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A balanced view of motor control

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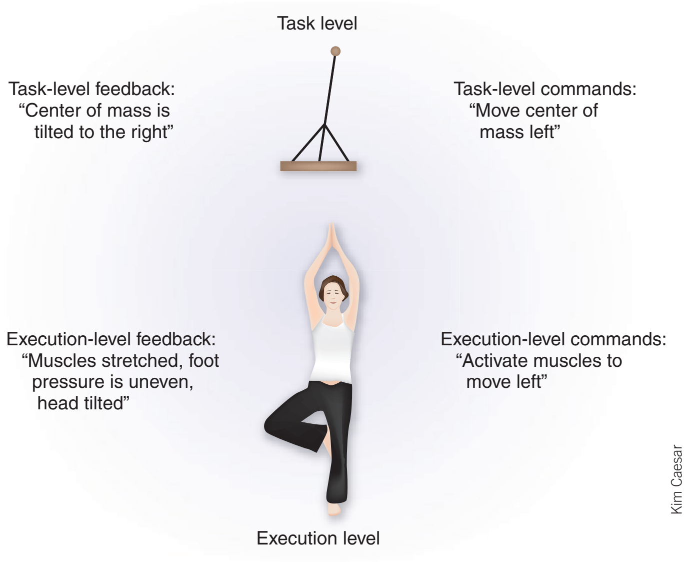
Maintaining balance requires the translation of a high-level command—“Keep the body’s center of mass over the feet”—to low-level adjustments in individual muscles and joints. A new paper finds that a simple translation between these two levels of control provides a robust explanation for responses to several types of perturbations.



Kim Caesar

Figure 1 A hierarchical controller for balance. In this scheme, control is divided between two levels: an execution level involving the regulation of variables such as muscle forces or head position, and a task level involving the regulation of behaviorally relevant variables such as the location of the center of mass relative to the base of support. At this task level, control might use a relatively simple model, such as the inverted pendulum shown. Changes in execution-level variables such as muscle stretches or foot pressure distributions are interpreted as a change in the task variable of center of mass. The task-level controller responds to this change by issuing a command to shift the center of mass back to upright. This task-level command is then translated into an execution-level command to activate the appropriate muscles in order to restore balance. Lockhart and Ting[1] suggest that the CNS might perform a simple translation between task-level variables and execution-level commands in the control of balance.

We all strive for balance in our lives. Many of us, however, have long ago abandoned the dream of balancing our personal and professional lives. For myself, I’m usually happy most days to just stay upright. Luckily for my self-esteem, new research by Lockhart and Ting[1] in this issue suggests that achieving such balance is no minor achievement, but instead involves a sophisticated process of sensorimotor coordination.

Balancing places great demands on the motor system. Small, subtle perturbations can potentially cause rapid and profound failure—that is, falling down. Such perturbations therefore need to be efficiently encoded and translated into appropriate compensatory motor commands. Spring-like properties of muscles, local spinal interneuronal reflexes, and systems throughout the CNS all combine to produce appropriate compensation[2]. How the motor system accomplishes this process, coordinating these different systems into an integrated, adaptive behavior, is a fundamental issue of motor control.

Lockhart and Ting[1] examine these questions in the context of hierarchical control[2–4]. Their hierarchical controller (**Fig. 1**) has two layers: an ‘execution’ level and a ‘task’ level. At the execution level, control is concerned with low-level variables that define the details of motor performance. In the case of balance, these execution variables might be the lengths and forces in each muscle, the angles of the different joints or the orientation of the head in space. Execution-level variables are typically high dimensional and complex, consisting of the vast number of separate elements within sensorimotor systems. At the task level, in contrast, control is concerned with high-level variables that define the nature of the task being performed. In the case of postural control, these are often described by the relationship between the body’s center of mass and the base of limb support; if our center of mass deviates too far from this support base, we fall over.

Lockhart and Ting[1] used several complementary and innovative approaches to examine how the CNS translates between task-level variables and execution-level variables. In the study, cats were first trained to stand on four separate force plates[5,6]. The entire platform was then rapidly displaced and the resulting muscle activation patterns and body kinematics measured. These types of perturbations are similar to those we might experience when riding on the subway or (more optimistically) when walking on the beach. Cats, like humans, are able to compensate readily and maintain their balance.

The authors then investigated the strategies used by the CNS to achieve this control. In particular, they focused on explaining the time course of muscle activations. Most

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muscles show a complex temporal pattern in response to these perturbations, with a phasic burst followed by a sustained plateau. How is this temporal pattern generated? What is its role in maintaining balance?

Studies examining such neural control strategies often simply regress observed activity to potential control variables. The regression coefficients thus identified are then interpreted as indicating how important each variable is for control. Although such analyses have been useful, they do not necessarily demonstrate whether the identified control strategy is actually effective.

To examine these issues, Lockhart and Ting developed a new analysis[1]. As in a standard regression analysis, they attempted to explain the muscle activation patterns in terms of potential control variables. In addition, however, they required that the predicted muscle activations actually achieve balance control. That is, they required that the low-level execution variable of muscle activation satisfy the demands of the high-level task.

Specifically, they used a simple biomechanical model of an inverted pendulum controlled by a single muscle. They then perturbed the base of support in the model along the same trajectory that was applied experimentally to the cat. As in standard analyses, they found the weighting coefficients for the position, velocity and acceleration of the center of mass that best explained the observed muscle activation. Going further, though, they required the resulting model pendulum trajectory to match that observed for the cat. By requiring that the modeled muscle activation match both the experimental muscle activity and the observed center of mass kinematics, this analysis constrains the explanation of the observed muscle activation to be effective for control. Thus, this analysis assesses whether the execution-level variable of muscle activity can be explained in terms of task-level control. If it can be, that would suggest that the CNS simply translates between task and execution levels.

The results of the study support the existence of such a simple translation. In particular, the temporal pattern of muscle activations could be explained quite well using this analysis. This goodness of fit was found for all muscles examined, irrespective of their mechanical action. This result further suggests that the translation is relatively global across a wide set of muscles, further simplifying the control problem.

The authors then performed a critical test of the robustness of these fits. They fixed the feedback gains found in the above analysis and used these gains to predict the muscle activations observed in a more complex perturbation in which the platform was initially displaced in one direction and then rapidly displaced in the opposite direction. The same feedback gains explained the often temporally complex responses to these dual-step perturbations. This ability provides a strong demonstration that the authors' analysis did not produce an arbitrary fit to the data but, instead, identified a control strategy used by the CNS.

Lockhart and Ting[1] next examined the efficacy of this control strategy. They applied techniques from optimal control theory to their inverted pendulum model to find the temporal activation pattern that minimized the amount of effort and the error in control. They found that the optimal patterns were similar to those found experimentally. Thus, although the control strategy used by the CNS was simple, it was nonetheless effective and close to optimal.

As a final test of their approach, the authors investigated whether feedback gains are alterable by examining the changes in control after peripheral neuropathy caused by pyridoxine overdose[6]. Pyridoxine overdose causes a profound loss of group I muscle and cutaneous afferents. Animals are initially ataxic after such an overdose, gradually recovering postural ability over the course of two weeks, although their balance control remains impaired.

The authors show that this residual impairment can be explained as an alteration in feedback control strategy. In particular, they show that the main alteration is a loss of acceleration feedback control. Because of this loss, cats no longer produce the initial transient burst of muscle activation, resulting in the appearance of a delayed muscle activation[6]. A similar temporal activation profile is predicted by their optimal control analysis when the acceleration signal is removed, suggesting that the CNS has reweighted its feedback gains to compensate optimally for the peripheral neuropathy.

This study is significant for several reasons. First, it provides a new explanation of muscle activation patterns in terms of a simple task-level feedback controller. As shown by its ability to predict the responses to complex perturbations and the consequences of peripheral neuropathy, this explanation provides important insights into balance control.

Further, this work suggests that there might be a relatively simple translation between task and execution variables used within a hierarchical controller. This simplicity is attractive, as the transformations between these different levels are potentially highly complex. It will be interesting to see whether the explanations of the temporal aspects of muscle activations demonstrated in this study can be extended to explain how the particular balance of muscle activations is chosen in these responses. As described in the paper, previous work by these authors and others has suggested that muscle activations are produced through the combination of muscle synergies[7,8]. It should be possible to incorporate such muscle synergies into the control framework of this study and examine whether it can explain both spatial and temporal muscle activation patterns.

More broadly, the optimal control framework used in the study holds the potential to provide a succinct explanation for a wide variety of phenomena in motor control[9,10]. There are of course several difficulties in this approach, such as defining the cost function to be optimized. And it is not clear that full optimality is always critical: might the CNS be satisfied sometimes with being 'good enough'? Fundamental to this approach, though, is a unified appreciation of the entirety of motor control: the properties of both sensory and motor systems, along with the biomechanical plant, must all be accounted for. Thus, it is neither purely motor nor sensory, but is a truly balanced, sensorimotor approach.

The results of this study therefore reaffirm the importance of balance, both for responding to perturbations and for studying how those perturbations are compensated for. Ideally, such a balanced approach to balance control might encourage a balanced lifestyle for researchers. In the meantime, I'll just go for a bike ride and try not to fall down.

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