**Biological
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Dynamic primitives of motor behavior

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Abstract We present in outline a theory of sensorimotor control based on dynamic primitives, which we define as attractors. To account for the broad class of human interactive behaviors—especially tool use—we propose three distinct primitives: submovements, oscillations, and mechanical impedances, the latter necessary for interaction with objects. Owing to the fundamental features of the neuromuscular system—most notably, its slow response—we argue that encoding in terms of parameterized primitives may be an essential simplification required for learning, performance, and retention of complex skills. Primitives may simultaneously and sequentially be combined to produce observable forces and motions. This may be achieved by defining a virtual trajectory composed of submovements and/or oscillations interacting with impedances. Identifying primitives requires care: in principle, overlapping submovements would be sufficient to compose all observed movements but biological evidence shows that oscillations are a distinct primitive. Conversely, we suggest that kinematic synergies, frequently discussed as primitives of complex actions, may be an emergent consequence of neuromuscular impedance. To illustrate how these dynamic primitives may account for complex actions, we briefly review three types of interactive behaviors: constrained motion, impact tasks, and manipulation of dynamic objects.

Keywords Discrete · Submovement · Rhythmic · Oscillation · Impedance · Primitive

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1 Introduction

Over the past decades, research on sensorimotor control has gained momentum as is evident in new journals, conferences, and more highly visible publications. This growth in both fundamental and applied motor neuroscience is partly spurred by applications to rehabilitation, robotics, and brain-machine interfaces. Though welcome, the sheer number of studies, experimental and computational, has reached a point where cohesive understanding seems beyond any single person's ability. A fundamental mathematical theory would be advantageous to organize and structure this data. We believe that with advances in computational and theoretical work over the past decades, a theory has come within reach. The goal of this paper is to integrate some recurring fundamental concepts into an outline of a comprehensive theoretical framework.

To establish a foundation for a theory of human sensorimotor control that is reliable and incrementally revisable, it is necessary to go beyond the usual practice of developing a model for a narrowly specified sensorimotor task. Many such models have described mechanisms and control structures that may underlie a specific behavior. These models have employed different mathematical tools, ranging from Bayesian statistics to nonlinear dynamics and optimal feedback control, to name just a few. While useful, insights gained thereby have proven difficult to integrate with other models (which are often seen as competing theories) and more or less impossible to generalize. In our view, the best way to develop

a fundamental mathematical theory of human sensorimotor control is to start with broader strokes.

Rather than choosing a suitable exemplary task, our approach is to address a fundamental and broad class of actions: tool use, a hallmark of human behavior. While some animals have been shown capable of making and using tools, this ability remains the distinctive signature that has given humans an evolutionary advantage (Boesch and Boesch 1990; Hunt 1996; Johnson-Frey 2004; Kenward et al. 2005). Hence, we propose a framework for how humans physically interact with and manipulate objects. This class of behavior intentionally goes beyond the typical study of isolated controlled experimental movements, such as walking on level ground without challenges like obstacles or uneven terrain, or reaching and pointing without interacting with objects. Examples of interactive tasks range from opening a door to carrying a cup of coffee, or more exotic skills such as fly casting or cracking a whip.

Where to begin? Any competent theory must address the prominent limitations of the human neuromuscular system. One of the most critical features of the neuromuscular system is that neurons and muscles are slow. The fastest neural transmission speed in humans is no more than 120 m/s (animals' conduction speed is slower and less economical), which still compares very poorly with information transmission in electro-mechanical systems such as robots, which can conservatively be estimated at 10^8 m/s, about a million times faster (Kandel et al. 2000). Furthermore, muscles are slow. The typical twitch contraction time[1] for the human biceps brachii is about 50 ms (Kandel et al. 2000). Assuming a linearized model to approximate this behavior implies a bandwidth of about 3 Hz. In comparison, electromechanical technology routinely achieves bandwidths in excess of hundreds of Hz (electro-magnetics) to thousands of Hz (electro-hydraulics).

Despite slow muscles and neural delays, humans achieve astonishing dexterity manipulating objects—and especially using tools—far superior to anything yet achieved in robotic systems. Slow neuromechanical response implies that *prediction* using some form of internal representation is a key aspect of human motor control, yet the nature of that representation remains unclear (Crevecoeur et al. 2010). Consider fly casting or cracking a whip: These objects comprise flexible materials that interact with complex fluid dynamics. Physics-based models of their behavior tax even modern supercomputers. The likelihood that anything resembling a physics-based model underlies real-time control of these objects seems slim, yet some humans can manipulate them with astonishing skill. Even the mundane task of carrying a cup of coffee without spilling is surprisingly challenging because complex nonlinear dynamics relate motions of the cup to motions of the coffee. How are these complex objects managed?

2 Dynamic primitives

How does the human system perform so well despite its limitations? We believe that the answer lies in the distinctive character of human motor control. Mounting evidence indicates that sensorimotor control relies on a composition of primitive dynamic actions (Sternad et al. 2000a; Thoroughman and Shadmehr 2000; Flash and Hochner 2005; Kargo and Giszter 2008; Sternad 2008; Sing et al 2009; Degallier and Ijspeert 2010; Dominici et al. 2011). We propose that *human motor control is encoded solely in terms of these primitive dynamic actions*.

Encoding control using primitives could dramatically simplify the control of physical interaction with complex dynamic objects. Returning to the example of cracking a whip: it is sufficient to generate a large sweeping arm movement (to put energy into the whip) and superimpose on it a precisely timed wrist "flick" (to propagate a wave along the whip). Each of these primitive actions may be specified by a small number of parameters. The acquisition and retention of such a skill would consist of finding and retaining suitable parameters of the primitive actions and how to combine them. That, of course, may require extensive practice but, once learned, only that small set of parameters need be retained and retrieved.

The idea that motor control is accomplished by combining primitive elements is not at all new, but the full extent of its ramifications for motor control may not yet have been fully articulated. The search for primitive elements that generate actions dates back at least a century. Sherrington proposed stereotyped neuromuscular responses to sensory events—the *reflex*—as building blocks of more complex actions (Sherrington 1906; Gallistel 1980; Elliott et al. 2001). The subsequent wave of behaviorist psychology explored how stimulus-response relations (S-R units) could become an "alphabet" for complex behavior. Learning a new action would comprise "chaining" such S-R units or reflexes such that each reflexive action resulted in sensory events that "triggered" the next (Bässler 1986).

More recently, the concept of a *synergy* has gained popularity, although this concept also has a long history and has been given many alternative meanings. The term often refers to stereotyped patterns of simultaneous motion of multiple joints or simultaneous activation of multiple muscles that may simplify control (Bernstein 1967; Tuller et al. 1982; Cheung et al. 2005; Flash and Hochner 2005; Latash 2008; Soechting and Flanders 2008). A common theme is that a synergy provides *dimensionality reduction*. For example, in geometric terms, if the set of all joint angles defines

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[1] Twitch contraction time is the time from an impulsive stimulus (e.g., electrical) to peak isometric tension.

a *configuration space*, a pattern of simultaneous motion of multiple joints defines a curve or subspace within this configuration space. If joint motions are confined to that subspace, yet account for most of the observed variance, this implies that the central nervous system (CNS) may simplify control of the high-dimensional musculo-skeletal system by selecting commands in the lower-dimensional subspace defined by synergies. Importantly, this common account of synergies constitutes an *algebraic constraint*, not a dynamic object. Even time-varying synergies are not dynamic objects, but constitute a kinematic constraint with time included as one of the variables related by the constraint (d'Avella et al. 2003; d'Avella et al. 2006). Reducing the dimension of commands alone is not sufficient to account for how humans control complex dynamic objects. For that, the primitives of control should themselves be dynamic objects.

Discrete and rhythmic movements have been proposed to indicate two classes of primitive actions (Schaal et al. 2000; Sternad et al. 2000a). They have been termed *dynamic* primitives as they refer to patterns of behavior that may robustly emerge from dynamic systems. To explain, two of the prominent behaviors exhibited by nonlinear dynamic systems are *point attractors* and *limit cycles*; a point attractor may describe a discrete movement to a stable posture; a limit cycle may describe a rhythmic movement. Even some of the simplest dynamic systems can exhibit these behaviors as may be seen by considering the class of negative-resistance oscillators from engineering (Strauss 1970). Those second-order dynamic systems can exhibit robustly sustained oscillation (limit cycle behavior) or stable convergence to a single state (point attractor behavior) and changing the value of a single parameter is sufficient to select or induce a transition between these two alternatives. More biologically plausible models of neural oscillators exhibit similar properties, thereby lending support for these mechanisms generating observable behavior (Fitzhugh 1961; Nagumo and Arimoto 1962; Matsuoka 1985; Ronsse et al 2009).

We define dynamic primitives as patterns of behavior that robustly emerge from dynamic systems, that is, as *attractors*. For example, a general representation of a dynamic system describes the evolution of behavior in a finite-dimensional state space, $\dot{\mathbf{x}} = f(\mathbf{x})$ where $\mathbf{x} \in R^n$ for finite n. An attractor is a subset of state-space with at least two properties. First, it is an *invariant set*: if the system begins in an invariant set, it never leaves it. Second, that invariant set is *attractive*: if the system starts sufficiently close to it, the system will ultimately converge to the attractor. Attractor sets may have many forms. A *point attractor* is a single point in state-space. An attractor set that is a closed path (or orbit) defines a *limit cycle*. There are alternatives: Any path in state-space—any trajectory—may be an attractor set; this may describe discrete reaching movements, which exhibit trajectory stability (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi

1994; Won and Hogan 1995; Burdet et al. 2001). Other subsets of state-space (e.g., manifolds) may also be attractors; these may describe synergies. Even the prodigiously complex objects known as *strange attractors* with fractal geometry may be attractor sets of chaotic dynamic systems which may arise in more complex actions (Strogatz 1994).

One important consequence of this definition of dynamic primitives is that an attractor exhibits a degree of robustness that might be termed "temporary permanence" (permanence due to robustness to perturbation; temporary because dynamic primitives, like the phonemes of verbal communication, may have limited duration). The pattern of behavior described by the invariant set (e.g., limit cycle oscillation, trajectory, etc.) will re-emerge after perturbation, at least for sufficiently small perturbations.

Another important consequence of this definition of dynamic primitives as attractors is that it points to experiments that might test their objective reality (at least in principle). Owing to the robustness of the attractor, a dynamic primitive should manifest as a common pattern of behavior observable in different contexts and despite the presence of noise or perturbations. This feature may lend itself to experimental testing.

2.1 Submovements

An important requirement for a theory based on primitives is that it should be possible to combine the elements to generate a repertoire of behavior. Are discrete and rhythmic movements suitable primitives? In short, no. In our previous work, we proposed precise quantitative definitions of discrete and rhythmic movements (Hogan and Sternad 2007). Our definitions were deliberately confined to the behavioral or observational level, remaining silent about possible generative processes that might give rise to these observations. For a movement to be discrete (i.e., distinct from other movements), we reasoned that any consistent definition requires that it should begin and end with a period of no movement. With that definition, discrete movements can only be sequenced and cannot overlap in time. This would severely restrict the repertoire that could be generated.

To overcome this limitation, we propose that *submovements* are primitive dynamic elements of motor behavior. In essence, submovements are like discrete movements, but they may overlap in time. A submovement is conceived as a *coordinative atom*: just as atoms are primitive units of chemical reactions, submovements are elements of dynamic coordination used to compose motor behavior. Just as atoms have complex internal structure, submovements may require complex patterns of neuromuscular activity to instantiate the dynamic process from which a submovement emerges as an attractor. Those patterns are like "subroutines" that can be called to compose behavior.

The possibility that observable movements are composed of submovements is by no means a new idea. As early as 1899, Woodworth noted that voluntary movements appear to be accomplished as a series of corrective submovements Woodworth (1899); comprehensive and highly-cited reviews are in Meyer et al (1988) and Elliott et al. (2001). More recent work showed that the earliest movements made by patients recovering after a paralyzing stroke were composed of submovements with remarkably stereotyped speed profiles, even for different patients with different lesions (Krebs et al. 1999). This degree of robustness or "temporary permanence" makes a compelling case that submovements are indeed a primitive dynamic element of human motor behavior. Further support is found in the analysis of infant reaching movements, which initially exhibit submovements but become essentially continuous at around 6 months of age (von Hofsten 1991; Berthier 1996).

Motor behavior composed of submovements would simplify prediction of the sensory consequences of motor actions and facilitate detection of errors based on sensory information (Burdet and Milner 1998). A study of submovement changes during recovery after stroke showed that the time between adjacent submovements decreased for patients in the subacute phase (less than 1 month post-stroke), but not for patients in the chronic phase (greater than 12 months post-stroke). Submovements became more overlapped for all patients, but more markedly for those in the subacute phase (Rohrer et al. 2004; Dipietro 2012). This is consistent with performance optimization by first "tuning" a forward model to improve predictability and subsequently an inverse model, as suggested by Bhushan and Shadmehr (1999).

We define a submovement as an attractor that describes a smooth sigmoidal transition of a variable from one value to another with a stereotyped time profile. For limb position, the variable is a vector in some coordinate frame, e.g., hand position in visually-relevant coordinates, $X = [x_1, x_2 \ldots x_n]^t$. Each coordinate's speed profile has the same shape which is non-zero for a finite duration $d = e - b$, where b is the time when the submovement begins and e is the time it ends, i.e., it has *finite support*:

$$\dot{x}_j(t) = \hat{v}_j \sigma(t), \quad j = 1 \ldots n$$

where $\hat{v}_j$ is the peak speed of element j; $\sigma(t) > 0$ iff $b < t < e$ and $\sigma(t) = 0$ if $t \le b$ or $e \le t$. The speed profile has only one peak: there is only one point $t_p \in (b, e)$ at which $\dot{\sigma}(t_p) = 0$, and at that point $\sigma(t_p) = 1$.

Note that this definition is deliberately confined to the behavioral or observational level, remaining silent about possible generative dynamic processes that might give rise to these observations. However, some constraints on those processes can be identified. Given the available physiological evidence, a dynamic process with a point attractor is not sufficient; trajectory, rather than final position, is controlled

(Bizzi et al. 1984; Won and Hogan 1995). Because of its stereotyped time-profile, this dynamic primitive may be termed a "trajectory attractor."

Submovements may be considered as *basis functions* and combined with overlap in time to produce a wide range of motion profiles. Though several combination operators are possible, linear vector superposition of discrete point-to-point reaching movements has been shown to provide an accurate description of movement trajectories in which a target shifts abruptly (Flash and Henis 1991). Combining m submovements yields

$$\dot{x}_j(t) = \sum_{k=1}^{m} \hat{v}_{jk} \sigma(t | b_k, d_k), \quad j = 1 \ldots n$$

where each submovement k has the same shape but may have different peak speed $\hat{v}_{jk}$, start time b_k and duration d_k. If submovements are dynamic primitives and exhibit the stability of discrete movements, the appropriate attractor set may be a trajectory in state space.

2.2 Oscillations—composites or primitives?

From a strictly mathematical perspective, rhythmic movements might not be primitive. They could be described parsimoniously as a composite of elementary back-to-back discrete submovements—i.e. overlapping submovements in opposite directions. However, our goal is not just a mathematical formalism but an account of biological sensorimotor behavior. Rhythmic movement is very old phylogenetically and available evidence indicates that oscillatory behavior is a *distinct* dynamic primitive of biological motor control (and not a composite of submovements) (Brown 1911; Brown 1914; Grillner and Wallen 1985; Schaal et al. 2004).

The term "rhythmic" is a loosely-defined umbrella term with numerous variations and degrees of periodicity as discussed in Hogan and Sternad (2007). To render precision, we denote the corresponding dynamic primitive as an *oscillation*. Describing limb position as a vector quantity, $x = [x_1, x_2 \ldots x_n]^t$, we define the primitive as an attractor that describes almost-periodic motion:

$$|x_j(t) - x_j(t + \Delta t + lT)|$$
$$< \varepsilon_j \forall t, l = \pm 0, 1, 2, \ldots, j = 1 \ldots n,$$

where T is a constant (its smallest value is the period), $|\Delta t| < \delta$, and ε_j and δ are small constants. This definition allows for the ubiquitous fluctuations exhibited in biological behavior, whether due to stochastic processes (noise) or deterministic chaos (Raftery et al 2008). The main point of this definition is that the *average* time course of an almost-periodic behavior is strictly periodic. The amplitude and phase of each vector component may differ, but all components exhibit an average time-variation with the same smoothly-varying shape and period, T.

As with submovements, this definition is deliberately confined to the behavioral or observational level, remaining silent about possible generative processes that might give rise to these observations. However, it seems reasonable to conjecture that oscillations emerge from a generative dynamic process with a limit cycle attractor (Rabinovich et al 2006).

2.3 Mechanical impedance

Submovements and oscillations may provide a basis for unconstrained movements, but contact and physical interaction are essential for that quintessentially human ability, object manipulation and the use of tools. To account for contact and physical interaction with objects, a third class of dynamic primitives is required, mechanical impedance. Loosely speaking, mechanical impedance is a generalization of stiffness to encompass nonlinear dynamic behavior (Hogan 1985). Mathematically, it is a *dynamic operator* that determines the force (time-history) evoked by an imposed displacement (time-history). The force and displacement must be *energetically conjugate*; that is, they must refer to the same point(s) so that incremental mechanical work dW may be defined, i.e.,

$$dW = \mathbf{f}^t d\mathbf{x} = \sum_{j=1}^{n} f_j dx_j$$

where $\mathbf{x} = [x_1, x_2 \ldots x_n]^t$ is a vector of positions and $\mathbf{f} = [f_1, f_2 \ldots f_n]^t$ is a vector of forces, both defined with respect to any suitable coordinate frame. A mechanical impedance operator $\mathbf{Z}$ maps displacement onto the conjugate force.

$$\mathbf{Z} : \Delta\mathbf{x}(t) \to \mathbf{f}(t)$$

The form of this mapping may be nonlinear and time varying. For convenience, we usually assume a state-determined representation

$$\dot{\mathbf{z}} = Z_s(\mathbf{z}, \Delta\mathbf{x}, t)$$
$$\mathbf{f} = Z_o(\mathbf{z}, \Delta\mathbf{x}, t)$$

where $\mathbf{z} = [z_1, z_2 \ldots]^t$ is a vector of state variables and Z_s and Z_o are algebraic functions. For brevity, we often omit the "mechanical" prefix. A time-invariant linearized form of a state-determined impedance model may be represented as a square matrix of transfer functions of arbitrary order that relate input displacements to output forces.

The displacement inputs need not be at the same physical location in space, provided they can be paired with energetically conjugate forces. For example, the several joints of the upper extremity (shoulder, elbow, wrist, etc.) are in different physical locations. The limb configuration may be described using joint angles, $\boldsymbol{\theta} = [\theta_1, \theta_2 \ldots \theta_n]^t$, a special case of *generalized coordinates* (Goldstein 1980). The corresponding *generalized forces* (joint torques) $\boldsymbol{\tau} = [\tau_1, \tau_2 \ldots \tau_n]^t$ are defined such that incremental mechanical work may be defined.

$$dW = \boldsymbol{\tau}^t d\boldsymbol{\theta} = \sum_{j=1}^{n} \tau_j d\theta_j$$

Joint mechanical impedance maps joint angular displacements onto the evoked joint torques.

$$\mathbf{Z}_{\text{joint}} : \Delta\boldsymbol{\theta}(t) \to \boldsymbol{\tau}(t)$$

Like submovements and oscillations, humans can voluntarily control mechanical impedance. The most obvious way is by co-contraction of antagonist muscle groups. Opposing muscle groups may be activated simultaneously without changing the net muscle-generated torque about a joint. If so, because mammalian muscle impedance increases with muscle force, the net mechanical impedance about the joint may increase and it usually does[2]. This is because the net mechanical impedance at a point is always the unsigned (positive) sum of the component mechanical impedances acting at that point. Mechanical impedance is also influenced by feedback loops, especially those involving muscle spindles and Golgi tendon organs at the spinal level or higher (Nichols and Houk 1976; Hoffer and Andreassen 1984). It is known that the gains of these feedback pathways are highly modifiable, either via gamma motoneuron activity or via descending drive to spinal interneuron pools (Prochazka et al. 2000).

Is mechanical impedance a dynamic primitive in the sense we have proposed above? An important fact is that mechanical impedance is extremely robust to contact and interaction. The force and motion of the hand are exquisitely sensitive to contact with objects and to the mechanical dynamics of the contacted objects. By coupling the object dynamics to those of the hand and arm, contact, and physical interaction may change the *structure* of the dynamics that give rise to behavior. For example, if the hand dynamics were described by a second-order model (e.g., to describe limit-cycle oscillation) and the object dynamics were described by a second-order model (e.g., a mass restrained by a damped spring), the coupled system may exhibit fourth-order dynamics. This is why stability may, in general, be compromised by contact. For a detailed discussion, see (Hogan 1990). In contrast, mechanical impedance at the hand is a property that emerges solely from the dynamics of the neuromechanical system supporting the hand. It is completely independent of the behavior of any object contacted, or even of any contact at all, and exhibits the robustness we require for a dynamic primitive.

Another remarkable feature of mechanical impedance is that, when coupled to skeletal inertia, *nonlinear impedances may be combined by linear superposition* (Hogan 1985). That

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2 A nonlinear relation between joint angle and muscle length may introduce a "kinematic stiffness" which acts to reduce the joint stiffness as muscle force increases (Hogan 1990). The increase of muscle impedance with force usually predominates.

is, given a set of different impedances $\{\mathbf{Z}_1, \mathbf{Z}_2, \ldots \mathbf{Z}_k\}$ appropriate for different aspects of a task, the total impedance is

$$\mathbf{Z}_{\text{total}} = \sum_{k=1}^{m} \mathbf{Z}_k$$

even if any or all of the component impedances $\mathbf{Z}_k$ are nonlinear. These are among the reasons why modulating mechanical impedance is a particularly efficacious way to control interaction tasks (Toffin et al. 2003; Hogan and Buerger 2004; Franklin et al. 2007). They are also the reasons we believe that mechanical impedance is an essential dynamic primitive for contact tasks.

3 Combining dynamic primitives

A theory based on dynamic primitives requires specification of how those primitives may be combined. Mechanical impedance describes how displacement of points of contact affects the forces exerted at those points. Of course, input from the CNS also influences forces exerted (if there is an object to withstand it) or motion (if no object impedes motion) and both CNS commands and contact events may occur sequentially or simultaneously. For example, carrying a cup of coffee requires movement to contact the cup, then exertion of force on the cup to pick it up, and both simultaneously to transport the cup. It is therefore essential to specify how the different dynamic primitives interact to produce observable forces and/or motions.

To do so, we use the concept of a *virtual trajectory*, denoted by $\mathbf{x}_0$. It summarizes the net motion due to commands from the CNS when the force exerted is identically zero. One advantage of this construct is that the virtual trajectory summarizes CNS motion commands in terms directly comparable to the actual motion. We make the mild assumption that the mechanical impedance is such that if the force is identically zero, the corresponding displacement is also identically zero, $\mathbf{f} \equiv 0 \Rightarrow \Delta\mathbf{x} \equiv 0$. In words: if force and all of its time derivatives and integrals are identically zero, then the corresponding displacement and all of its time derivatives and integrals are also identically zero. This allows us to *define* the displacement input to the impedance operator, $\Delta\mathbf{x}$, to be the difference between virtual and actual trajectories $\Delta\mathbf{x} = \mathbf{x}_0 - \mathbf{x}$ (in joint coordinates, $\Delta\boldsymbol{\theta} = \boldsymbol{\theta}_0 - \boldsymbol{\theta}$) (Hogan 1985).

An advantage of this construction is that the combination of dynamic primitives—submovements, oscillations, and impedances—defines a nonlinear extension of the *equivalent networks,* widely used in engineering to describe physical interaction between dynamic systems, e.g., an audio amplifier and the speakers it drives (Hogan 1985; Johnson 2003; Johnson 2003). According to our view of dynamic primitives,

the virtual trajectory $\mathbf{x}_0(t)$ specified by the CNS may be composed of *submovements* and/or *oscillations*. Based on the difference between virtual and actual trajectories, *impedances* (also specified by the CNS) determine the forces evoked by contact. With this representation, much of the prior engineering insight about dynamic interaction in machines may be extended to help understand physical interaction between humans and their tools.

A virtual trajectory, $\mathbf{x}_0(t)$, can be measured experimentally, at least in principle (Latash 1992; Latash and Gottlieb 1992). It may be inferred from a measurement of mechanical impedance, $\mathbf{Z}$, force, $\mathbf{f}(t)$, and actual motion, $\mathbf{x}(t)$. Impedance maps displacement onto the conjugate force.

$$\mathbf{Z} : \Delta\mathbf{x}(t) \rightarrow \mathbf{f}(t)$$

Its inverse, in a region where it exists, maps force onto the conjugate displacement.

$$\mathbf{Z}^{-1} : \mathbf{f}(t) \rightarrow \Delta\mathbf{x}(t)$$

Thus, the virtual trajectory may be inferred from

$$\mathbf{x}_0(t) = \mathbf{x}(t) + \mathbf{Z}^{-1}\{\mathbf{f}(t)\}$$

To illustrate with a simple scalar example, a linear spring of stiffness, k, may be characterized by

$$f = k(x_0 - x)$$

where f and x are conjugate in the sense that incremental mechanical work done by the spring is defined by $dW = f\,dx$. The virtual trajectory x_0 is the "other end" of the spring. Knowing x, f and k, it can be inferred from

$$x_0 = x + f/k$$

provided $k \neq 0$. In the more general case, estimating a virtual trajectory may be challenging. The central problem is that estimates are exquisitely sensitive to the *assumed* order of the neuromuscular impedance model used to infer a virtual trajectory—see (Gomi and Kawato 1996), but compare with (Gribble et al. 1998). However, there is no fundamental reason it cannot be determined and model-independent experimental methods have been demonstrated (Hodgson and Hogan 2000).

The virtual trajectory is closely related to the equilibrium-point hypothesis, but is also distinct from it in important ways (Feldman 1966; Feldman 1986; Feldman and Latash 2005). A common theme running through the several variants of the equilibrium-point hypothesis is the proposal that the CNS encodes motor commands as time-varying equilibrium postures. However, if neuromuscular mechanics is such as to define an equilibrium configuration for the limbs (specifically, if mechanical impedance is locally invertible, such that $\mathbf{Z}^{-1}$ exists) then an instantaneous equilibrium point (virtual trajectory) may *always* be defined, no matter what the CNS may command. Thus, the mere existence of an equilibrium

point, though not guaranteed ($\mathbf{Z}^{-1}$ might not exist), is not by itself very surprising and does not provide compelling evidence about how the CNS encodes motor commands.

We propose that what is learned, encoded, and retrieved are the parameters of dynamic primitives, rather than any details of behavior. The essence of our perspective is that dynamic primitives are attractors, which emerge from underlying dynamic processes. A virtual trajectory composed of submovements or oscillations (or both), as well as the mechanical impedance required to manage contact and physical interaction with objects, may emerge from generative processes that underlie a combination of submovements, oscillations, and impedances.

3.1 Kinematic synergies may emerge from muscle mechanical impedance

The idea that the CNS simplifies control of its many degrees of freedom by imposing (and taking advantage of) patterns of coordination has considerable appeal, and synergies are often considered to be primitive elements of motor behavior (Tuller et al. 1982). However, it is important to distinguish between primitives and composites. As we next show, at least some types of synergies may in fact be composites, a consequence of muscle mechanical impedance.

Synergistic patterns of joint motion (which we have termed *kinematic synergies*) have been reported in the lower limb motions of cats and humans (Lacquaniti and Maioli 1994; Ivanenko et al. 2007; Dominici et al. 2011). Here, we show how, if muscle impedance is taken into account, these kinematic synergies may be an emergent consequence of *muscle tone*. The term "muscle tone" generally refers to patterns of sustained or *tonic* muscle activation that simultaneously engage agonists and antagonists, and upon which time-varying or *phasic* muscle activation is superimposed (Adams et al. 1997). Abnormal tone, common after neurological injury, occurs when some muscle or group of muscles is hyperactive or hypoactive (Sanger et al. 2003). Following from the robust observations about mammalian muscle that stiffness increases with force, the simultaneous activation of all muscles in a limb—uni-articular or poly-articular or both—will impose a non-zero stiffness about each of the joints (Smith 1981; 1984; Kandel et al. 2000). Thereby, the joint stiffness matrix $\mathbf{K}_\theta$ becomes non-singular.

To see how a kinematic synergy may emerge, consider joint angles $\boldsymbol{\theta} = [\theta_1, \theta_2 \ldots \theta_n]^t$ as coordinates of a configuration space. A synergy defines a curve in that space. Denoting distance along that curve by s_1, the curve is defined by a set of algebraic relations, $\theta_j = S_{j1}(s_1), j = 1 \ldots n$ or, in compact notation, $\boldsymbol{\theta} = \mathbf{S}_1(s_1)$. A set of p synergies defines an array of equations $\theta_j = S_{ji}(s_i), j = 1 \ldots n, i = 1 \ldots p$ or $\boldsymbol{\theta} = \mathbf{S}(\mathbf{s})$ where $\mathbf{s} = [s_1, s_2 \ldots s_p]^t$. The parameters $\mathbf{s} =$

$[s_1, s_2 \ldots s_p]^t$ define the coordinates of a subspace of configuration space (if $p < n$) or the entire configuration space (if $p = n$). The equations $\boldsymbol{\theta} = \mathbf{S}(\mathbf{s})$ define a transformation between the new coordinates $\mathbf{s}$ and old coordinates $\boldsymbol{\theta}$. A locally linear relation between displacements in the old and new coordinates is obtained by differentiation

$$d\boldsymbol{\theta} = [\partial\boldsymbol{\theta}/\partial\mathbf{s}]\,d\mathbf{s} = \boldsymbol{\psi}(\boldsymbol{\theta})d\mathbf{s}$$

where $\boldsymbol{\psi}(\boldsymbol{\theta})$ is the Jacobian matrix associated with the transformation.

Consider the set of kinematic relations between joint angles and the coordinates of some point on the limb, e.g., the hand, $\mathbf{x} = \mathbf{L}(\boldsymbol{\theta})$. The relations between displacements and forces are

$$d\mathbf{x} = [\partial\mathbf{L}/\partial\boldsymbol{\theta}]\,d\boldsymbol{\theta} = \mathbf{J}(\boldsymbol{\theta})d\boldsymbol{\theta}, \text{ and } \boldsymbol{\tau} = \mathbf{J}(\boldsymbol{\theta})^t\mathbf{f}$$

where $\mathbf{J}$ is the Jacobian matrix associated with the change from joint to hand coordinates. Joint coordinate compliance, the inverse of stiffness, is defined by $d\boldsymbol{\theta} = \mathbf{C}_\theta d\boldsymbol{\tau}$ where $\mathbf{C}_\theta = \mathbf{K}_\theta^{-1}$. Differentiating the relation between torques and forces yields

$$d\boldsymbol{\tau} = \mathbf{J}(\boldsymbol{\theta})^t d\mathbf{f} + \boldsymbol{\Gamma}(\boldsymbol{\theta})d\boldsymbol{\theta} \text{ where } \boldsymbol{\Gamma}(\boldsymbol{\theta}) = [\partial\mathbf{J}(\boldsymbol{\theta})^t/\partial\boldsymbol{\theta}]\mathbf{f}$$

A little algebra yields

$$d\boldsymbol{\theta} = \left[(\mathbf{K}_\theta - \boldsymbol{\Gamma})^{-1}\mathbf{J}^t(\mathbf{J}(\mathbf{K}_\theta - \boldsymbol{\Gamma})^{-1}\mathbf{J}^t)^{-1}\right]d\mathbf{x}$$

assuming the required inverses exist Mussa-Ivaldi and Hogan (1991). The term in brackets defines a locally linear relation between displacements in hand coordinates and joint coordinates. Displacement of the hand by $d\mathbf{x}$ results in a displacement of the joints by $d\boldsymbol{\theta}$, similar to what is achieved by a displacement $d\mathbf{s}$ in the subspace defined by synergies. Thus, $(\mathbf{K}_\theta - \boldsymbol{\Gamma})^{-1}\mathbf{J}^t(\mathbf{J}(\mathbf{K}_\theta - \boldsymbol{\Gamma})^{-1}\mathbf{J}^t)^{-1}$ is a particular instantiation of $\boldsymbol{\psi}(\boldsymbol{\theta})$.

Moreover, that locally linear relation may be integrated to yield $\boldsymbol{\theta} = \boldsymbol{\Upsilon}(\mathbf{x})$ which is a particular instantiation of $\boldsymbol{\theta} = \mathbf{S}(\mathbf{s})$. Note that the inverse Jacobian is not required, thus there may be many more joint angles than hand coordinates. It therefore follows that, given a suitable joint stiffness, hand displacements determine a set of joint motion synergies (Mussa-Ivaldi and Hogan 1991). A controller that implements the hand displacement $\mathbf{x}$ and the joint stiffness $\mathbf{K}_\theta$ implements a kinematic synergy corresponding to that joint stiffness. Furthermore, different joint stiffnesses yield different kinematic synergies (Fig. 1).

Simultaneous tonic activation of all the muscles in a limb will impose a joint stiffness that will, in turn, impose a synergy. Abnormal tonic muscle activation will impose a different joint stiffness and, as a result, a different synergy. Such abnormal synergies have been considered a sign of persistent neuromotor deficits. In fact, they may be a consequence of

Fig. 1 Simulation of a planar arm with three joints. Zero displacement of the hand from the equilibrium posture is shown black. The hand (tip) positions of the three final postures are in the same locations in both panels. Different joint synergies result from different joint stiffnesses (k11: shoulder; k22: elbow; k33: wrist). Left: A stiffer shoulder resists deflection and promotes collinearity of hand, wrist and elbow. Right: A stiffer elbow resists deflection. Modified from a figure in (Mussa-Ivaldi and Hogan 1991) where details of the simulation may be found.

k11=-10; k22=-1; k33=-1   k11=-1; k22=-10; k33=-1
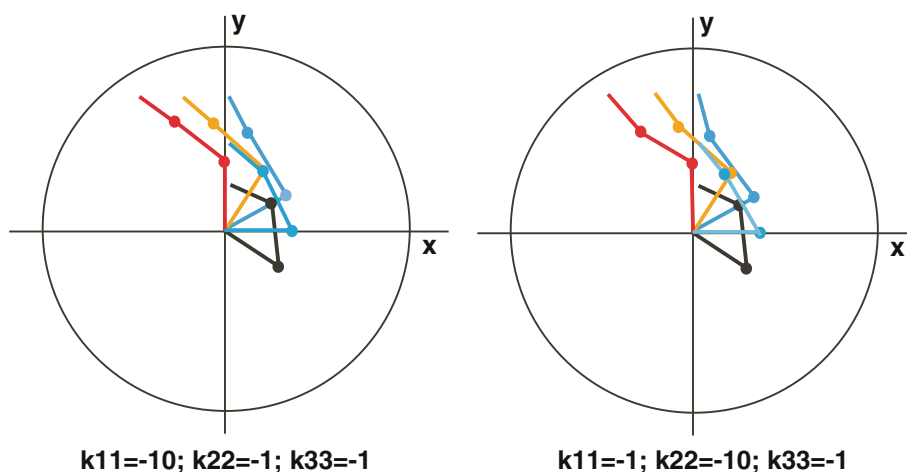
abnormal muscle tone, common in persons with neuromotor deficits. "Re-tuning" of abnormal synergies as measured by the clinical Fugl-Meyer scale accounts for a significant portion of recovery (Dipietro et al. 2007). This may be due to an underlying "re-tuning" of muscle tone, which may also accompany recovery.

For clarity, the above analysis considered only steady-state conditions, but it may readily be extended to include dynamics and yields a similar result. A controller that implements hand motion and joint mechanical impedance also implements a kinematic synergy. Different mechanical impedances yield different synergies and time-varying mechanical impedance may yield time-varying kinematic synergies. Of course, this analysis describes a mechanism for generating only one form of synergy, at the level of joint motions; other synergies may be generated in different ways. Nevertheless, the analysis shows that muscle mechanical impedance may provide a simple solution to Bernstein's "degrees-of-freedom problem" (Bernstein 1967). Whether this solution is employed in the neuro-mechanical system remains to be established by future research.

4 Example applications of dynamic primitives

4.1 Kinematically constrained motions

While much of the motor neuroscience literature has studied simple reaching movements, kinematically constrained motions, such as opening a door or a drawer, are equally ubiquitous in everyday life and, in fact, may be especially informative. Consider the task of negotiating a circular constraint, e.g., opening a door or turning a crank. With negligible friction, minimal mechanical work is required to comply with a constraint, and forces tangential to the constraint are close to zero. Normal forces, however, may be substantial

and their pattern may reveal coordinative strategies used in this context. For example, one strategy for negotiating contact with an object is to learn the exact shape of the constraint imposed by the object in sufficient detail to generate a motion to follow it. Imperfect knowledge of the constraint or imperfect execution of the planned motion might evoke forces normal to the constraint. These, however, should be small and decline with practice. In contrast, a strategy based on taking advantage of low mechanical impedance may succeed *with a minimal representation of the constraint*. With low hand impedance, it is possible to negotiate the constraint with a virtual trajectory comprising a small number of primitive submovements that are not confined to follow the constraint.

Figure 2 shows exemplary data from a simple experiment in which unimpaired human subjects rotated a circular crank in the vertical plane using shoulder and elbow movements (Russell 1990). The circular constraint is shown as the dotted line. Using measured forces exerted on the crank and an estimate of the two-degree-of-freedom mechanical stiffness of the shoulder and elbow, the underlying virtual trajectories were estimated as outlined above. The continuous lines in Fig. 2 show the estimated virtual trajectories (dark line: upward motion; light line: downward motion). In both cases, the virtual trajectories show a clear segmentation into two nearly linear segments or submovements. While these observations should be interpreted with caution due to the very approximate nature of the estimates, they are highly suggestive that this task is learned and parsimoniously represented in terms of dynamic primitives.

4.2 Impact tasks

Object manipulation frequently involves abrupt transitions between free and interactive motion, which can evoke impacts many times briefer than the fastest neuromechanical response times. Consider striking a tennis ball with a racket
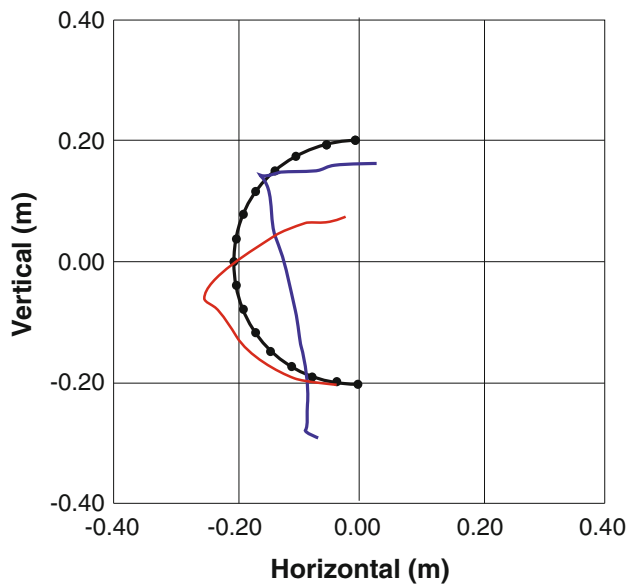
Fig. 2 Negotiating a circular constraint (*dotted line*) with its center at the coordinate origin. Estimated virtual trajectories for up (*thick blue line*) and down (*thin red line*) suggest two submovements.

Fig. 3 Rhythmic ball-bouncing. *Top* ball and racket kinematics. *Middle* wrist and elbow kinematics. *Bottom* EMG of antagonist forearm muscles. Flexor and extensor exhibit similar modulation.

where the actual contact duration is on the order of 5 to 30 ms. Pre-tuning impedance enables a controlled reaction to contact that can overcome the limitations of neuromotor delays. Impedance due to spinal reflex feedback enables reactions faster than those mediated by supra-spinal feedback; intrinsic muscle impedance enables even faster reactions, the so-called "preflexes" (Loeb 1995). Each of these different contributions to overall impedance operates at a different time-scale and therefore may be a distinct dynamic primitive. Whether they are independent impedance primitives is (to the best of our knowledge) a topic for future research.

Sternad and colleagues have studied how humans learn to control impacts in a simple ball-and-racket task (Sternad et al. 2001; Katsumata et al. 2003; Dijkstra et al. 2004; Wei et al. 2008). In a virtual environment, a simulated ball was dropped from a known height and struck to return to that height with the ball and racket motion confined to the vertical direction (Fig. 3). Remarkably, subjects learnt to exploit task dynamics with practice, probably to simplify performance (Sternad et al. 2000b, 2001). Owing to the brevity of the impact, mechanical impedance plays a central role. Pilot data showed increasing co-contraction of antagonist forearm muscles before impact, which elevates mechanical impedance (Fig. 3).

In contrast to rhythmically bouncing a ball, success on a single bounce requires anticipatory action based on a stored representation of the task dynamics. That representation may be quite simple—for example, it may be sufficient to learn and retrieve no more than the onset and amplitude of an appropriate submovement—but, some internal representa-
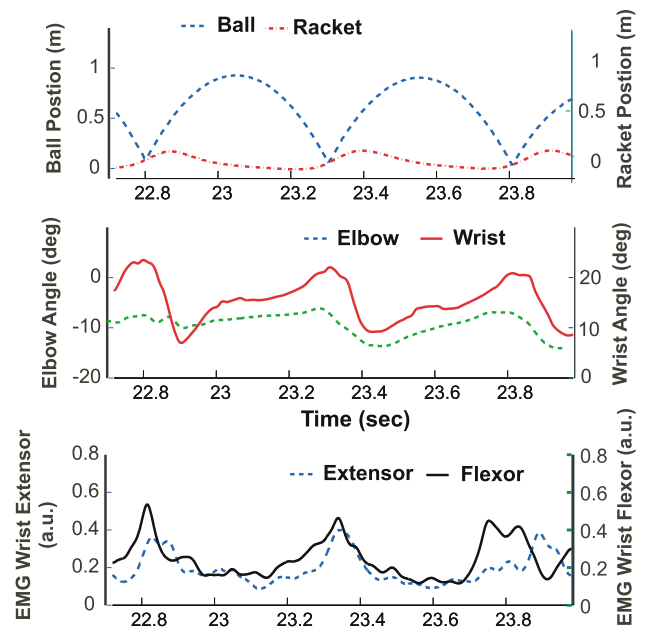
tion is required. Conversely, rhythmically bouncing the ball may not require anticipation or any internal representation of the task. In principle, it may be accomplished by a cycle-to-cycle feedback process, e.g., using ball height on the previous bounce to correct the parameters of a primitive oscillation (e.g., amplitude and frequency) with no stored or recalled representation of task dynamics (de Rugy et al. 2003; Siegler et al 2010). Furthermore, if the task dynamics are sufficiently oscillatory, i.e., nearly lossless collisions, rhythmic bouncing may capitalize on *synchronization due to entrainment* (a characteristic exhibited by nonlinear dynamic oscillators) to reduce performance variability even without visual feedback of bounce height. In fact, experimental studies show that variability of ball height is greater in discrete performance than in rhythmic performance, consistent with this speculation (Fig. 4).

4.3 Continuous dynamic interaction

Continuous interaction with dynamic objects is even more difficult than impact tasks, yet humans frequently wield objects with prodigiously complex dynamic behavior (that was why we mentioned fly-casting or cracking a whip). Even carrying a cup of coffee might be a challenge though most of us manage it with ease. Physical contact with the cup couples the dynamics of the liquid to the controller dynamics. Though it may not be obvious, coupling may compromise stability (Hogan 1990). From robotics, we know that one effective (though perhaps conservative) solution is to
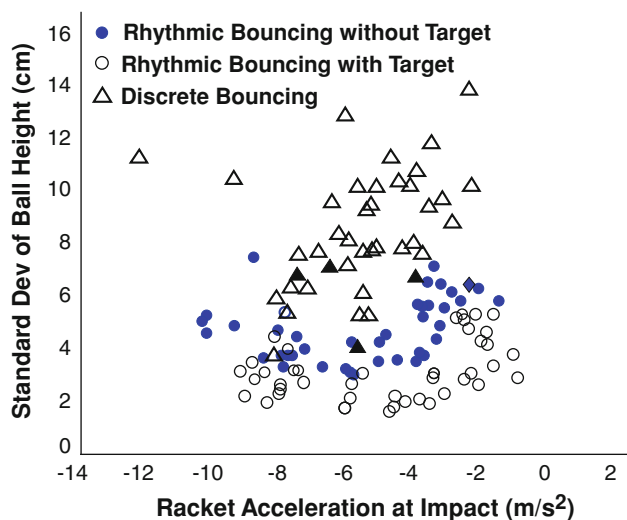
Fig. 4 Variability of discrete vs. rhythmic bouncing. Rhythmic bouncing exhibits similar variability with and without a visual target. Discrete bouncing exhibits significantly greater variability.

adjust mechanical impedance at the point of contact so that it exhibits the dynamic behavior of a passive object, which is sufficient to yield robust stability while interacting with a wide class of objects (Colgate and Hogan 1988; Hogan 1988). Some of the evident human skill at manipulating objects with complicated dynamics may arise from the fact that intrinsic muscular and skeletal impedance is dynamically passive. Whether this is a general principle of human motor behavior remains to be established.

Even aside from maintaining stability, achieving acceptable performance may be challenging. Some initial forays into this area suggest that our formulation based on dynamic primitives may account for observable behavior. However, extensive further investigation is required (Hasson et al. 2012a,b).

5 Levels of analysis

To understand how dynamic primitives might account for human sensorimotor control and use of tools, we distinguish between (at least) three levels of analysis: an *observational level* of overt, measurable behavior; a *combinatorial level* at which the dynamic primitives may be combined; and a *physiological level* from which the dynamic primitives may actually arise—e.g., through a combination of muscular and/or neural dynamics giving rise to submovements, oscillations, and impedances. These levels are loosely analogous to Marr's three levels of analysis—computational, algorithmic, and implementational (Marr 1982). However, Marr's levels refer to computation or information-processing, e.g., for vision. Sensorimotor control and the use of tools may also require

computation or information processing but, in addition, requires dynamics and control of physical interaction, which are not adequately subsumed under information processing.

The distinction between these levels is important. Discrete movements at the *observational* level may result from a sequence of overlapping *submovements*, which are dynamic primitives at the *combinatorial level*. Studies at the *physiological* level are essential to identify primitives unambiguously. To emphasize this point, note that from a purely mathematical perspective, oscillatory dynamic primitives are superfluous. Rhythmic movements at the observational level might be composed of a sequence of back-to-back submovements. However, studies of human neurophysiology have clearly shown that the brain regions involved in rhythmic movements are distinct from those involved in discrete movements. In animals, specialized neural circuitry for generating rhythms—central pattern generators—have been identified in spinal and supra-spinal regions. Hence, this physiological evidence indicates that oscillation is not a composite of submovements but a primitive element in its own right.

Conversely, synergies at the *observational* level of kinematics (joint motion) might appear to be primitive elements of motor coordination. However, they may in fact be composites which emerge as consequences of the interaction among dynamic primitives at the *combinatorial* level of muscle tone. Further work is needed to explore this possibility.

A failure to distinguish between these levels—observational, combinatorial, and physiological—all too frequently confounds sensorimotor neuroscience. The definitions of dynamic primitives we propose here describe *product* rather than *process*. That is, in an attempt to establish a foundation, we focused on the phenomenology of motor behavior, not on hypothesized mechanisms that may give rise to that observable behavior. For clarity, we defined dynamic primitives in the mechanical domain of motions and forces at the interface between the neuromechanical system and an object being manipulated. If the available observational variables are at a different level of the neuromechanical system—e.g., muscle activations (EMG), neural firing rates, etc.—a similar approach may, in principle, be applicable, though care may be required.

Dynamic primitives analogous to submovements and oscillations may be definable at any level (though the former may need to be re-labeled). The case for impedances is more subtle. The definition and properties of mechanical impedance which we have invoked here (including linear superposition of nonlinear primitives) may be applied at different locations—the muscle-tendon interface, the foot-ground interface, the finger-tool interface, etc.—provided significant energetic interaction is involved such that mechanical impedance may be defined. However, an important consideration is that operations on signals which carry information (e.g. neural firing rates) are not subject to the

constraints imposed on energetic interaction (e.g. conservation of energy and production of entropy). Whether plausible dynamic primitives with properties analogous to mechanical impedance may be defined for levels involving information processing alone remains to be determined.

6 Prospect

The elements of a theory based on dynamic primitives which we have outlined here are necessarily crude. Much needs to be done to formulate a reliable, i.e., falsifiable theory (Ajemian and Hogan 2010). To begin, experiments should critically test—attempt to falsify—hypotheses derived from the theory, but, in addition, a practical theory should be *incrementally revisable*. History has taught that any sufficiently ambitious theory will inevitably be contradicted by some experimental observations. However, this does not mean that it should be discarded outright. Valuable theories should not be discarded, but, if possible, revised to accommodate new knowledge. Sometimes, those revisions are small incremental changes; sometimes they are profound re-formulations that make the consequences more accessible[3]. Theory building is an iterative, ongoing process.

Important aspects of any theory need to be tested and established experimentally. One prominent example in the theoretical framework we propose is the composition operator. In the above, we assumed that linear composition was sufficient. This is well justified: linear superposition may be applied to submovements, oscillations, and impedances, even if the latter are highly nonlinear dynamic objects. However, available studies indicate that linear superposition does not adequately describe the combination of submovements and oscillations. There appears to be a phase constraint which cannot be accounted for by linear superposition (de Rugy and Sternad 2003). Further work is required to identify which composition operator may best describe human behavior.

Another open question is how many different primitives of each class (submovements, oscillations, and impedances) are required. Here, a clear understanding of the three levels—observational, combinatorial, and physiological—may be especially useful. For example, it is a fact of mathematics[4] that any sufficiently smooth function may be approximated to any degree of precision by a finite set of finite-support basis functions. This means that it is impossible to disprove a theory that movements are composed of submovements based on kinematic observations alone. However, physiological observations may resolve this fundamental ambiguity.

As mentioned above, for oscillations, it is the physiological evidence which leads us to postulate them as a distinct dynamic primitive.

In the above, we assumed that a single submovement shape, $\sigma(t)$, determines the speed profile of each element of a limb position vector. Though there is experimental evidence to support this assumption in simple reaching and constrained-motion tasks, its generality has not been established (Atkeson and Hollerbach 1985; Russell 1990; Flash and Henis 1991; Krebs et al. 1999). Similarly, mechanical impedance may result from intrinsic muscle properties and/or from the action of spinal (or higher) reflex feedback. Both may be controlled by the CNS. Are they distinct primitives? Or are intrinsic and feedback-generated contributions to impedance fundamentally linked? Probing further, is this set of three classes complete? Are further distinct classes of primitives required? For example, are muscle synergies a distinct type of dynamic primitive? Or are they a completely different kind of coordinative object? Clearly, further research is needed.

Here, we encounter one of the delightful paradoxes of research: while one of the stronger motivations for developing a theory is to organize and codify the burgeoning volume of experimental data, to articulate that theory and make it convincing, we need still more experimental data. New experiments are needed at all levels. Behavioral studies can reveal patterns and invariances that are obscured at the level of neurons; neurophysiological studies can reveal biological constraints that are masked at the behavioral level; analysis and simulation can reveal the consequences of hypothesized generative dynamic processes. Success will require a continuing dialog between theory and experiment at all levels: theory to suggest revealing experiments; experiments to indicate required revisions of a theory. There is plenty yet to be done.

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[3] Consider Oliver Heaviside's reformulation of Clerk Maxwell's twenty equations of electrodynamics into the much simpler formulation we teach today (Ajemian and Hogan 2010).

[4] A generalization of Fourier's Theorem.

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