

What can we expect from models of motor control?

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Abstract: The lambda model of servocontrol seems superior to the alpha model in terms of dealing with the mechanical complexities of nonlinear and multiarticular muscles. Both, however, can be trivialized by noting that the "control variable" may simply be the sum of descending influences at propriospinal interneurons in the case of the lambda model or in the muscles themselves in the case of the alpha model. The notion that the brain explicitly computes output in terms of any such control variables may be an engineering metaphor, useful for conceptual understanding but not for generating predictive hypotheses about higher motor circuitry.

The lambda model for sensorimotor control is clearly a much richer source of biomechanical and neurophysiological insights than the oversimplified alpha model that now dominates many textbooks. Rather than concentrating on the lambda model's mathematical details (which may have frightened off those who demand simple explanations for complicated phenomena), let us concentrate on its general features.

Consistency with anatomical facts. It is certainly a great step forward to recognize the importance, even predominance, of motor command pathways that interact with segmental sensory feedback before they reach the motoneurons (Illert et al. 1981; Jankowska et al. 1973). Such interactions have often been viewed as a descending modulation of local reflexes, but Feldman and Levin (F&L) imply correctly that the same circuitry permits the motor output to be generated during the event by the proprioceptive signals themselves, played out around an interneuronal set point established by the descending signals. What is less clear is the need for *any* direct, unmodulated command signal to motoneurons to act as "the control variable." Even monosynaptic excitation of motoneurons is often subject to presynaptic inhibition from somatosensory afferents (Hultborn et al. 1987). By appropriately weighting the relative effects of descending and peripheral signals on the various interneurons, it should be possible to account both for the presence of motor output in the absence of sensory feedback and for its obvious pathologies. Such a unified approach would also account more gracefully for the obvious differences in dependence on proprioceptive feedback in systems such as the eye and neck that, despite F&L's fancy footwork, seem to operate in a very different mode from limbs.

As F&L point out, the lambda hypothesis actually makes it plausible for the motor cortex to generate descending commands in end-point coordinates, as suggested by Georgopoulos (1991) and colleagues. If the complex distribution and sequence of activation patterns of motoneurons had to be computed explicitly by the brain, there would simply not be enough computational machinery between the motor cortex and the spinal cord to perform the transformation. Instead, the brain can shift the operating point of the spinal interneurons that actually elaborate the observable motor program. The spinal circuitry can also take into account the posture-dependent background of afferent activity and can generate rapid and goal-directed responses to perturbations. It is worth noting that these "preenabled" responses are often far more sophisticated than might be expected from the simple homonymous reflexes that are usually associated with spinal cord circuitry (Cole et al. 1984; Gracco & Abbs 1985). This is, of course, the result of the widespread convergence and divergence of inputs and outputs mediated by the same spinal interneurons responsible for conveying most of the descending control to the motoneurons (Schomburg 1990).

Consistency with biomechanical facts. The lambda model is probably better than the alpha model at coping with the mechanical dynamics of multiarticular limbs and muscles, but much work remains to be done. The analyses presented by F&L assume that

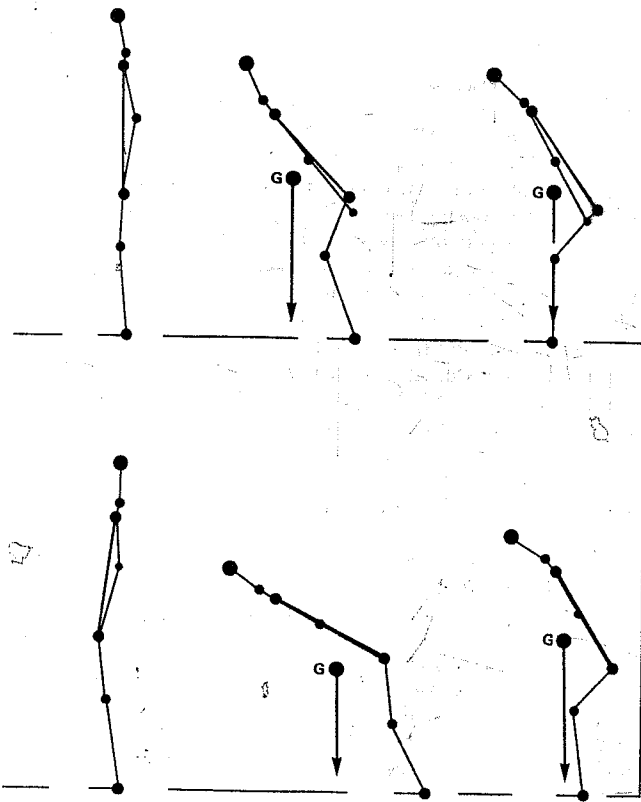


Figure 1 (Lestienne et al.). Body configuration in normal gravity and in weightlessness. Multi-segmental, two-legged human model showing the angular combination among four joints (neck, hip, knee, and ankle) before (left) and on day two (middle) and day seven (right) of a seven-day space flight. Upper figures: "normal terrestrial" standing posture. Lower figures: voluntary 7° forward tilt. In both situations goggles were used to stabilize the visual surroundings (stabilized vision). Notice the exaggerated forward posture on day two. In this posture, the projection of the body's center of gravity is located very far from the subtended polygon. On day seven, immediately following postural reorganization, the body is in equilibrium with respect to a hypothetical field of terrestrial gravity, whereas the execution of the postural reorganization was not totally successful in attaining an erect posture (adapted from Lestienne & Gurfinkel 1988).

of terrestrial gravity. The resulting angular combination among the four joints highlighted the mechanism of movement production by bringing backward the barycenter of the body mass into the vicinity of the foot support. This reorganization of body configuration has been confirmed by the redistribution of tonic activity of the leg muscles controlling the ankle, knee, and hip joints during space flight (Clement et al. 1984; 1985; Lestienne et al. 1994).

* In conclusion, we believe that the experimentally testable arguments developed here reinforce the statement of Feldman & Levin concerning the role of the neuronal body scheme, which "forces the neuronal structure to find a new steady-state distribution of activity which restores the correct geometric relationship associated with the new body configuration" (sect. 6, para. 2).

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motoneuron activation (as measured by EMG) is closely related to force output, an assumption that breaks down for large and rapid movements and brief perturbations. The effects of cross-bridge dynamics and connective tissue elasticity are large and complex, but they weigh much more heavily on alpha-like models that must compute motoneuronal activation explicitly.

It will also be a challenge to see whether the lambda model can account for the activation of muscles on the basis of their ability to cause acceleration at a particular joint, as opposed to torque. Zajac and Gordon (1989) have pointed out that, depending on posture, activating a muscle can produce accelerations at joints that it does not cross; even more paradoxically, it may accelerate a joint that it does cross in a direction opposite to that predicted by its torque. Such complexities seem to be dealt with appropriately by the nervous system but they are completely beyond the scope of alpha models. For the lambda model to account for them, it seems likely that it will need a considerable refinement of the rudimentary but promising approach to kinesthesia presented by F&L.

Consistency with scientific method. It is distressing to see how quickly attempts to cope with reality tend to trivialize all such models into tautologies. For the lambda model, elimination of private line paths to motoneurons causes the control variable in the brain to become simply the sum of all descending influences on spinal circuitry. For the alpha model, the motoneuronal output to the muscles themselves is the control variable, resulting in a trajectory of purely mechanical equilibria (which are under no constraint to be either realized or realizable during a movement). Neither constitutes a testable hypothesis, so what is an experimentalist to do?

At these levels of abstraction, models are more like metaphors than theories. When we read an inspiring novel dealing with a universal theme, we believe that we have gained insight, but we do not insist on going out and reliving the life of the protagonist to test its validity. Instead, we hope these insights will lead us indirectly to make wiser choices in our daily lives. Both the alpha and lambda models are metaphors for aspects of the much richer workings of the real brain. Personally, I find the former like a child's cartoon and the latter like an intriguing short story. Even if someone writes a great novel, however, it would not be the only book I would ever read to understand all there is to know about life or motor control.

Can the λ model benefit from understanding human adaptation in weightlessness (and vice versa)?

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Abstract: Parameters of the lambda model seem tightly linked to certain characteristics of human performance influenced by weightlessness. This commentary suggests that there is a valuable opportunity to probe the lambda model using the changed environment experienced during space flight. The likely benefits are a better model and a better understanding of the consequences of weightlessness for human performance.

The consequences of the changed inertial environment of space flight for human performance are not fully understood, but both the scientific and anecdotal evidence indicate the consequences can be profound. Reports of space motion sickness, disturbances in motion control and spatial orientation, visual disturbance, and experiences ofvection are common during the adaptive period early in flight (Reschke et al. 1994). Many of the same disturbances also manifest themselves immediately following the crew's return to Earth. Humans in weightlessness for extended durations also exhibit a number of physiological changes, including changes in bone density, muscle mass, and strength, all of which are

considered attributable to a changed loading history (Whalen 1993). Given that nominal contact with support surfaces during orbital flight has momentum characteristics significantly different from those experienced on Earth, Whalen (1993) argued that the significant decrease in daily external loading history is critical to the process of musculoskeletal adaptation during space flight.

Because humans adapt to operate efficiently and effectively within the ambient environment, it is likely that the consequences of a modified loading history for human performance are much more extensive than the physiological changes referred to by Whalen. The dynamics observed during human-environment interactions are modulated by the inertial, stiffness, and viscosity characteristics of the musculoskeletal system. The control of intersegmental energy flow is critical in many activities, as evidenced by performance decrements seen under conditions of vibration (e.g., Burstöm & Lundström 1994). Thus, appropriate modulation and attenuation of energy flow is critical for effective performance under conditions of multisegmental motion. Because the dynamics of human-environment interaction during weightlessness are qualitatively different from those found in the terrestrial environment, adaptation to weightlessness will entail a fundamental change in the overall viscoelastic characteristics of the musculoskeletal system.

If adapting to weightlessness has implications for the attenuation of energy flow, then this adapted state will be inappropriate for effective and robust postflight terrestrial behavior. The capacity to attenuate the transmission of energy through the body at the moment of heel strike during locomotion is directly influenced by changes in the characteristics of the musculoskeletal shock absorbers, including the viscoelastic properties of joints (Voloshin et al. 1981). Together, the stiffness, viscosity, and inertial properties of the musculoskeletal system contribute to the ability to conserve, dissipate, direct, and/or exploit such energy. It is quite possible that a potent factor influencing postflight human performance is the compromised ability to attenuate energy flow through the body (McDonald et al. 1994). This maladapted effort to manage energy flow will result in inappropriate energy transfer among contiguous body segments and could cause disturbances in both lower limb coordination and head-eye coordination seen during postflight locomotion.

The I model lends itself to a direct exploration of the mechanisms underlying this adaptation to weightlessness. In turn, human performance in, and adaptation to, weightlessness lend themselves to direct testing of certain predictions of the I model. The question to be posed for the I model is: How does this process of adaptation unfold? If one were to express the adaptive phenomena in light of I model parameters, where exactly should we expect to see change? For example, Feldman & Levin (F&L) admit that there is the possibility that as yet undefined control variables (CVs) may influence muscle stiffness (sect. 4, para. 3). Is it possible that such a CV is related to the energy transmissibility of the musculoskeletal system? Grillner (1972) demonstrated that the earliest response to the disturbances encountered in walking occur as a result of the intrinsic stiffness of muscle. Perhaps one feature of adaptation to weightlessness is a change in the dynamics of this response mechanism?

Finally, one is naturally led to questions of a directly operational nature. For example, would a description of adaptation to weightlessness in terms of the I model lead to the identification of measures we could adopt to alleviate the deleterious aspects of adaptation? As the model currently stands, what kind of sensorimotor disturbances would the model predict in response to the changed inertial environment of weightlessness? Because the parameters of the I model seem tightly linked to certain characteristics of human performance influenced by weightlessness, there is a valuable opportunity to probe the model using the changed inertial environment experienced during orbital flight. The likely benefits are a better model and a better understanding of the consequences of weightlessness for human performance.