Using perturbations to probe neural control: from standing to walking

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Sensory information is critical for the neural control of human bipedal balance, as human bipedal stance is inherently unstable, requiring a sophisticated control system to maintain upright. Studies of human standing have shown how three primary sensory systems interact through principles such as multisensory reweighting to insure the most reliable estimates of body dynamics so that control processes result in flexible stable upright standing. Although the nonlinearity of reweighting is prominent when sensory conditions change, such as when a previously static visual scene begins to move, under fixed sensory conditions linearizing around the fixed point of upright stance can usefully approximate standing balance. Thus, the inherent appeal of studying balance during standing is that well-known linear time invariant (LTI) methods can be used for system identification and analysis.

In the frequency domain, the LTI approach uses a *closed-loop* frequency response function (FRF) to characterize the effect of a perturbation on the standing control system. This system consists of two processes: the mapping from muscle motor commands to sway (the plant) and the mapping from sway to muscle motor commands (feedback), where we consider rectified EMG signals as a proxy for muscle motor commands. The plant depends on musculotendon dynamics and body dynamics. Feedback depends on sensory dynamics, sensory integration, and the control strategy. The joint input-output (JIO) method of closed-loop system identification (CLSI) uses closed-loop FRFs used to identify both the plant and feedback *open-loop* FRFs. Such analysis has shown that the control strategy for standing is to minimize "neural effort" rather than the common assumption of body sway minimization.

In contrast to standing, the neural control of walking must stabilize a limit cycle rather than a fixed point. One can linearize around the limit cycle, but even under this simplifying approximation one must consider how neural feedback control using sensory information varies with phase of the gait cycle. This phase-dependent neural feedback control must be suited to the specific feature of walking, including that: 1) the center of mass travels outside the base of support during walking; and 2) sensory modalities such as vision play multiple roles during walking, such as navigation and obstacle avoidance. It remains an open question whether the current conceptual understanding of the neural control of standing maps onto that during walking.

To develop system identification methods to study walking, we must develop an analogue to the FRF. We do this by first estimating the phase $\theta(t)$ of the gait cycle and considering the given response variable to be a function of θ, so that the system is approximately linear time periodic (LTP). The analogue of a FRF for a LTP system is a harmonic transfer functions (HTF), which describes how input at frequency f produces outputs at multiple frequencies $f + kf_0$, where f_0 is the gait frequency and k is any integer. We use HTFs to describe the effect of a small perturbation both on the response variable and on estimated phase. These two HTFs can be converted to the time domain and combined together to obtain a phase-dependent impulse response function (IRF) that characterizes the effect of a small brief perturbation at any phase of the gait cycle. A key advantage to this method is that the IRF is, to first order, independent of the method used to estimate phase.

We have applied this approach to probe walking on a treadmill under various conditions, for example, walking while perturbed by a moving visual scene. When the visual scene moved forward, the subjects sped up and moved forward on the treadmill, a response caused not only by the expected increased activation of plantarflexors in late stance, but also by the increased activation of dorsiflexors in early stance. Thus, our results suggest a much more flexible control scheme for walking than that predicted by models that emphasize control at push-off.