control signals that result in successful task completion while allowing for variance in trajectory parameters not relevant to the task. We also argue that muscle synergies activated through the stimulation of specific loci along the spinal cord provide evidence for the existence of a vocabulary of motor primitives that can be combined, either simultaneously or sequentially, to generate a broad repertoire of complex movements.

I. INTRODUCTION

Moving in a coordinated, graceful and efficient way is not a simple art. The study of motor behavior in animals and in artificial systems has revolutionized our ideas on intelligence. Contrary to older views of intelligence that placed all emphasis on “high level” logical reasoning, Herbert Simon, Nobel laureate for Economics, once predicted that it will be easier to create an artificial college professor than an artificial bulldozer driver. More recently, Llinas [1] has argued that the very existence of the nervous system may be traced back phylogenetically to the first multicellular organisms, such as the sea squirt, that were endowed with the ability - and with the challenge - to move in the environment. The complexity of motor behavior has become more evident to neurobiologists as robotic engineers have identified the computations involved in controlling the motion of artificial manipulators [2]. Here, we present some perspectives on neural control

of movement in a broad spectrum of vertebrates, ranging from fish to human. What is common to these studies is the focus on the information processing that the nervous system is capable of carrying out with an efficiency and robustness that still surpasses the most advanced artificial systems. In fact, the nervous system is routinely engaged in solving problems that engineers must deal with to control systems such as robotic devices and Autonomous Underwater Vehicles (AUV).

Differential equations provide the means for investigating this kind of dynamical systems. Engineers and physicists have developed computational tools for integrating differential equations, both ordinary and partial, and for solving problems such as the flow around a flapping foil or the motion of a robotic arm. However, the study of complex systems [3] has highlighted some limitations in the use of traditional analytical tools. The main concept behind current approaches to complex dynamical systems has been succinctly stated by Cvitanovic [4]:

“Armed with a computer and a great deal of skill, one can obtain a numerical solution to a nonlinear PDE. The real question is: once a solution is found, what is to be done with it? ...Dynamics drives a given spatially extended system through a repertoire of unstable patterns; as we watch a “turbulent” system evolve, every so often we catch a glimpse of a familiar pattern. For any finite spatial resolution, the system follows approximately for a finite time a pattern belonging to a finite alphabet of admissible patterns, and the long-term dynamics can be thought of as a walk through the space of such patterns, just as chaotic dynamics with a low-dimensional attractor can be thought of as a succession of nearly periodic (but unstable) motions.” A similar argument leads to the conclusion that, in order to generate and control complex behaviors, the brain needs not to explicitly solve a system of coupled equations. A more plausible mechanism is the construction of a vocabulary of

fundamental patterns, or primitives that are combined sequentially and in parallel for producing a broad repertoire of coordinated actions. This concept appears to be at the basis of neural control of movement and is the central theme of this review.

The nervous system of fish, and more generally of vertebrates, is evidently capable of solving complex problems, such as reaching for food while avoiding obstacles in an unsteady current. It is generally accepted that the type of neural computation underlying such behaviors is based on the utilization of previously learned patterns as a means to analyze and generate new ones. Thus, the idea of solving hard control problems by combining the elements of a finite vocabulary of primitives has become one of the

key concepts in the neurobiology of the motor system. This review is a discussion of the computational and physiological basis for this approach, for developing intelligent control systems for a new generation of Biorobotic Autonomous Undersea Vehicles (BAUV).

II. NEURAL CONTROL OF MECHANICAL SYSTEMS

A general feature of biological systems is redundancy of muscles and degrees of freedom. This issue is specifically discussed by Colgate and Lynch [5] in the context of fish navigation, through a distinction between *shape* and *group* variables.

The execution of the simplest action requires the accurate coordination of several muscles. In robotic

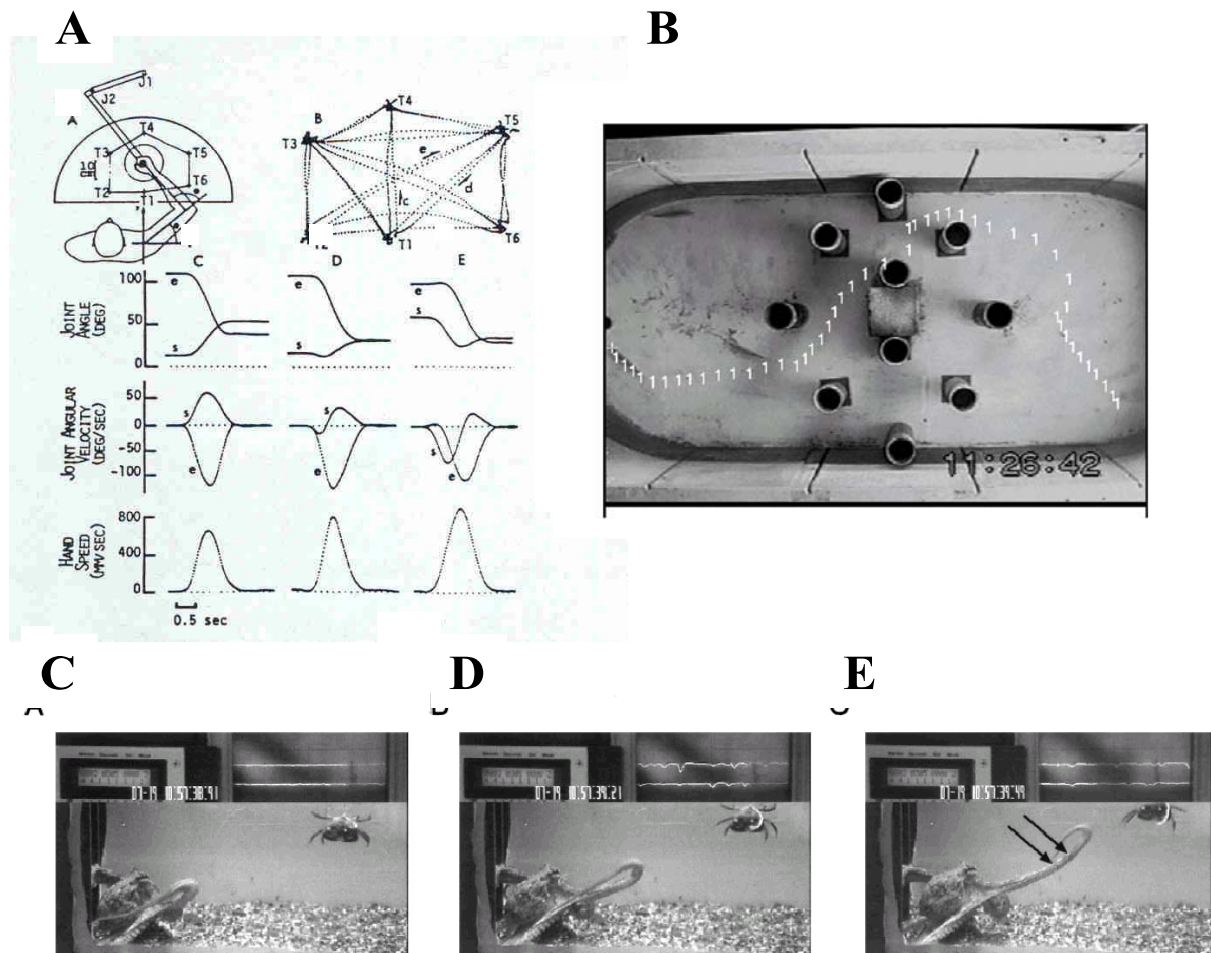


Figure 1. *Three examples of smoothness in endpoint motion.* A. Reaching movements of the hand take place along straight line segments. The temporal profiles of hand speed display a symmetric bell-shaped pattern for all trajectories. In contrast, the joint angular velocities have different temporal profiles in different movements (From Morasso, 1981). B. Digitized trajectory of a bluefish. The path is a smooth curve among the obstacles. (From Bandyopadhyay2002). C. Three video frames of an octopus reaching for a target. The bending point of the tentacle follows a straight path with a unimodal velocity profile (From Gutfreund et al. 1998).

systems, engineers coordinate the action of multiple motors by writing computer code that specifies how the motors must be activated for achieving the desired robot motion and for rejecting unexpected disturbances. Vertebrate animals use a different mechanism. Nature achieves something akin to programming through the biological mechanisms of synaptic plasticity [6-9], that is by the variation in efficacy of neural transmission brought about by past history of pre- and post-synaptic signals.

Robots and animals differ in another important way. Robots (at least the most conventional ones) have fixed mechanical structure and dimensions. In contrast, the mechanics of muscles, bones and ligaments change over time: the length and functionality of the body changes dramatically with growth. This is particularly evident in species, such as the Lamprey, characterized by a sharp transition from larval to adult stages. As a lamprey grows in size, its central nervous system must update the muscle commands that generate an undulation involving the entire body length in a single cycle. Both artificial and natural devices must face the challenges of a changing environment. Because of body and environmental changes, the central nervous system must continuously adapt motor commands to new mechanical conditions. Adaptation - the ability to carry previously learned motor skills into new mechanical contexts - is the most distinctive feature of biological motor systems and is widely investigated by neurobiologists [10-14].

The geometrical nature of the operations that the brain must carry out in the recognition of objects and in the execution of movements is a central issue in neural information processing. In particular, some critical operations in the generation and control of movements can be formulated as coordinate transformations. Sensory information about the state of motion of the body comes from a variety of signal sources, each being concerned with a particular mechanical variable. For example, skeletal muscles are endowed with fusiform sensors that measure the muscle strain and its rate of change [15]. Muscles are also endowed, at the junction with tendons, with Golgi tendon organs [16] that sense variations in muscle force. Other receptors are sensitive to the displacement of the joints, to pain, to temperature, etc. Signals from other sensory organs, like the eyes and the vestibular organs, provide information about the position of the body and of its parts with respect to the

environment. This variety of sensory channels is matched by a relatively uniform motor structure. The neural signals controlling muscle contractions are generated by the motoneurons, which are located inside the grey matter of the spinal cord. Muscles are partitioned into groups of fibers - called motor units - that receive common innervation from a single motoneuron. The force generated by a muscle is graded by a distribution of neural activities over the motoneurons. Each motor unit generates tension. As motor units are connected both in series and in parallel within a muscle, either tensions (parallel) or strains (series) are combined additively.

While there are several possible coordinate systems to describe different sensory and motor signals, these coordinate systems fall quite naturally into three classes: actuator coordinates, generalized coordinates and endpoint coordinates [17]. This nomenclature comes mostly from the analysis of arm movements, but is readily extended to more diverse situations including underwater maneuvering.

1) Endpoint coordinates

Endpoint coordinates are appropriate for describing the goal of an action and the interaction with the environment. These coordinates simplify the description of symmetries that are present in the external environment. Perhaps the most striking of these is the Euclidean symmetry, the invariance of distance under rotations and translations. This symmetry can be observed in the environment within which organisms move. The dimensionality of endpoint space is generally rather low. The state of a moving rigid body is adequately described by six position coordinates (3 translations and 3 angles). Accordingly, the force applied to the body is a 6-dimensional force/torque vector. In a target reaching task, the position of a point target relative to the body is given by 3 coordinates (e.g. the Cartesian coordinates of the target with respect to a frame fixed in the body). Human hand movements tend to be spontaneously organized in endpoint coordinates: the kinematics of reaching is generally a maximally smooth trajectory - i.e. a straight line with bell-shaped velocity profile - when described in the coordinates of the hand [18, 19] (Figure 1A). This is remarkable because the kinematics of a multi-jointed limb define a curved manifold which does not match the symmetries of Euclidean space. Similar observations were made recently [20] in reaching movements of the octopus (Figure 1C): a stereotyped tentacle motion, characterized by a bending wave traveling along the tentacle, leads to a kinematically simple

movement of the bending point that moves in a radial nearly rectilinear direction toward the target. This bending motion does not appear to be produced as a passive whip, but rather by a continuously propagating wave of muscle activity. This insures a repeatable velocity profile and a quasi-planar motion of the limb. The observations by Bandyopadhyay et al. [21] of trajectories of blue fish and mackerel in an obstacle-ridden tank illustrate a similar result: the trajectories appeared to be smooth and determined by the location of the obstacles rather than by the dynamics of the body (Figure 1B). These findings from such radically different systems suggest that the central nervous system plans movements in endpoint coordinates and that this planning is enforced by a control system that to a significant extent is capable of overcoming the passive dynamics of the body. However, as discussed below, in other instances the control system appears to take advantage of passive dynamical properties, such as the muscles' built-in stability.

2) Actuator Coordinates

Actuator coordinates [22] afford the most direct representation for the motor output of the central nervous system. A *position* in this coordinate system may be, for example, a collection of muscle lengths, $l = (l_1, l_2, \dots, l_M)$. Accordingly, a force in the same coordinate system is a collection of muscle tensions, $f = (f_1, f_2, \dots, f_M)$.

Unlike generalized coordinates, actuator coordinates do not constitute a system of mechanically independent variables: one cannot set arbitrary values to all l_i without eventually violating a kinematic constraint.

The dimension of actuator space may vary depending upon the level of detail in the physiological analysis. Many studies have focused on simplified models, in which a single joint is operated by a pair of muscles acting as reciprocal (agonist/antagonist) actuators. If several degrees of freedom are involved in the motion and multiple muscle groups are considered, the dimension of the actuator space will increase, typically by one order of magnitude. At the most detailed level, individual motor units may be considered as actuator elements. In this case, the dimension of the actuator space can reach hundreds of thousands.

3) Generalized Coordinates

A different way of describing body motions is to provide the set of joint angles that define the orientation of each skeletal segment either with

respect to fixed axes in space or with respect to the neighboring segments. Joint angles are a particular instance of *generalized coordinates*. Generalized coordinates are independent variables suitable for describing the dynamics of a system [23, 24].

Given a set of generalized coordinates one may define a *generalized force* vector. As the kinematics of the body are often approximated by a tree of rigid links, interconnected by joints with one to three rotational degrees of freedom, the corresponding generalized forces are the torque components generated at each joint by the muscles and by the external environment. The dynamics of the body or of its parts are described by systems of coupled differential equations relating the generalized coordinates to their first and second time derivatives and to the generalized forces.

In vector notation, the dynamics equations for a multi-jointed limb can be written as:

$$M(q)\ddot{q} + G(q, \dot{q}) + E(q, \dot{q}, t) = C(q, \dot{q}, u(t)) \quad (1)$$

where $q = (q_1, q_2, \dots, q_N)$ is the limb configuration in joint-angle coordinates, $\dot{q}$ and $\ddot{q}$ are respectively the first (velocity) and second (acceleration) time derivatives of q , M is a $N \times N$ matrix of inertia (that is configuration-dependent), $G(q, \dot{q})$ is a vector of centripetal and Coriolis torques [25] and $E(q, \dot{q}, t)$ is a vector of external torques, which, in general, depends upon the state of motion of the limb and also upon time (see also Equation 9 in [5]). The whole left side of Equation 1 represents the torque due to inertial properties and to the action of the environment (part of which may be considered as "noise"). The term $C(\cdot)$ on the right side stands for the net torque generated by the muscles. The time-function $u(t)$ is a control vector representing, for example, a set of neural signals directed to the motoneurons or a representation of a desired limb position at time t . An additional term, to be added on the right side of Equation 1, is the noise associated with the control signal.

4) Redundancy

A distinctive feature of biological control systems is what appears to be an overabundance of controlled elements and of degrees of freedom [26]. This is in striking contrast with the traditional design of robotic systems, where the number of actuators and of degrees of freedom matches the dimension of the task space. However, advanced robotics technologies have recognized the value of design that allows for "extra"

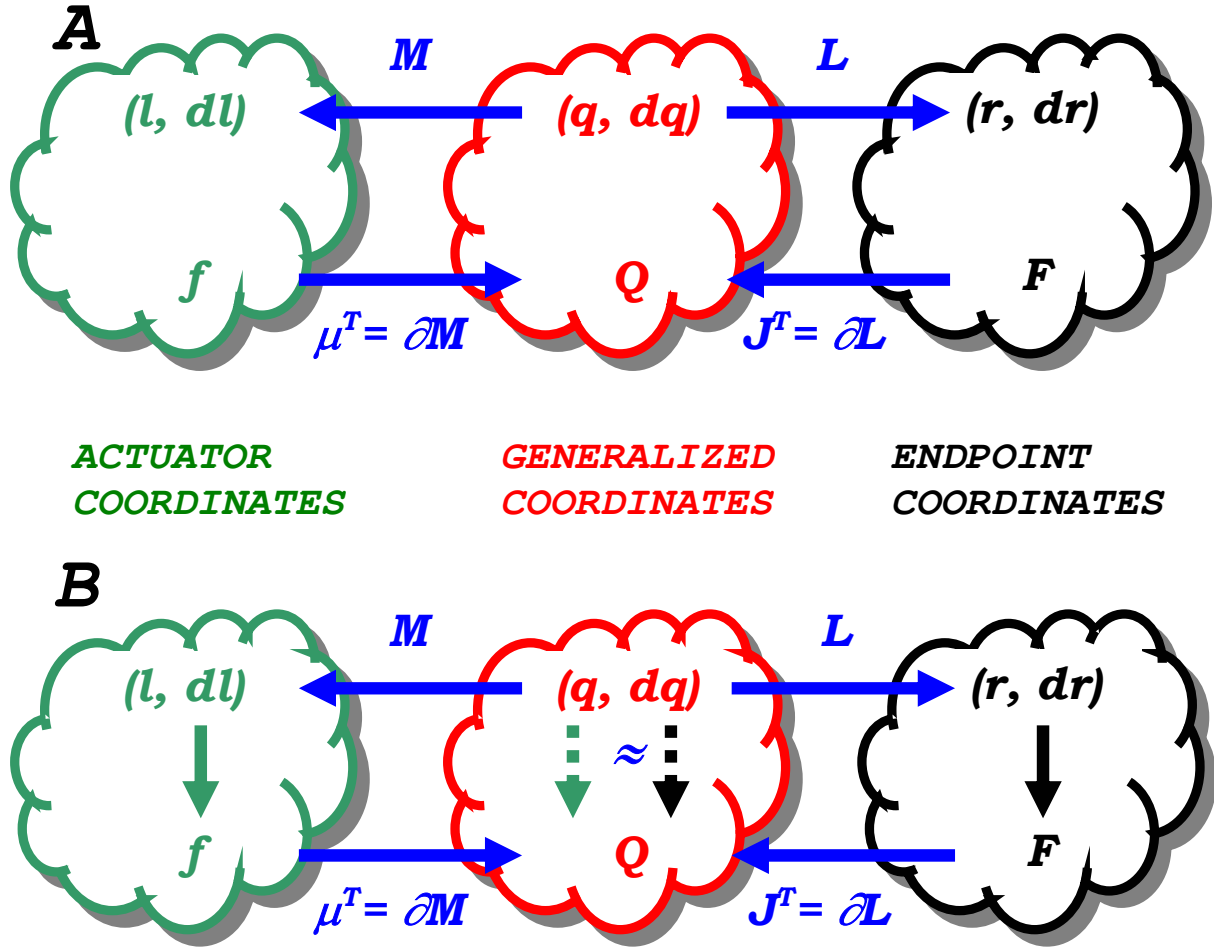


Figure 2. Coordinate transformations for planning and control (see text).

degrees of freedom in favor of greater versatility and dexterity [2, 27, 28]. Ultimately, the term “redundancy” can be considered as a misnomer because it does not acknowledge that the dimension of a task may well exceed the dimension of mere kinematics. For example, Hogan [29] has pointed out the important role played by what appear to be “extra” degrees of freedom of a limb in modulating the impedance of the limb endpoint in face of an expected impact.

The importance of redundancy as a means for providing alternative (or “equivalent”) ways to achieve a goal in face of variable operating conditions was recognized a century ago by Bernstein [26], who also described the computational problems arising from the presence of an imbalance between the number of degrees of freedom and the demands of a task. The computational problem is illustrated by the graph of Figure 2A, representing the maps of force

and position in a serial limb, such as the arm, or the body of a fish. On the right-end side of the diagram are the representations of state and force variables in endpoint coordinates. These variables are observed at the interface with the environment; for example, the position of the fingertip and the contact force at the same point. On the opposite end are descriptions in actuator coordinates. Note that the force generated by the muscular system is a (generally non-linear and non-invertible) function mapping the state of motion of the muscles - collectively indicated by the pair $l, \dot{l}$ of muscle lengths and their rates of change - and the muscle activations u , into a vector f of muscle tensions. The generalized coordinates are an intermediate representation - typically joint angle variables - between actuators and endpoint. The directions of the arrows correspond to the directions in which kinematic and force transformations are well-posed. For example, the joint angles map into

endpoint position via a direct kinematics function L , and into muscle length via a function M . Both functions are generally non-invertible, although for different reasons: the same endpoint position corresponds to a “null-space” of joint configurations, whereas an arbitrary set of muscle lengths may not be allowed, as it may have no corresponding image in configuration space. Forces map in a dual, reciprocal way, through the Jacobians of the corresponding kinematic functions, ∂L and ∂M .

5) Motor planning and control

The graph in Figure 2A highlights the computational challenge associated with the redundancy of the musculoskeletal apparatus: the non-invertibility of the transformations between actuator, generalized and endpoint variables. It is not evident, based on this graph, how a movement plan such as a desired motion of the endpoint can be mapped by the nervous system to a corresponding command for the muscles. An answer to this problem may be offered by the impedance properties of the muscular apparatus [30-34]. The spring-like and viscous properties of the muscles provide a computational “bridge” between motion and force variables, as illustrated in Figure 2-B. While the transformation from a desired motion to a set of control signals u may be ill-defined, a plan of action may be implemented as an approximation of a desired *force field* by an appropriate tuning of viscoelastic actuators [35, 36]. The force field generated by the combined viscoelastic behavior of the muscles under a pattern of activation $u(t)$ is, in generalized coordinates:

$$Q = \varphi_f(q, \dot{q}, u(t)) = \partial M(q)^T f(l(q), \dot{l}(q), u(t)) \quad (2)$$

Note that the above expression does not involve any ill-posed inverse mapping.

The planning of a desired behavior can in turn be expressed as a force field that maps a state of the endpoint (for example, a heading direction) into a corrective force:

$$F = F(x, \dot{x}, t) \quad (3)$$

This is a way to represent what some researchers would call a “policy” [37], a prescribed action in response to an observed state. The policy can be represented as a force field in generalized coordinates:

$$Q = \psi_F(q, \dot{q}, t) = \partial L(q)^T F(x(q), \dot{x}(q), t). \quad (4)$$

The definition of this field is also free of ill-posed inverse transformations.

Therefore, the biological implementation of a

planned policy can be seen as the approximation

$$\varphi_f(q, \dot{q}, u(t)) \approx \psi_F(q, \dot{q}, t) \quad (5)$$

through the appropriate choice of $u(t)$. We discuss below how this approximation may be implemented by the neural structures of the spinal cord.

6) Noise and uncertainty

The representation of motor plans and of actuator commands as force fields is directly related to the control of movements in uncertain and noisy environments. This is perhaps one of the most distinctive feature of biological controllers. Unlike most robots, biological systems have evolved to interact with environments that change in unpredictable ways. Muscles and sense organs are abundant but noisy and subject to variations in their transduction properties [38]. Under these conditions, adaptability appears to be more valuable than precision. Indeed, force field approximation (Equation 5) does not insure the precise execution of a planned motion $q(t)$. The approximating field would provide at most a prescription for driving the system in face of external perturbations. Perhaps the most critical feature of this approach is to ensure the stability of the resulting behavior. Biological organisms are not as precise as many machines. But they typically tolerate errors and recover from them much better.

The external environment is not the only source of noise. The analysis of motor unit activities [39] indicates that the variance of these signals is tightly coupled with the signals’ amplitude. Harris and Wolpert [40] have proposed that the smoothness of natural motions observed in different motor behaviors (arm and eye movements, for example) may be accounted for by assuming that the biological controller minimizes the final error, while being subject to signal dependent noise. This proposal is based on the idea that violations of smoothness, such as a large swing in a trajectory, are associated with large-amplitude control signals. Given that the signal variance accumulates additively along a movement, the net expected outcome of a jerky motion is a larger variance at the final point. Similar considerations are at the basis of a more general framework proposed recently by Todorov and Jordan [41], who observed that in the presence of redundancy, one may identify within the space of control signals a lower-dimensional “task relevant” manifold. This manifold contains the combinations of motor commands that have a direct impact on the achievement of the established goal. Because of redundancy, at each point

of this manifold there is a “null space” of control signals that do not affect the execution of the task. For example, when we place the index finger on a letter key, we may do so with an infinity of arm configurations. A common observation across a variety of behaviors is that variability tends to be higher in the task-irrelevant dimensions. Todorov and Jordan [41] consider this to be a direct consequence of optimal feedback control. According to this scheme, the control system aims at minimizing the expected final error in the presence of signal dependent noise. While the outcomes of the optimization may depend upon the specific distribution of variability among the system of actuators, the simulations presented by these authors indicate a general tendency of the control system to displace the variance in the task-irrelevant dimensions, so as to achieve a higher degree of precision in the task-relevant dimensions. This view of the biological control system brings about two important (although yet to be proven valid) concepts:

- a. that the control system is not concerned with the explicit planning of trajectories but rather with the attainment of final goals with the least amount of variance and
- b. that the space spanned by the task-irrelevant dimensions plays the role of a “variance buffer”, where the noise generated by the control signals has the largest effect so as to attain a higher performance in the space defined by the task.

While this is a promising approach, with interesting implications for the design of biomimetic controllers, the evidence for the explicit planning of trajectories remains rather strong. In some cases, the regularity of trajectories in endpoint coordinates is hard to be accounted for by mechanisms - such as the minimization of the effects of signal-dependent noise - that depend upon the geometrical, mechanical and control properties of the musculoskeletal system and of the neural controller.

III. THE ORGANIZATION OF MUSCLE SYNERGIES IN THE SPINAL CORD

The spinal cord is the final output stage of the motor system. Every muscle is innervated by motoneurons located in the ventral portion of the spinal grey matter. This system of motoneurons is comparable to a switchboard that drives an artificial mechanism. But there is more than a switchboard in the spinal cord. In addition to the motoneurons, the spinal grey matter contains a large population of nerve cells, the interneurons, whose functions are not

yet fully understood. Spinal interneurons may form connections with motoneurons that innervate several different muscles.

In a series of experiments [42-46], the activity induced by chemical and electrical stimulation of the spinal interneurons of the frog was found to spread to several groups of motoneurons. This distribution of activity was not random but imposed a specific balance of muscle contractions. The mechanical outcome of the evoked synergistic contraction of multiple muscles was captured by a force field (Figure 3). The activation of a group of muscles generated a force that was recorded by a sensor at the endpoint of the limb. This force vector changed in amplitude and direction according to the position of the limb. The resulting force field converged toward a location in the reachable space of the limb - a stable equilibrium point. At this location, the force vanished and a small displacement of the endpoint in any direction induced a restoring force. The analysis of the force field induced by stimulation of the spinal interneurons revealed that such activation leads to the generation of a stable posture.

In these experiments, the stimulating electrodes

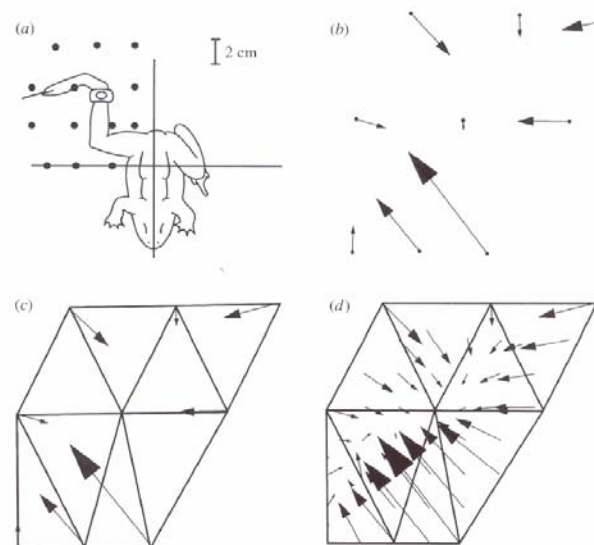


Figure 3. Force fields induced by microstimulation of the spinal cord in spinalized frogs. (A) The hindlimb was placed at a number of locations on the horizontal plane (indicated by the dots). At each location, a stimulus was applied at a fixed site in the lumbar spinal cord. The ensuing force was measured by a 6-axes force transducer. (B) Peak force vectors recorded at the nine locations shown in (A). The workspace of the hindlimb was partitioned into a set of non-overlapping triangles. Each vertex is a tested point. The force vectors recorded on the three vertices are used to estimate, by linear interpolation, the forces in the interior of the triangle. (D) Interpolated force field. (From Bizzi et al. 1991).

were placed in different loci of the lumbar spinal cord. The conclusion of these mapping studies is that there were at least four areas from which distinct types of convergent force fields were elicited. This is a strikingly small number of distinct force fields, given the broad combinatorial space generated by the set of leg muscles.

Perhaps the most interesting aspect of these investigations was the discovery that the fields induced by the focal activation of the cord follow a principle of vectorial summation [47]: when two separate sites in the spinal cord were simultaneously active, the resulting force field was the vector sum of the force fields induced by the separate activation of each site. This discovery led to a new hypothesis for explaining movement and posture based on combining a few basic elements. The few force fields stored in the spinal cord may be viewed as representing motor primitives from which, through superposition, a vast number of movements can be formed by impulses conveyed via supraspinal pathways. According to this view, the supraspinal signals would establish the level of activation for each module.

In this review, we take the concept of primitive to be defined quite generally as an elementary control function emerging from the combination of neural activity and muscle mechanics. Here, the term “elementary” is not intended to mean “simple”, but rather “basic” or “fundamental”, in the same sense that is typically attributed to basis functions. In this respect, motor primitives need not to be confined to the spinal cord (see [48]). The microstimulation experiments suggest that the circuitry in the spinal cord - and perhaps also in other areas of the nervous system - is organized in independent units, or modules. While each module generates a specific field, more complex behaviors may be produced by superposition of the fields generated by concurrently active modules. Thus, one may regard these force fields as independent elements of an internal model of dynamics. In particular, the finding of vector summation suggests that under descending supraspinal commands, the fields expressed by the spinal cord may form a broad repertoire:

$$\Gamma = \left\{ C_s(q, \dot{q}, t | c_f) = \sum_f c_f \varphi_f(q, \dot{q}, t) \right\} \quad (6)$$

Each element of Γ is generated by descending commands that select a group of synergies through the weighting coefficients c_f . In this view, the neural control system may approximate a target field

$\psi_F(q, \dot{q}, t)$ by finding the element of Γ that is closest to the target field.

Field approximation has been directly applied to the generation of a desired trajectory, $q_D(t)$, in generalized coordinates [35, 36]. In this case, one may attempt to generate the appropriate controller by finding the parameters c_f which minimize the difference between forces generated by the passive dynamics and those generated by control field along the desired trajectory.

If the residual error could be reduced to zero, then the corresponding controller would produce exactly the desired trajectory. If, instead, there is a non-zero residual, then the problem of generating acceptable approximations becomes a question of local stability. Residual forces may be regarded as a perturbation of the dynamics, and one needs to insure that this perturbation does not lead to a motion that diverges from the desired trajectory. A study of Lohmiller and Slotine [49] showed that the combination of control modules is stable if the modules are “contracting” - a condition germane to exponential stability.

If the modules corresponding to muscle synergies are stable, then the possibility of combining them provides the central nervous system with something equivalent to movement representation. The movements of a limb can be considered as “points” in an abstract geometrical space, where the force fields produced by a set of modules play a role equivalent to that of coordinate axes, and the selection parameters that generate a particular movement may be regarded as generalized projections of this movement along these axes.

IV. CENTRAL PATTERN GENERATORS AS A BASIS FOR NEUROCONTROL

The generation of rhythmic motor patterns is crucial to the alternation of activity between antagonistic abductor and adductor muscle groups that drive the motion of pectoral fins ([50] this volume – See Figure 8). The need for such rhythmic patterns of neural activity is not restricted to the motion of fin systems; it also appears in the axial locomotor system of fishes and aquatic amphibians, whose swimming movements are generated by waves of left-right alternating motor activity that travel rostral-caudally along the body and propel the animal through the water [51]. The coordinated alternation of flexion and extension of leg muscles in walking [52] is yet another, quite more complex example of this type of

rhythmic neural activity associated with a variety of locomotor behaviors.

A large body of information on the neural control of rhythmic movements in the invertebrates and vertebrates [53, 54] indicates that such rhythmic motor patterns are produced by central pattern generators (CPGs): central neuronal circuits whose activation can produce rhythmic patterns in the absence of sensory or descending inputs that carry specific timing information [55]. The best evidence for the existence of such circuitry is provided by preparations in which neuronal tissue is removed from the animal and placed in a dish. The observation of “fictive motor patterns”, which would drive actual movements if connected to muscles, in conditions in which there are no remaining pathways for sensory input or for timing information provided by the environment, is conclusive proof for the existence of CPGs. The activation of these circuits depends on neuromodulators that are normally supplied by descending pathways and that can be applied directly to the saline bath in the case of in-vitro preparations.

The CPGs are networks typically composed of subnetworks of neurons, not necessarily identical. Each subnetwork is capable of producing a rhythmic output; the various outputs need to be coordinated to provide proper relative timing. The role of the various subnetworks depends on the membrane properties of the corresponding neurons. Bursting neurons, which fire endogenously or in the presence of neurotransmitters, provide timing through their oscillatory activity. Features of this activity that determine the overall temporal properties of the CPG are: cycle period, burst duration, duty cycle (the ratio

of burst duration to cycle period) and the phase of firing (delay relative to the firing of other subnetworks). Other neurons that play an important role in CPGs are bistable neurons, which generate “plateau potentials” – periods of sustained depolarization – controlled by depolarizing and hyperpolarizing pulses. These neurons can provide a discharge pattern that outlasts their excitatory drive [56]. Another important component of CPGs is inhibitory neurons, which control the timing of activity of neurons that fire in post-inhibitory rebound. The dynamical properties of the CPG network depend on the intrinsic properties of the neurons that populate the corresponding subnetworks, and on the time-dependent properties of the synapses among them.

There are two general mechanisms for rhythmic production in CPG networks [55]: pacemaker driven networks and networks with emergent rhythms. In pacemaker driven networks, a subnetwork of oscillating neurons can drive nonbursting neurons into an alternating oscillatory pattern. Pacemaker neurons are typically found in CPG networks that are always active, such as those involved in breathing [57]. In contrast, emergent rhythms arise as a consequence of synaptic coupling among neurons that are not intrinsic oscillators. The simplest example of such a CPG is the so called “half-center oscillator”, in which two subnetworks of mutually inhibiting neurons produce alternating patterns of activity [58, 59]. Reciprocal inhibition is a core feature of almost all known CPG networks.

Among the most thoroughly studied examples of half-center oscillator networks are those that generate swimming-related patterns along the spinal cord of tadpoles, leeches, and lampreys. These animals swim using multiple body segments and organizing left-right alternations in each segment so as to produce a wave of body contraction that propels them through water. Each segment can produce fictive motor patterns that organize the local swimming movements. Each segmental CPG can be seen as two mutually inhibiting halves (Figure 4), each one comprising burst-generating premotor interneurons.

This neural system can generate and control a variety of motor behaviors: local asymmetries in the oscillatory patterns induce controlled changes of direction while the mean frequency of the CPGs regulates forward or backward velocity. This structure is quite similar to the one proposed as a model for the extensor/flexor rhythms in fin locomotion ([50] this

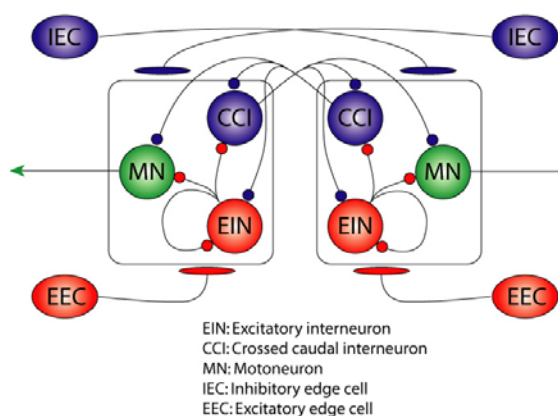


Figure 4. Schematic structure of the half-center oscillator network in the Lamprey (courtesy of Simon Alford)

volume - See Fig 11). The activity of CPGs must be highly adaptive as lampreys swim and maneuver amid variable currents and in media of variable density. Lampreys are predators and their control system has evolved a rich repertoire of escape and attack maneuvers.

In addition, like every biological controller, the spinal CPGs are capable of adapting their operation to a variety of body and environmental changes. Across its life-span, the body of a lamprey undergoes a tremendous change in size, which can range from a few inches in length to a few feet. As this process takes place, the CPGs must change frequency and relative phase across segments, as well as their net power output. While the mechanisms through which these adaptive changes take place are an object of current research [12, 60, 61], there is evidence that inputs from a distributed system of mechanoreceptors located within the lateral edges of the spinal cord [62, 63] play a critical regulatory and error-correction function. These receptors (edge cells) provide direct feedback about the local bending of the body in relation to the output of the CPGs.

The output of these segmental oscillators needs to be coordinated by ascending and descending fibers so as to maintain the required phase relation between adjacent segments [64] needed to produce a wave of activity whose wavelength remains essentially equal to body length over a wide range of swimming speeds. This careful coordination of local CPG networks associated with individual segments is an example of a complex locomotor behavior generated through a well-orchestrated combination of motor primitives.

V. INTERNAL MODELS AS A BASIS FOR ADAPTIVE BEHAVIOR

The ability to generate a variety of complex behaviors cannot be attained by just storing the control signals for each action and recalling these signals when subsequently needed [65, 66]. Simple considerations about the geometrical space of meaningful behaviors are sufficient to establish that this approach would be inadequate [67]. To achieve its typical competence, the motor system must take advantage of experience for going beyond experience itself, by constructing internal representations of the controlled dynamics. These representations allow the nervous system to generate new behaviors and to handle situations that have not yet been encountered. A vivid illustration of this is offered by recent work of

Atkeson and Schaal [68, 69], who studied the task of balancing an inverted pendulum on the hand of a robotic arm. The balancing task can be accomplished by humans without much effort. Therefore, the simplest way to execute the same task with a robot arm seemed to be that of copying with the robot every movement of a human expert. When Atkeson and Schaal tried this direct imitation approach they found that it failed: even if the hand movements were carefully copied by the robot, the smallest amount of uncertainty associated with sensing and acting did not allow the pendulum to remain balanced. This does not mean that imitation of successful behavior is not a valid strategy [70, 71]. Quite on the contrary, the robot learned to act successfully when the data from the observed demonstrations were used not to mimic the expert's movements but to build an internal representation of the dynamics associated with the task. Such a representation may be constructed by a search procedure starting from some arbitrary initial model that specifies the action to be taken at every possible state. Then, the data from experience of trials and errors are used to iteratively update the model parameters until some optimal, or at least satisfactory performance is attained. It turns out that in most cases, search procedures are effective only if the starting point – the initial assumptions about the dynamic model – is not too far from the correct representation. The work of Atkeson and Schaal shows that imitation is a useful strategy when it provides the learner with a good starting point for the subsequent refinement of an internal model by a search procedure.

The term "internal model" refers two distinct mathematical transformations: 1) the transformation from a motor command to the consequent behavior and 2) the transformation from a desired behavior to the corresponding motor command [10, 72-75]. A model of the first kind is called a "forward model". Forward models provide the controller with the means not only to predict the expected outcome of a command, but also to estimate the current state in the presence of feedback delays [76, 77]. A representation of the mapping from planned actions to motor commands is called an "inverse model". Studies by Kawato, Wolpert and Miall [78, 79] have proposed that the neural structures within the cerebellum perform sensory-motor operations equivalent to a combination of multiple forward and inverse models. Strong evidence for the biological and behavioral relevance of internal models has been provided by numerous experiments [80, 81]. Some

of these experiments involved the adaptation of arm movements to a perturbing force field generated by an instrumented manipulandum. The major findings of these studies are as follows: 1) when exposed to a complex but deterministic field of velocity-dependent forces, arm movements are first distorted and, after repeated practice, the initial kinematics are recovered; 2) if, after adaptation, the field is suddenly removed, after-effects are clearly visible as mirror images of the initial perturbations [10]; 3) adaptation is achieved by the central nervous system through the formation of a local map that associates the states (positions and velocities) visited during the training period with the corresponding forces [82, 83]; 4) after adaptation this map - that is the internal model of the field - undergoes a process of consolidation [84]. In order to generate the appropriate command for a desired movement of the arm, an inverse model must take into account that multi-joint inertia depends on limb position and velocity. Therefore, an inverse model must be informed about the current state of motion of the limb. This information may come in one of two ways: 1) from the input to the inverse model that specifies where the limb should be or 2) from a prediction of the current state based on delayed sensory feedback and on the past history of motor commands. Bhushan and Shadmehr [85] have found compelling evidence for the second way. Their experimental results are consistent with the hypothesis that we learn to compensate changes in limb dynamics by a process that involves the combined adaptation of a forward and of an inverse model of the limb

VI. ARCHITECTURES FOR NEURAL COMPUTATION

The various computational tasks described in preceding sections of this article are best suited for different neural network architectures.

Force field vectors, whose amplitude and direction depend on the position of a limb as described by its endpoint coordinates x , have been mapped out in experiments based on microstimulation of spinal interneurons in the frog [43, 44]. The resulting force fields exhibit an interesting property: they converge toward a stable equilibrium point in the space of attainable limb positions. To the extent that these force fields have zero curl, a condition met in related experiments on human subjects [33], it is possible to construct a scalar potential function, $U(x)$, such that the observed force field is given by the gradient $\nabla U(x)$. The existence of a single stable equilibrium

point for the force field corresponds to the existence of a unique minimum for the potential function $U(x)$. This, together with a dissipative component, can then be interpreted as a Lyapunov function that describes the dynamics of an *attractor neural network* [86]. The existence of a relatively small number of distinct force fields associated with a large set of muscle elements could thus be modeled through an equivalently small number of attractor neural networks, each one of them constructed so as to reproduce the flow of the corresponding force field. The Lyapunov function associated with each one of these networks describes the basin of attraction of the corresponding stable fixed point. Movements generated as a combination of these few force field primitives can be represented through a “*mixture of expert networks*” [87] constructed as a linear superposition of individual modules that would be, in this case, the attractor neural networks associated with the force field primitives.

The implementation of a desired trajectory $x(t)$ in the endpoint coordinate representation requires a map from the state of the endpoint, as described by $(x, \dot{x})$, into a force $F(x, \dot{x}, t)$ that might also depend explicitly on time (see Equation 3). This map from a *state* into an *action* can be easily captured in the framework of a *layered neural network* [88]. Training a layered neural network to implement the desired map from states into actions requires a training set, which can be obtained in the context of imitative learning [68]. The detailed observation of policies implemented so as to achieve a desired trajectory, in conjunction with the determination of endpoint state variables, could provide the data needed to train a layered neural network using a standard back-propagation algorithm. Further training, based on generating actual trajectories and comparing them to desired trajectories so as to obtain an error signal, will be necessary to provide the layered network with some degree of robustness against noise and/or uncertainty in the input (sensory information on current state) or the output (actuated policy).

Of particular importance for the accurate execution of movements is the use of a control function $u(t)$ (see Equation 1), which can take the form of activation signals to motoneurons (in the language of actuator coordinates) or of a desired limb position (in the language of endpoint coordinates). The motion described by Equation 1 can be interpreted as an iterative map in a $2N$ -dimensional tangent bundle [24], that is in a manifold spanned by the generalized

coordinates, $q = (q_1, q_2, \dots, q_N)$, and the generalized velocities, $\dot{q} = (\dot{q}_1, \dot{q}_2, \dots, \dot{q}_N)$. When complemented with N equations of the form $\dot{q}_i = dq_i/dt$, $1 \leq i \leq N$, the N equations for $\ddot{q}_i$ (compactly expressed by Equation 1) define unique trajectories in the $(q, \dot{q})$ manifold. The state of the system at time $(t+dt)$ is uniquely and completely determined by the state at time t , and by the control signal $u(t)$.

The appropriate neural network architecture to represent the action of the control signal on the $(q, \dot{q})$ manifold is intermediate to the fully recurrent architecture of attractor neural networks and the purely feedforward architecture of layered neural networks. We specifically refer here to networks such as those described by Jordan [89], which consist of a two-layered feedforward network whose intermediate layer receives as input not only the external input, but also a copy of its own state at the preceding time step. This additional input provides mechanisms for implementing lateral connections which result in dynamical recurrence within the intermediate layer. For the control problem of interest here, the intermediate layer would encode for the state $(q, \dot{q})$ of the system at time $(t+dt)$, as a function of its two inputs: the control signal and the state at time t . The connections from the intermediate layer to the output layer can be adjusted so as to implement the map L from generalized to endpoint coordinates (Figure 2). A comparison between actual and desired endpoint trajectories would generate an error signal to be backpropagated into the network for adjusting the connections that describe the effect of the control signal on the state and on the output of the system.

This brief discussion suggests that the computational demands of the execution and control of movements incorporates many facets, whose description in terms of neural computation involves different models, ranging from fully recurrent to purely feedforward architectures and including hybrid models between these extremes. The choice of a suitable architecture in an artificial emulation of a neural system depends on the emphasis and the specific formulation of the problem, be it in the format of generating appropriate policies for endpoint coordinates or of characterizing the effects of control signals on the dynamics in generalized coordinates.

CONCLUSIONS

The control of natural movements, such as

underwater maneuvering and manipulation, involves the ability to solve complex mathematical problems. Our current knowledge of biological system suggest that the living organisms approach this task not by solving explicitly large systems of differential equations but by combining building blocks of primitives that implement elementary motor behaviors. Some of these primitives are embedded in the genetic design of the nervous system. Others arise in each individual from the experience of mechanical interactions with the environment and from a variety of learning mechanisms. The peripheral structures of the vertebrate's nervous systems, coupled with the muscle viscoelastic properties, lead to the definition of a family of mechanical waves, or time-dependent force fields. The nervous system modulates these waves and combines them to generate a rich repertoire of adaptable behaviors. This approach can be translated in modular design of controllers for dealing with the complex dynamics of underwater maneuvers.

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