The λ-Based Equilibrium Point (EP) Hypothesis 1990-1999

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The primacy of the abstract

How abstract are the ideas required to address biological movement? Consider the question posed by Arthur Winfree (1987, p. 253), the foremost theoretician on temporal order in biology and chemistry: "How does a gymnast calculate forces and rates for hundreds of muscles with millisecond precision while whirling from one maneuver to the next?" For Winfree, the answer is not forthcoming in the language of kinematic and kinetic variables. The gymnast's reproducible precision is a more flexible exactitude than the kind we know how to write equations about. It is a kind of exactitude best described and reasoned about in geometry, specifically, the type of geometry that ignores conventional geometric properties (e.g., distance and angle). For Winfree, the gymnast's reproducible precision is a *topological exactitude*.

A similar (but slightly more modest) appeal to an abstract geometrical notion characterizes Feldman's EP hypothesis. That notion is λ, a kind of spatial threshold that is neither a mechanical nor a physiological variable in any orthodox senses of those terms. When referred to the individual muscle, λ is a collective variable expressing current states of the central and peripheral nervous systems, multiple motor and sensory units, and properties of muscle tissue (Feldman, 1986). When referred to a whole body configuration, the generalization of λ is a collective variable comprising all aspects of the constituent muscle and joint λ variables nested within it (Feldman, 1996; Feldman & Levin, 1995). At each of its manifest scales, generalized λ operates as the origin of a spatial reference frame. To change origin is to produce forces in the manner understood for shifting physical frames of reference. Recognition of the scale invariance of this geometrical property with its force producing consequences was a primary theoretical achievement of Feldman's work in the 1990s.

Self evidently, λ is abstract—sufficiently so, apparently, as to shroud the variable in doubt and controversy and to entice calls for its immediate demise (e.g., Gottlieb, 1998). In our view, the dubiety and criticism expressed in the 1990s were motivated in significant degree by the *fallacy of misplaced concreteness* (Whitehead, 1925). The fallacy is committed when one treats an analytic or abstract relationship (which λ most assuredly is) as though it were a concrete entity. The antagonists of λ make the fallacy, but they are not alone. The agonists are also susceptible to the fallacy as reflected in a continuing search for the material grounding of λ's character. Common concretions of λ are as a feature of a physical spring or as an isolable component of the neurophysiology.

Within the burgeoning science of complex systems it has become necessary to be wary of inappropriate concretion. Historically, an observation of quantitative and qualitative features common to different systems would invite a search for a common underlying material cause. For complex physical, chemical and biological systems, however, evidence of similitude frequently requires a very different search and level of explanation (e.g., Goodwin, 1994; Hilborn, 1994). What is sought is *a common geometry in the abstract state space of the dynamics of the systems in question*. A view from the sidelines of the developments of the λ model in the 1990s and the debates surrounding them suggests that the model's contribution to a general theory of coordination will grow as the appreciation of its abstract nature matures.

Theoretical developments of the 1990s in overview

Feldman and Levin's (1995) seminal target article in *Behavioral and Brain Sciences* was a comprehensive and ambitious extension of the λ model. The expansion included (a) the nature of control variables and their relation to reflexes and biomechanical properties of the motor system, (b) multi-joint and multi-muscle redundancy, (c) the equivocal relationship between muscle activity and observed movements, (d) the posture-movement problem, (e) the differences between state and parameter based control of biological movement systems and (f) the emergent nature of kinematic, force and EMG patterns treated as the solution of a nonlinear neuromuscular system and its interaction with the world. However, the most important development was arguably the extension of the concept of physical reference frame from a one-dimensional quantity (threshold muscle length) to the level of actions that spans all the degrees of freedom available to the organism including ones at the extra-personal level (Feldman, 1996). This extension promises both theory and method for studying environmentally embedded action.

Control variables: Parameters not system states

Not surprisingly, the 1990s saw Feldman pressing his fundamental theme: control is via parameters not states. In the formalism of mechanics the manifestation of force on a system depends explicitly on the system's phase (the system states of initial position and initial velocity) and implicitly on the system's parameters (numerical constants that are independent of phase and time). Parameters are independently specified constants (e.g. mass, elastic and friction coefficients) and express the highly particular way in which the system is coupled to the imposed forces. They give the system its identity. Their influences persist throughout the changes in the system's phases and are made manifest by the system's equilibrium state. As the theoretical biologist Robert Rosen (1988, 1990) observed, a system's parameters in the formalism of Newton's mechanics constitute *formal* cause. They differ, therefore, from the force on the system—the *efficient* cause determining the system's motion—and from the initial phase of the system—the *material* cause defining what the force acts upon.

Feldman underscores that the parameters of biological movement are changeable (they are not the fixed quantities of idealized physical systems such as a pendulum). As such they can function as control variables. They differ from one movement to another with their constancy during a movement giving that movement its identity. In his λ model, control is by formal cause. Efficient cause—the forces and the state transitions that express them—are emergent consequences. A moving body segment describable by its states (e.g., EMG activity and velocity) is controlled by parameters that are completely independent of those states (Feldman, Adamovich & Levin, 1995; Feldman, Ostry, Levin et al., 1998). One suspects that this subtlety of the argument, namely, that formal cause is controlled, but efficient cause is not, contributes to the doubts and controversies alluded to above. The EMG-force control hypothesis opposing Feldman's λ model during the 1990s promotes direct manipulation of efficient cause.

To elaborate slightly, the λ model defines control variables in terms of stability. Such variables include reciprocal activation, co-activation and μ (e.g., Feldman & Levin, 1995) that change a body segment's equilibrium under the varying dynamic relations between the muscular configuration of the segment and external forces. These variables are not related to the mechanical characteristics of the segment itself, but are specified in the context of the abstract relation between the body segment and its environment (loading conditions).

The mass-spring analogy

As foreshadowed above, the slim elegance of the λ model encourages the fallacy of misplaced concreteness. This is especially so when viewing the abstract condition expressed by λ through the metaphor of a mass-spring system. The resistance of a mass-spring system to changes in its current equilibrium state is explained in terms of stiffness (resistance to position dependent changes) and damping (resistance to velocity based changes). These are relatively well-understood mechanical properties of materials that can, in principle, be extrapolated to active biological tissue. Perhaps the resistance to perturbation implicit in Feldman's EP hypothesis is understandable in strictly biomechanical terms?

The foregoing assumption seems to be behind a major criticism of the λ model by Gomi and Kawato (1996). They estimated the mechanical stiffness and damping of an arm experimentally (by means of a high-performance manipulandum) and used the estimates to compute shifts in the arm's equilibrium points and determine, thereby, the equilibrium trajectory. The velocity profiles of the observed and estimated trajectories did not match. Although Feldman et al. (1998) questioned the linearity assumptions behind the stiffness estimations and Gribble et al. (1998) provided experimental alternatives, the mismatch reported by Gomi and Kawato was seen by many as a basic contradiction of the λ model.

A resolution of this conundrum motivated by the misapplied concretion fallacy is rather simple. Experimental estimation of the arm's stiffness is at best an approximation of a mechanical quantity and is not equivalent to the abstract notion of an equilibrium-restoring disposition implicit in the λ model. Consider an oscillator dynamic (limit cycle or otherwise) used to describe rhythmic movements of the arm. The model equation includes linear and nonlinear stiffness terms together with friction terms, both dissipative and restorative (a friction function). Modulation of these terms produces qualitative changes in the movement trajectory. The terms in question, however, are not mechanical properties of the arm, but system variables that are parameterized to produce a stable trajectory. While the oscillator terms represent the reluctance that the system exhibits in moving away from its equilibrium state, they cannot be simplified into something merely mechanical or merely physiological.

For the latter reasons and more, the λ model has had a continued impact on the dynamical systems approach. Mitra et al (1997) decomposed (nearly) the control variables required for rhythmic arm movements by parsing the number of active degrees of freedom or first order autonomous differential equations required to reconstruct the movement trajectory in phase space. They found that the system was adequately captured by three degrees of freedom, which could stand for the independent modulation of Feldman's R, C and μ commands.

Literal readings of the mass-spring analogy in the 1990s led to other falsifiable predictions about the λ model. Of particular note was the study by Lackner and DiZio (1994). It is widely understood that transient perturbations do not thwart a mass-spring system's achievement of its equilibrium point—the equifinality principle. Lackner and Dizio showed, however, that Coriolis force perturbations applied to subjects in a dark rotating room produced large endpoint and path deviations in normal reaching movements. The Lackner-Dizio results have also been considered by many to be in contradiction of the λ model. Again, a more abstract perspective with stability as its focus suggests circumspection. At issue is the study of similarity and dissimilarity in sets of λ-based characteristic functions. Perturbations of particular kinds and/or magnitudes preserve the λ-based characteristic functions within a similarity class, that is, preserve stability; others do not. The experimental and theoretical challenge is a formal account of equivalence neighborhoods and the complementary conditions of bifurcation. Feldman (1986) had suggested experimental circumstances of non-equifinal behavior (see also Latash, 1993) and highlighted their relevance to the Coriolis-force experiments in a review (Feldman et al., 1998).

A further point might be helpful. All systems that have an attractor or position dependence of any kind behave in a manner that is similar to that of a spring. The more a linear spring deviates from its state of rest the stronger is its disposition to return to the state of rest. The equifinality assumption, although true for simple springs, cannot be true for the body. First, by the very nature of the λ model, the spring analogy refers to the whole neuromuscular system and its relationship to the environment. Second, not all systems with position-dependent force generation exhibit the property of equifinality. Thus, the demonstrations of Lackner and DiZio (1995) challenged the analogy of the arm as a simplified mass-spring system, but did not disprove the EP hypothesis.

New lines of research

The 1990s saw the application of the principles of the λ model in investigating movement pathologies (e.g., Archambault et al., 1999; Levin & Feldman, 1994). The decade also saw Feldman and his colleagues develop experimental paradigms for studying the assembly and superposition of synergies. They demonstrated that the CNS organizes simple synergies or units of coordination for solving the redundancy problem in trunk assisted reaching movements. Consider, for example, the act of reaching for an object on a table while bending forward at the same time. Experiments suggest that it is achieved by superposing an arm-transport synergy and a compensatory synergy that affects the arm's geometric configuration (Pigeon & Feldman, 1999).

In summary

The EP hypothesis emerged relatively unscathed from this most active decade, despite the high-profile criticisms. The misunderstandings do continue of course and a full comprehension of the hypothesis eludes most students of movement. The leading issue of the scientific level of explanation befitting the richness of the control variables encompassing mechanics, physiology, and much more, remains the central challenge.

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