nature neuroscience

Optimal sensorimotor transformations for balance

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Here we have identified a sensorimotor transformation that is used by a mammalian nervous system to produce a multijoint motor behavior. Using a simple biomechanical model, a delayed-feedback rule based on an optimal tradeoff between postural error and neural effort explained patterns of muscle activation in response to a sudden loss of balance in cats. Following the loss of large sensory afferents, changes in these muscle-activation patterns reflected an optimal reweighting of sensory feedback gains to minimize postural instability. Specifically, a loss of center-of-mass-acceleration information, which allowed for a rapid initial rise in the muscle activity in intact animals, was absent after large-fiber sensory neuropathy. Our results demonstrate that a simple and flexible neural feedback control strategy coordinates multiple muscles over time via a small set of extrinsic, task-level variables during complex multijoint natural movements.

The simple act of standing up is a common and essential motor behavior that is often taken for granted, even in uncertain and dynamic environments. Although humans are able to stand on a boat or walk over uneven terrain without much thought, the neural systems that regulate postural orientation and equilibrium continually integrate a large array of sensory inputs and coordinate multiple motor outputs to muscles throughout the body. Understanding how complex sensory patterns are transformed into an appropriate temporal sequence of motor commands is central to unraveling the complexities of the neural control of movement.

It has been shown recently that just a few motor command signals are used to generate spatial patterns of muscle activation during natural movements[1–4]. By using a single motor command signal to activate multiple muscles across the body in a group, called a 'muscle synergy', a multijoint motion can be produced. By adding a few additional motor command signals, a repertoire of complex motions becomes possible. The advantage of this scheme is that the set of motor command signals has substantially reduced dimension when compared with the total number of motor outputs[5], whether these are considered to be individual muscles or motor units. During a natural movement, these motor command signals are necessarily modulated over time[6,7]; however, the neural mechanisms that determine their temporal characteristics are not known.

In balance control in particular, motor command signals must be dynamically modulated in response to a suite of sensory information and cannot be generated by feedforward spinal pattern-generation mechanisms, such as those producing locomotion[3,8]. Sensory signals during a perturbation also depend dynamically on the ongoing motor response to the perturbation, making them difficult to study in a classical stimulus-response procedure. Moreover, because of redundancy in the multijointed musculoskeletal system, the relationships between specific joint-angle changes and muscle-activation patterns during the postural response are highly variable[9]. Thus, postural responses to perturbations cannot be explained by reflex loops acting on individual joint angles, but instead require substantial integration of multiple sensory modalities, presumably in the brainstem[10].

Because the center of mass (CoM) motion compactly encapsulates the relationship of the body to the extrinsic effects of gravity and external forces, we reasoned that the control of CoM dynamics would be important in the feedback regulation of balance. The best predictor of which muscles are activated during a postural response to perturbation is the horizontal direction of CoM motion[9,11]. CoM-motion variables are extrinsic, task-level variables that represent the net motion of the body with respect to the gravitational reference frame. In general, extrinsic, task-level variables represent the relative relationship of multiple body segments to the external environment and cannot be inferred from local anatomical variables such as joint angles or head displacement, except in the simplest of cases. Thus, task-level variables generally cannot be encoded by any one sensory signal or modality; rather, they must be estimated from many sensory modalities.

We hypothesized that an optimal and hierarchal feedback control organization based on extrinsic, task-level variables governs balance control, which is an automatic motor task that does not require trajectory planning or the involvement of higher brain centers[10]. Similar schemes have been proposed as a general organization principle for voluntary motor tasks[12–16]. We predicted that neural control mechanisms for temporal patterning of motor signals for balance control would be low in dimension, operating on a small set of feedback gains related to the control of the CoM[5]. We demonstrate that a simple model of the neuromechanical system—an inverted pendulum stabilized by a feedback rule—predicts the time course of motor command signals during balance control in both intact and sensory-loss cats. The pendulum dynamics nominally modeled CoM acceleration, velocity and position of the animal and were sufficient to specify the motor

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Received 5 July; accepted 24 August; published online 16 September 2007; doi:10.1038/nn1986