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Postural feedback responses scale with biomechanical constraints in human standing

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Abstract We tested whether human postural responses can be described in terms of feedback control gains, and whether these gains are scaled by the central nervous system to accommodate biomechanical constraints. A feedback control model can describe postural responses for a wide range of perturbations, but biomechanical constraints—such as on the torque that can be exerted on the ground—make a single set of feedback gains inappropriate for all perturbations. To observe how postural responses change with perturbation magnitude, we applied fast, backward perturbations of magnitudes 3–15 cm to 13 healthy young volunteers (4 men, 9 women, aged 20–32 years). We used a 3-segment, sagittal-plane biomechanical model and a linear state feedback controller to reproduce the observed postural responses. Optimization was used to identify the best-fit feedback control gains for each trial. Results showed that trajectories of joint angles and joint torques were scaled with perturbation magnitude. This scaling occurred gradually, rather than abruptly changing at magnitudes where biomechanical constraints became active. Feedback gains were found to fit reasonably well with data ($R^2=0.92$) and to be multivariate and heterogenic in character, meaning that the torque produced at any joint is generally a function of motions not only at the same joint, but other joints as well.

Hip gains increased and ankle gains decreased nearly linearly with perturbation magnitude, in accordance with biomechanical limitations on ground reaction torque. These results indicate that postural adjustments can be described as a single feedback control scheme, with scalable heterogenic gains that are adjusted according to biomechanical constraints.

Keywords Balance · Equilibrium · Posture · Motor control · Biomechanics

Introduction

The human posture control system accommodates a wide variety of perturbations to balance. The central nervous system (CNS) must select muscle activation patterns appropriate not only for an assortment of perturbation types and magnitudes (Diener et al. 1988; Horak and Nashner 1986), but also in accordance with biomechanical constraints such as those imposed by intersegmental dynamics and musculoskeletal geometry (Kuo and Zajac 1993). Postural responses can be described in terms of preprogrammed muscle activation patterns that are triggered by perturbations, with the appropriate response selected from among many possibilities (Nashner and McCollum 1985). For example, as the magnitude of a surface translation increases (Diener et al. 1988) or the base of support decreases (Horak and Nashner 1986), postural responses have been described as changing from a distal-to-proximal pattern of muscle activation to one with early activation of torso and hip muscles. It has been suggested that subjects change strategy due to biomechanical constraints such as a desire to avoid lifting the heels off the floor (Horak and Nashner 1986), but it is unclear whether the nervous system selects preprogrammed postural strategies according to such constraints. The seemingly infinite variety of possible postural responses, makes automatic postural responses difficult to store in the form of detailed movement trajectories (Schmidt and Lee

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1999). Postural responses might, alternatively, be generated dynamically through continuous feedback.

Continuous feedback has a number of functional advantages compared with the storage of preprogrammed movement patterns (Kuo 1995). First, feedback responses can be produced by relatively simple reflex circuitry, compared with the storage circuitry needed for a library of muscle activation patterns. Second, feedback can provide the dynamic stability that is needed to keep the body upright even during quiet standing, when there are no apparent external perturbations. Third, a single set of feedback gains can flexibly respond to multiple perturbations, because it is the interaction between a perturbation and the feedback system that generates the response. This means that a set of feedback gains, alone, might be sufficient to describe a range of responses appropriate to a context. In contrast, preprogrammed movement trajectories can restore the body to upright after a perturbation, but, despite their large storage requirements, cannot produce the dynamic stability required to remain upright.

The advantages of feedback do not, however, obviate the need for higher-level participation by the CNS, which must determine context (Horak et al. 1989) and select appropriate feedback gains. The postural context depends on biomechanical factors such as body and surface configuration, as well as task objectives such as the desire to remain upright without stepping versus the desire to return to equilibrium as fast as possible (Horak and Kuo 2000). Different contexts require different strategies (Adkin et al. 2000; Horak and Kuo 2000), each of which may require a different set of feedback gains. Previous studies have shown that in quiet standing, feedback gains are multivariate and can vary with sensory context (Kuo et al. 1998; Speers et al. 1998). Multivariate gains refer to the multiplicity of relationships between movement about a joint and the feedback torque generated about the same and other joints, as might result from heterogenic reflexes (Bonasera and Nichols 1994). The variety of postural responses to different perturbations (Allum and Honegger 1998; Horak et al. 1989; Runge et al. 1999; Diener et al. 1988; Hughes et al. 1995; Maki and Ostrovski 1993) might vary depending on biomechanical context.

The purpose of the present study was to test whether postural response can be described in terms of a continuous feedback control system, and to determine how a feedback description scales with perturbation magnitude. We hypothesized that postural responses gradually scale in accordance with biomechanical constraints such as limitations on allowable ankle torque, and that multiple, heterogenic feedback gains must participate in this scaling.

Methods

To examine human postural balance control under the influence of biomechanical constraints, we applied backward surface perturbations of a variety of magnitudes to subjects initially standing upright, and observed how their sagittal plane postural responses changed as

biomechanical constraints on ankle torque became increasingly constraining. We then used optimization to identify a set of feedback control gains for each trial that could produce similar behaviors in a biomechanical model and used these gains as a quantitative measure of postural control strategy. We examined the scaling of these gains with the magnitude of perturbations relative to biomechanical constraints.

Experimental data collection

We applied backward translations of the support surface to 13 healthy young-adult humans (4 men, 9 women) aged 20–32 years. All subjects gave informed consent based on protocols approved by the Oregon Health & Science University Institutional Review Board. Subjects were instructed to stand quietly in an upright position with their arms crossed over their chests, atop a movable support surface. They were instructed to recover from a perturbation by returning to their initial upright position, without stepping or lifting their heels off the ground if possible. The support surface was servo-controlled to produce fore-aft translations and was programmed to move backward with seven ramp displacements, all 275 ms in duration. The displacement magnitudes were 3, 4.5, 6, 7.5, 9, 12, and 15 cm, with average velocities of 0.11–0.55 m/s. Each perturbation occurred in blocks of 5 repeated trials of the same magnitude, with the blocks given in random order. The largest perturbation magnitude was designed to induce either lifting of the heels or stepping, to test a significant range of the subjects' balancing ability. During the rehearsals for the trials, subjects were allowed to experience the largest perturbation in order to be acquainted with the most challenging perturbation.

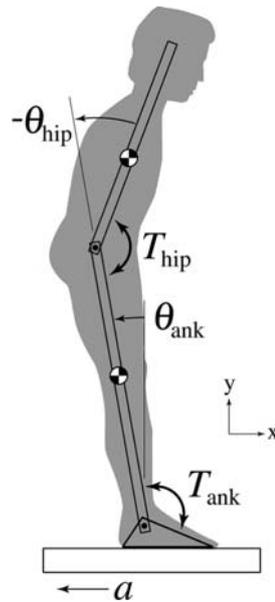
For each trial, kinematic and ground reaction force data were recorded for a total of 10 s, including 2 s prior to and 8 s after the onset of disturbance. Kinematic data were recorded at a sampling rate of 120 Hz using an optical Motion Analysis (Santa Rosa, Calif.) system with six cameras. Seven optical markers were used, located at the right shoulder (acromion), hip (greater trochanter), knee (lateral femoral condyle), ankle (lateral malleolus), toe, heel, and the platform surface. The marker positions were used to calculate the segment angles for the foot, shank, thigh, and trunk. All segment angles were referenced to zero, defined as the subject's preferred vertical upright position, with a positive sign for extension. Ground reaction forces and moments were recorded at a sampling rate of 480 Hz from force transducers located in the support surface. These data were then used to compute net joint torques, employing a least-squares inverse dynamics method (Kuo 1998).

Video records were used to examine whether subjects' postural responses were primarily confined to the sagittal plane. All subjects exhibited fairly consistent behavior between trials, except for one subject who exhibited highly asymmetrical and inconsistent movements outside of the sagittal plane. This subject's data were excluded from the subsequent analysis.

Identification of feedback gains

We used optimization methods to identify a set of feedback control gains characterizing each trial, so that the biomechanical model incorporating this feedback control would reproduce each trial's response. There were three components to this identification (described in detail in the Appendix): a biomechanical model of body dynamics, a linear feedback control to stabilize this model, and an optimization procedure to produce model responses with a best fit to the data. The biomechanical model was based on the equations of motion for a three-segment (feet, legs, trunk) linkage confined to the sagittal plane, with the feet flat on the support surface (Fig. 1). This model was first used for inverse dynamics computations on the experimental data to estimate joint torques (Kuo 1998). The same equations of motion were incorporated, in linearized form, in a feedback control model of postural responses to disturbances of the support surface (see Fig. 2). In this feedback paradigm, the body

Fig. 1 Biomechanical posture model in the sagittal plane, with three body segments (feet, legs, and head–arms–trunk), assuming little knee motion. Joint angles θ_{ank} and θ_{hip} are measured relative to the vertical upright position with a positive sign for extension. In experimental trials, the support surface (force platform) moved backward in various ramp displacements, a , ranging from 3 to 15 cm, all with duration of 275 ms



dynamics remain relatively fixed, and the CNS selects the feedback control gain matrix (K) to determine the dynamic postural behavior. Each entry in the gain matrix specifies the amount of torque produced at each joint proportional to deviations in joint angle and angular velocity. The response to a perturbation is then generated dynamically as a function of initial conditions and the perturbation magnitude, producing simulated state and torque trajectories over time.

To describe human postural responses in terms of the feedback control model, we used an optimization procedure to find the gain matrix K that would produce a response that best matched the experimentally determined kinematics and joint torques. One constraint was placed on the optimization, requiring a stable closed-loop system. To facilitate comparisons with data while accounting for differences in subject height and weight, we performed a series of normalizations to yield dimensionless quantities. We normalized perturbation magnitude data by body height, torque data by the product of body weight and height, and angular velocity data by the square root of the gravitational acceleration divided by body height, which is proportional to an inverted pendulum's natural frequency. The torque and velocity

normalizations account for the increased inertia and slower dynamics, respectively, that are expected of larger individuals.

We hypothesized that biomechanical constraints require the CNS to scale postural responses, in terms of feedback gains K , as a function of perturbation magnitude. In the absence of constraints, a fixed set of gains is sufficient to guarantee stability against any disturbance. But constraints such as the limitation on allowable ankle torque mean that the gains appropriate for small perturbations, when applied to larger perturbations, might lead to control responses that exceed the constraints. A different set of gains would then be required for larger perturbations.

We expect that the CNS could accommodate constraints with either a discrete or continuous change in control strategy, depending on how constraints are represented. Constraints that act in a discrete or on–off manner can select different strategies with a discrete gain switch, whereas constraints that act in a continuous manner can be used to weight strategies so that the control response changes more gradually with perturbation magnitude. Discrete constraints would be expected to produce constant gains that switch abruptly once a constraint becomes active (Fig. 3A), while continuous constraints would produce gains that scale gradually with perturbation magnitude (Fig. 3B). Experience with artificial neural networks suggests that constraints are more readily represented continuously in a neural system (Nauck et al. 1997), implying an expectation of gradual scaling.

To test for scaling of control responses, we averaged the normalized gain matrices for each perturbation, and tested whether these changed as a function of perturbation. Statistical tests were based on a level of significance of $P < 0.01$.

Results

Postural responses were found to gradually scale with perturbation magnitude, rather than abruptly when biomechanical constraints became active. This is demonstrated by continuously changing kinematic trajectories of joint angles and accelerations, and by trajectories of joint torques computed from inverse dynamics. We also found that a quantitative description, in terms of feedback control gains, also exhibited gradual scaling with perturbation magnitude.

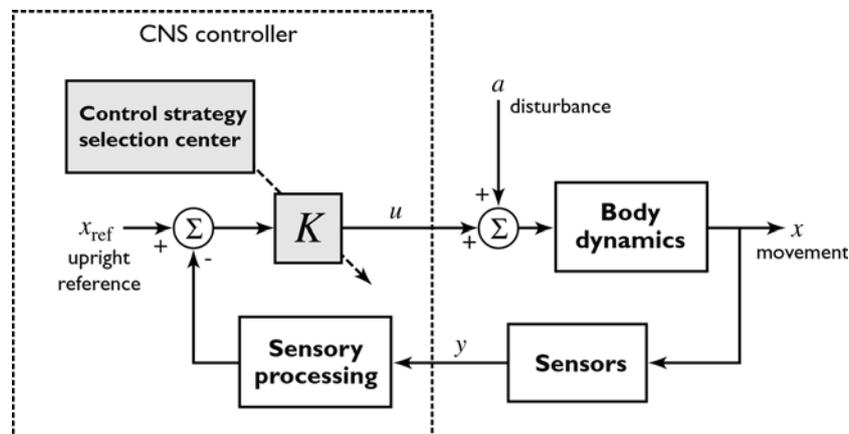


Fig. 2 Linear feedback control model, where K is a matrix of feedback gains producing joint torque commands u as a function of body movement x . Joint torques and disturbances act as force inputs to the body dynamics, resulting in movement that is detected by a variety of body sensors. Sensory information is then processed by the central nervous system (CNS) to estimate the positions and

velocities of the body segments, which are used to generate the compensatory joint torque commands u . The present model focuses on appropriate selection of K by the CNS in accordance with biomechanical constraints and body dynamics, and does not specifically model sensors and sensory processing

Subjects gradually scaled their postural responses with perturbation magnitude. This is qualitatively demonstrated by a typical subject's hip versus ankle joint trajectories, averaged over 5 trials, for each perturbation magnitude (Fig. 4A). Joint angular accelerations (Fig. 4B) exhibited a

bias toward combinations of hip and ankle acceleration in the ratio of approximately $-3:1$, as predicted from body dynamics and biomechanical constraints (Kuo and Zajac 1993). The gradual change in control strategy is seen most clearly by scaling of joint torques (Fig. 4C), with torque

Fig. 3A, B Expected scaling of postural responses with increasing perturbation magnitude, for **A** discrete and **B** continuous representation of biomechanical constraints. **A** A discrete representation implies that the postural control strategy will change only when biomechanical constraints (heel-off, *dashed line*) act to limit allowable joint torques. Trajectories of hip versus ankle torque (T_{hip} versus T_{ank}) will scale uniformly as perturbation magnitudes increase, and abruptly change when the strategy (i.e., feedback gain) is switched to satisfy the constraint on maximum allowable ankle torque. **B** A continuous representation will cause the CNS to gradually scale control strategies before constraints are active, yielding gradual changes in joint torque trajectories and feedback gains

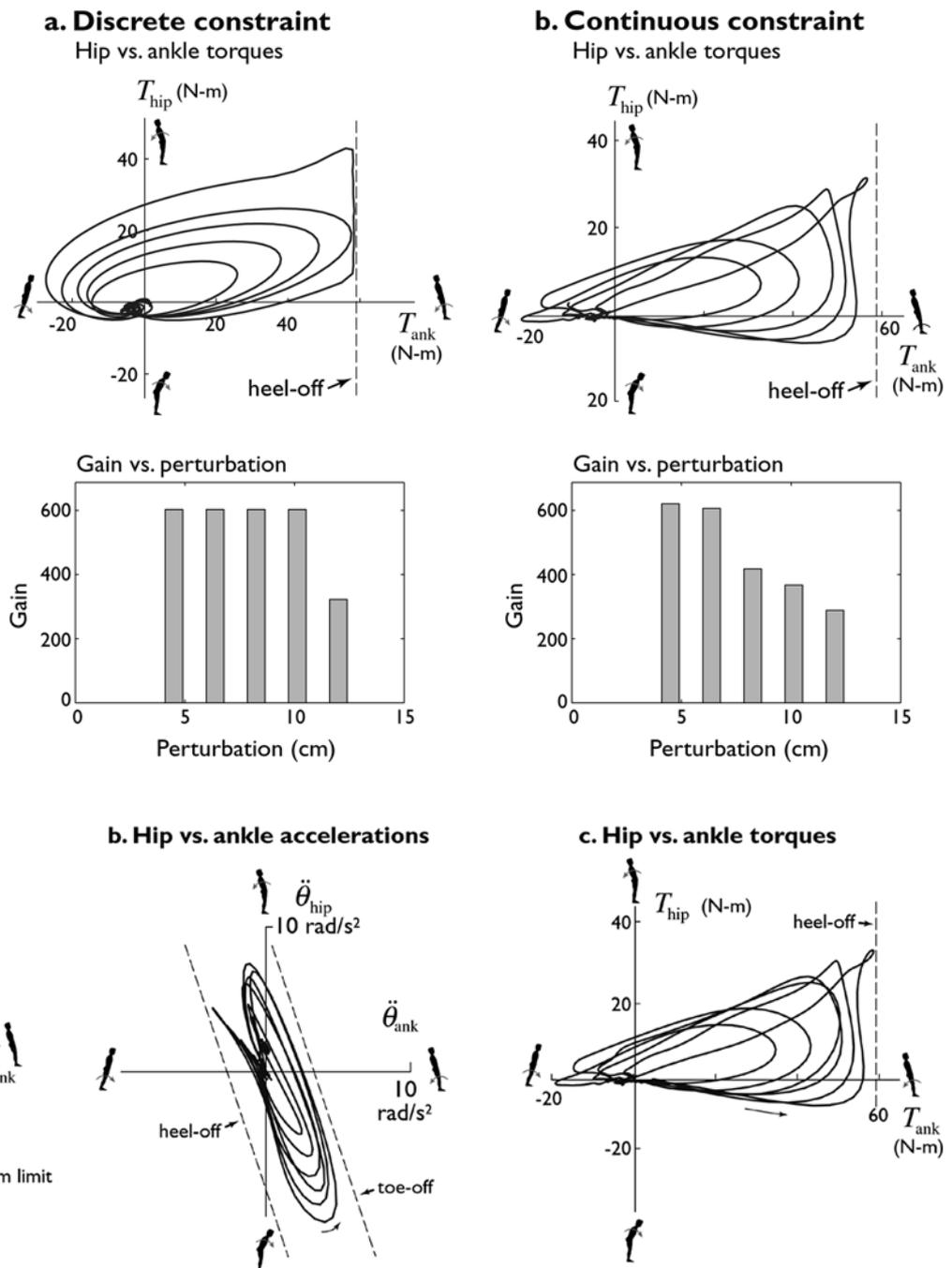


Fig. 4A-C Scaled postural responses for increasing perturbation magnitude, in terms of joint angle, joint angular accelerations, and joint torques. **A** Hip versus ankle joint angle trajectories, averaged over 5 trials for each perturbation, were found to scale gradually with perturbation magnitude. All trajectories remained within the boundaries in ankle-hip joint space for which the center of gravity remains within the base of support (com limits, *dashed lines*). **B** Hip versus ankle joint angular acceleration trajectories were also found to scale gradually. All trajectories remained within the limits on allowable movements that keep the feet flat on the ground (heel-off

and toe-off acceleration constraints, *dashed lines*). The dominant combination of hip and ankle accelerations was approximately $-3:1$, due to body dynamics, musculoskeletal geometry, and other biomechanical constraints (Kuo and Zajac 1993). **C** Hip versus ankle joint torque trajectories were also found to scale gradually, with a change in the trajectory shape as perturbation magnitude increased, in order to stabilize the body while keeping ankle torque below the maximum allowable to keep the feet flat on the ground (heel-off joint torque constraint, *dashed line*). Data shown are means for a representative subject

trajectories changing as perturbation magnitude increased, in order to accommodate the limitation on allowable ankle torque while keeping the feet flat on the ground.

The feedback control model was able to reproduce each postural control trajectory with one set of time-invariant feedback gains for each trial (Fig. 5). Optimization yielded model trajectories that fit experimental data with a mean $R^2=0.92\pm0.04$ (SD). The poorest fits were for the smallest perturbations (3 cm), because postural responses were very small in magnitude, and for the largest perturbations (15 cm), because some subjects tended to lift their heels or bend their knees slightly, making the 3-segment model a less accurate representation of the overall movement.

We found that six of the eight identified feedback gains contributed significantly to postural responses (see Fig. 6 for absolute gains for one subject; Fig. 7 for normalized gains averaged over all subjects). The largest gain was for the inverted pendulum mode, $T_{\text{ank}}/\theta_{\text{ank}}$ (ankle torque relative to ankle motion), at approximately 700 Nm/rad. The remaining three position gains were smaller, on the order of 200 Nm/rad. Gains related to velocity were largest for ankle torque, $T_{\text{ank}}/\dot{\theta}_{\text{ank}}$ and $T_{\text{ank}}/\dot{\theta}_{\text{hip}}$, on the order of 80 Nm·s/rad. Two gains, $T_{\text{hip}}/\theta_{\text{ank}}$ and $T_{\text{hip}}/\dot{\theta}_{\text{ank}}$, were not significantly different from zero ($P>0.01$; see Table 1).

Feedback gains were also found to gradually scale with perturbation magnitude (Figs. 6, 7). Linear regressions on

Table 1 Linear regression coefficients ($\pm 95\%$ confidence interval) for scaled gains of all subjects. All gains but two, corresponding to the hip torque response to ankle position and velocity, were found to be significantly different from zero ($P<0.01$)

Gain	Linear regression	
	Slope	Intercept
$T_{\text{ank}}/\theta_{\text{ank}}$	-3.73 ± 1.45	0.80 ± 0.08
$T_{\text{ank}}/\theta_{\text{hip}}$	0.89 ± 0.47	0.10 ± 0.03
$T_{\text{ank}}/\dot{\theta}_{\text{ank}}$	-0.51 ± 0.83	0.15 ± 0.05
$T_{\text{ank}}/\dot{\theta}_{\text{hip}}$	-1.81 ± 0.53	0.19 ± 0.03
$T_{\text{hip}}/\theta_{\text{ank}}$	-0.43 ± 0.66	0.10 ± 0.04
$T_{\text{hip}}/\theta_{\text{hip}}$	0.45 ± 0.35	0.12 ± 0.02
$T_{\text{hip}}/\dot{\theta}_{\text{ank}}$	0.01 ± 0.42	0.02 ± 0.02
$T_{\text{hip}}/\dot{\theta}_{\text{hip}}$	-0.45 ± 0.25	0.06 ± 0.01

the gains as a function of perturbation magnitude demonstrated several significant trends ($P < 0.01$; see Table 1). The most significant trends were for $T_{\text{ank}}/\theta_{\text{ank}}$ and $T_{\text{ank}}/\dot{\theta}_{\text{ank}}$, both of which decreased with perturbation magnitude. In contrast, gains related to hip position increased with perturbation magnitude. Most of the gains related to angular velocities tended to decrease with increasing perturbation magnitude. Two of the gains, $T_{\text{hip}}/\theta_{\text{ank}}$ and $T_{\text{hip}}/\dot{\theta}_{\text{ank}}$, did not exhibit significant scaling.

Comparison of data with model fit

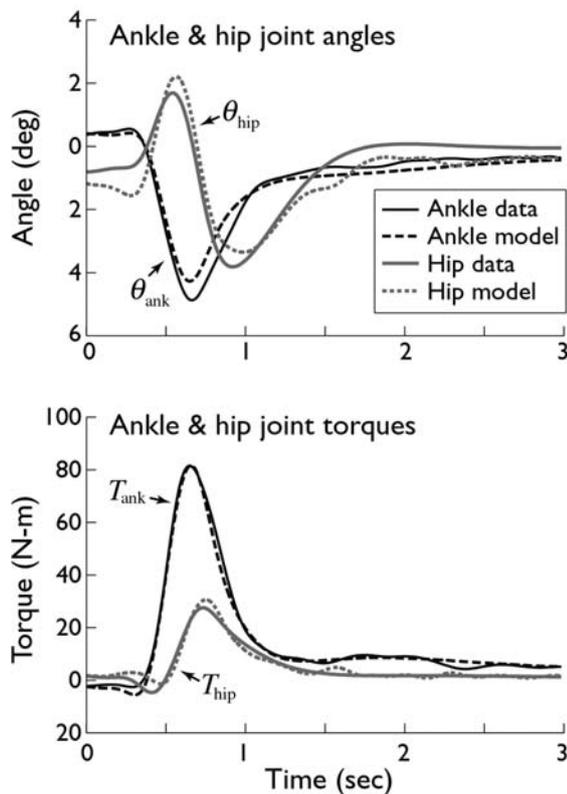


Fig. 5 Comparison of experimental data with model fit for a typical trial, for joint-angle time trajectories and joint torque trajectories. The mean R^2 for all trials was 0.92 ± 0.04 (SD)

Discussion

The results suggest that changes in strategy that accompany increasing postural perturbations could be explained by a continuous scaling of postural response feedback gains. Feedback alone was sufficient to reproduce postural responses, but the postural control model required multiple, heterogenic feedback gains in order to do so. In addition, the observed scaling of responses suggests that the nervous system may represent potentially discrete constraints (such as a threshold torque required before heel off) in a more continuous (and approximate) manner.

The heterogenic nature of the identified feedback gains means that postural responses could not be characterized by feedback of one joint's motion to produce torque about the same joint alone. Instead, there was significant feedback of ankle position and velocity to the hip, and vice versa. This is consistent with analysis of the feedback model, which predicts that such gains are in fact necessary for stability.

The observed scaling of feedback gains with perturbation magnitude indicates that the CNS adjusts postural responses in accordance with biomechanical constraints. The most prominent scaling effect was a decrease in the ankle feedback gain $T_{\text{ank}}/\theta_{\text{ank}}$ as perturbation magnitude increased. A reduction in this gain is mandated by the task constraint on allowable ankle torque. Without this decrease, larger perturbations would result in lifting the

Fig. 6 Scaled postural gains of one subject as a function of perturbation magnitude. Means and standard deviations (*error bars*) for each gain and perturbation. Gains are heterogenic, meaning that torque about one joint depends on movement about the same and other joints

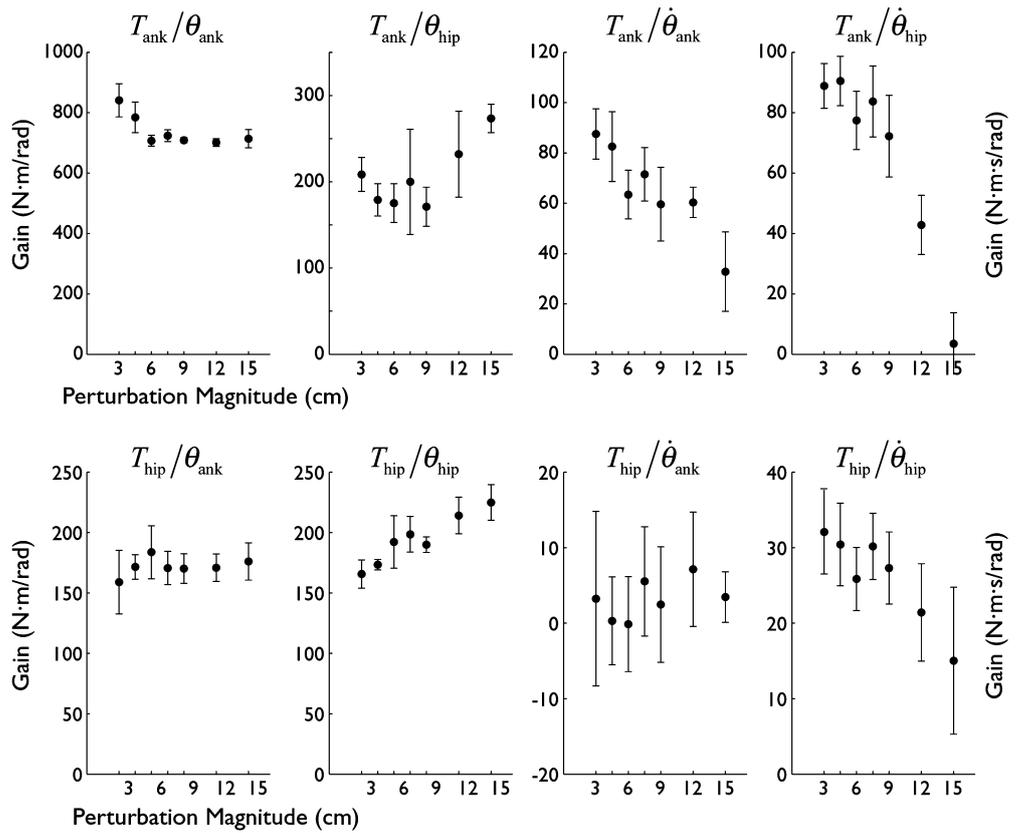
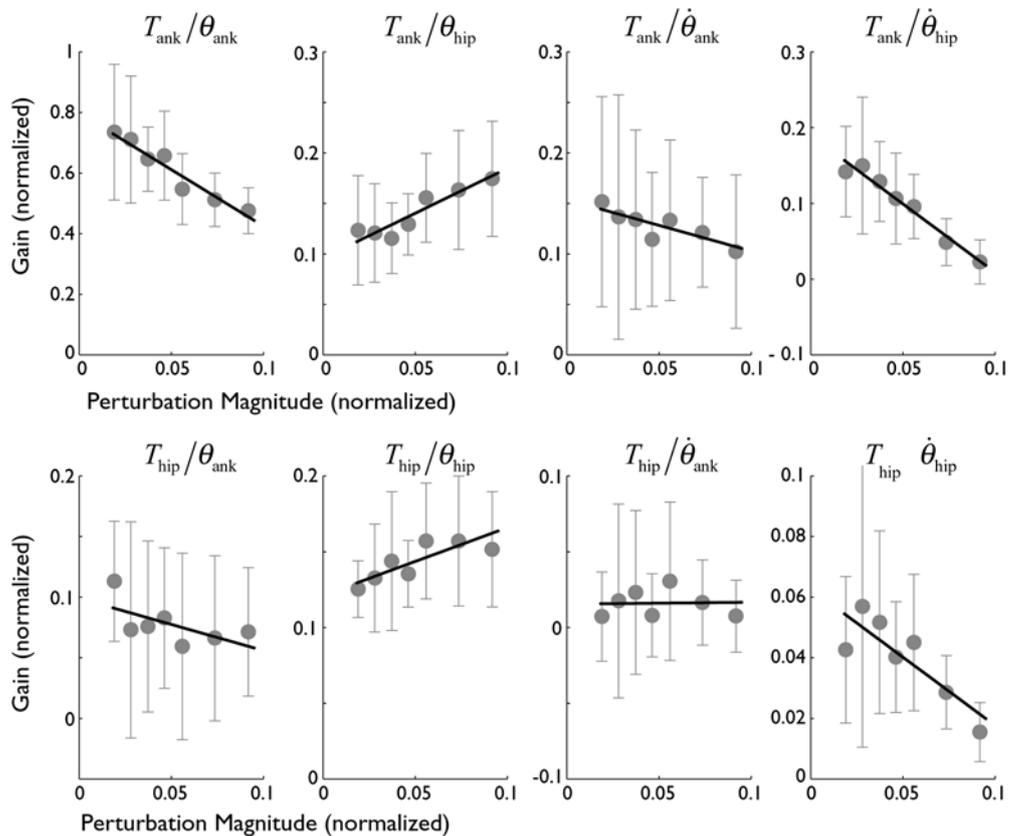


Fig. 7 Scaled postural gains averaged over all subjects as a function of perturbation magnitude. Means and standard deviations (*error bars*) for each gain and perturbation, along with a best linear fit as a function of normalized perturbation. Gains for ankle position and hip velocity decreased with increasing perturbation magnitude, while gains for hip position increased. These scaling trends indicate a reduction of inverted pendulum stabilization, and an increase in use of hip motion to keep the body upright while maintaining feet flat on the ground



heels from the ground. Instead, there was a change in ankle motion from a fast response, with very little overshoot to a slower response with substantial overshoot. In parallel with this change was an increase in both ankle and hip torque sensitivities to hip angle, $T_{\text{ank}}/\theta_{\text{hip}}$ and $T_{\text{hip}}/\theta_{\text{hip}}$, with perturbation magnitude. Stabilization for larger perturbations was therefore driven more by hip motion than for small perturbations, where the behavior bears a closer resemblance to a single inverted pendulum.

The gradual scaling of these feedback gains might also provide insight regarding how the CNS represents biomechanical constraints. The limitation on allowable ankle torque is represented mathematically as a discrete inequality constraint. But neural systems are better able to represent constraints in a more continuous (and approximate) manner (Nauck et al. 1997), using relative weightings to adjust the interaction between constraints. Such a continuous representation would result in gradually scaled changes in feedback gain that occur before the ankle torque constraint is actually reached, as was observed in our results.

It is instructive to compare the observed scaling behavior with the model's sensitivities to feedback gains. We evaluated this sensitivity by observing changes in the closed-loop system's eigenvalues as a function of deviations (of up to 50%) in the feedback gains from their identified values (see Fig. 8). The most important sensitivity was in ankle gain, $T_{\text{ank}}/\theta_{\text{ank}}$, which was the only gain whose sensitivity was sufficient to risk instability (i.e., an eigenvalue with positive real part). This means that the observed decrease in $T_{\text{ank}}/\theta_{\text{ank}}$, while necessary to keep ankle torque within its allowable value, would by itself come at the expense of a decrease in stability. Fortunately, however, the observed increase in hip gain $T_{\text{hip}}/\theta_{\text{hip}}$ acted to increase stability, so that the combined scaling of these gains only resulted in a small decrease in overall stability. This increase in hip gain is also consistent with previous reports of perturbation- and context-dependent continuous changes in postural responses from ankle to hip strategies (Nashner and McCollum 1985; Horak and Nashner 1986). Three other gains ($T_{\text{ank}}/\theta_{\text{hip}}$, $T_{\text{ank}}/\dot{\theta}_{\text{hip}}$, $T_{\text{hip}}/\dot{\theta}_{\text{hip}}$) were found to have relatively high sensitivity and were indeed found to scale

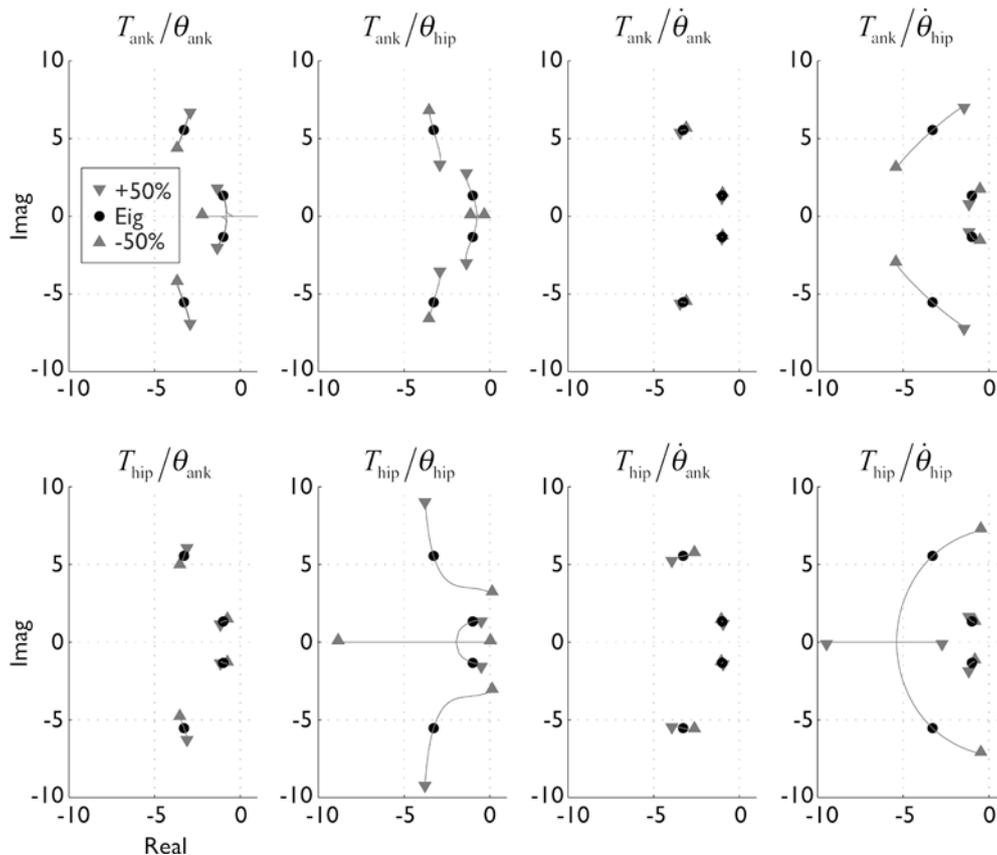


Fig. 8 Trajectories of closed-loop eigenvalues for gain variation. For the nominal gain defined by the averaged gain over all trials, each gain parameter was perturbed by $\pm 50\%$ from the nominal value, and corresponding closed-loop eigenvalues were displayed in the complex plane. Each eigenvalue's position describes a component of the overall dynamic response, with the distance to the left of the origin signifying the rate at which perturbations are reduced, and the vertical distance from the origin signifying the frequency of oscillations following perturbations. High sensitivities are identified

by large changes in eigenvalue positions with perturbed gains. This analysis shows that reduction of the gain of ankle torque relative to ankle position can result in unstable motion (signified by an eigenvalue to the right of the origin). Stability was preserved for all other gain variations, indicating a fair degree of robustness to errors in gain. The other most sensitive gains were those associated with hip position and velocity. These include production of ankle torque dependent on hip motion, indicating the importance of heterogenic gains to postural behavior

significantly with perturbation magnitude, but in a coordinated fashion that resulted in little effect on closed-loop stability. Of these, the most notable are the heterogenic gains producing ankle torque in response to hip motions. The relatively high sensitivity of the body's stability to these gains indicates the importance of accurately feeding back hip position and velocity information to drive the ankles. Finally, the remaining gains ($T_{\text{hip}}/\theta_{\text{ank}}$, $T_{\text{ank}}/\dot{\theta}_{\text{ank}}$, and $T_{\text{hip}}/\dot{\theta}_{\text{ank}}$) were found to have little effect on closed-loop stability. Unsurprisingly, observed changes in these same gains with perturbation magnitude were either relatively small or statistically insignificant.

The observed heterogeneity and scaling of feedback gains have implications regarding CNS control. Heterogenic feedback gains could in principle be explained by spinal reflex loops, many of which are multisynaptic and feed back to both agonists as well muscles crossing other joints (Bonasera and Nichols 1994). But the scaling of these gains also depends on context, in the form of perturbation magnitude, which is probably determined through sensory integration occurring at levels higher than the spinal cord (Allum and Honegger 1998), including the brainstem (Holstege 1998). Visual, vestibular, and proprioceptive signals appear to contribute to the determination of context and feedback responses, allowing for more complex control than would be possible with spinal reflexes alone (Horak and Macpherson 1996). This integration and the scaling of gains appear to be mediated by the cerebellum (Dietz 1993). Indeed, cerebellum-impaired patients have difficulty scaling postural (Nashner 1976; Horak et al. 1989; Kolb et al. 2001) and stepping (Timmann and Horak 1998) responses according to context. The basal ganglia also appear to contribute to scaling of posture, as evidenced by poor postural responses in patients suffering from Parkinson's disease (Horak et al. 1992, 1996).

We have thus far interpreted postural responses in terms of continuous feedback control, but this does not exclude a

feedforward interpretation in which a perturbation triggers a preprogrammed movement trajectory. Under the feedforward paradigm, the feedback parameters identified here should be thought of as a compact description of scaled preprogrammed trajectories, rather than as gains literally used in feedback. If the CNS stores a large library of preprogrammed movements, these responses might be encoded in a compact, parameterized form that can generate open-loop motor commands. Although there are clear differences in the physiological basis for feedback and feedforward postural responses, it is difficult to differentiate the two from a noninvasive, behavioral study. Although the present results show that feedback, alone, is sufficient to explain the gradual changes in postural responses, they cannot determine the actual contributions of feedforward and feedback to postural responses.

A limitation of this study is the use of linear, time-invariant feedback gains to fit experimental data. Many components of the postural feedback system, such as muscles and proprioceptors, have substantial nonlinear properties. Linear gains were nevertheless able to reproduce the measured postural responses with reasonable fidelity ($R^2=0.92\pm 0.04$). This may be due to the large influence of body dynamics, which are fairly linear about the operating point of upright stance (Kuo and Zajac 1993). It is also possible that the CNS linearizes the overall feedback to interface with these body dynamics. The fits might nonetheless be improved somewhat by the introduction by nonlinear or time-varying feedback gains, but at a large penalty in model complexity. In any case, the scaling of feedback with perturbation magnitude is a strongly nonlinear phenomenon—a purely linear system has fixed gains that are independent of perturbation magnitude. The scaling behaviors observed here might be likened to gain scheduling, a technique of control engineering where linear feedback gains are used, but with different gains being substituted depending on context or operating point.

Our model also did not include the time delays that are inherent in CNS feedback control. Human postural

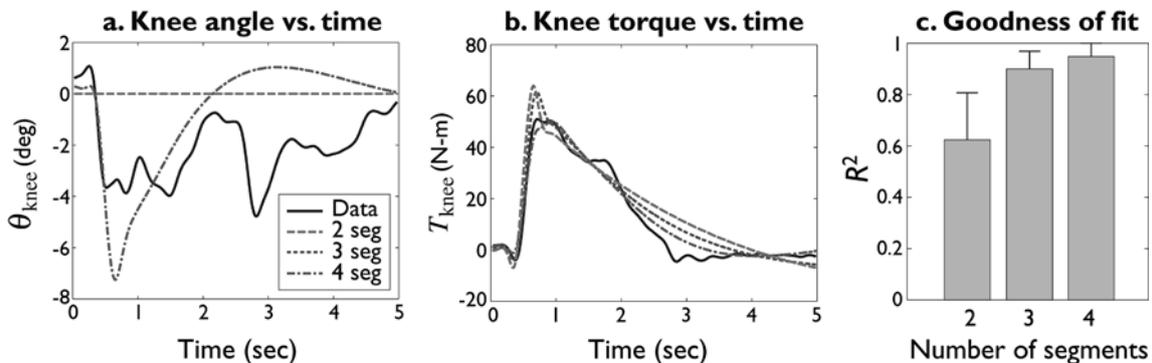


Fig. 9A-C Comparison of biomechanical models using 2–4 body segments, including the feet. **A** Feedback model fits of knee joint angle are zero for 2- and 3-segment models that lack knees, compared with the non-zero knee motion actually measured in a typical subject. **B** All models can be used to estimate the knee torque, even if the knee does not move. Because of the relatively small knee motion, even the 2-segment model produces a reasonable

fit to measured knee torque. **C** The degree of fit improves as the number of segments increases. The 3-segment (knees locked) model reproduces data reasonably well with only 8 feedback gains, compared with the 4-segment model, which requires 18 gains. R^2 values were 0.62 ± 0.18 , 0.90 ± 0.07 , and 0.94 ± 0.06 , for 2-, 3-, and 4-segment models, respectively

responses include instantaneous torques due to mechanical stiffness, short-latency responses due to spinal reflexes, and a variety of long-latency responses due to longer feedback loops (Nashner and Cordo 1981). To model these effects, we attempted fitting a model with a single time-delay parameter. We found, however, that the identified time delay was highly inconsistent from trial to trial and resulted in negligible improvement in fit. A single-delay parameter biases the identified feedback gains in favor of one time delay, but at the expense of others occurring at a wide range of latencies. A more complex model with several distributed time delays would produce better fits, but would probably not affect our general conclusions regarding scaling of postural responses and would come at the expense of a large increase in the number of model parameters.

Another limitation of this study was the use of a simple model of sagittal plane body motion, without knees. Because perturbations were only in the backward direction, subjects' responses were primarily in the sagittal plane, making this a reasonable simplification. Some knee motion, however, occurred in all trials, generally increasing with perturbation magnitude. To quantify the potential errors arising from our 3-segment model, we repeated the fitting of seven subjects' data with two alternative models. One was an even simpler model with only 2 segments, and the other a 4-segment model, including knee motion. Each additional degree of freedom allows for a better fit to the data, but the improvement gained from the inclusion of knees was found to be quite modest (see Fig. 9). This improvement comes at the expense of added complexity, in the form of 10 additional feedback gains related to knee motion. We found that many of these gains were difficult to identify uniquely, due to the relatively small amount of motion. Other gains such as $T_{\text{ank}}/\theta_{\text{ank}}$ and $T_{\text{hip}}/\theta_{\text{hip}}$ were found to exhibit the same scaling behaviors as for the 3-segment model. In contrast, a 2-segment model resulted in a much poorer fit to data, implying that there was substantial motion beyond that of an inverted pendulum. We therefore consider the simpler model without knees to be an appropriate compromise between model simplicity and fidelity to data for the case of forward body sway induced by backward surface translations. Inclusion of additional segments would be appropriate for perturbations that are larger in magnitude or are applied in different directions, where knee motion plays a larger role in the restoration of upright stance (Henry et al. 1998).

Finally, we note that the experimental conditions of this controlled study differ from what humans might typically encounter in the environment. We intentionally asked subjects to avoid stepping, in order to assess how that biomechanical constraint affects posture control. In many realistic situations subjects may prefer to step in response to a perturbation (Maki and Ostrovski 1993). But because any control task is subject to biomechanical constraints, the simplifications of the present study might nevertheless provide general insight as to how humans determine context and accommodate these constraints. Indeed, even when subjects step, there appears to be a continuous

downward scaling of postural responses as the stepping responses increase (Burleigh et al. 1994), and the stepping responses themselves can also be scaled to accommodate external constraints (Zettel et al. 2002). Even though stepping is biomechanically distinct from postural responses that keep the feet in place, it is possible that both types of strategies are scaled according to continuous representations of biomechanical constraints.

In summary, we found that postural responses were well represented in terms of a feedback control system with heterogenic feedback gains. These gains were found to scale gradually with perturbation size, indicating a continuous change in postural responses and suggesting that the CNS uses a continuous representation of biomechanical constraints. With increasing perturbation magnitude, subjects tended to decrease ankle feedback control, and increase control at the hip. This made it possible to accommodate biomechanical constraints on allowable ankle torque while preserving stability. The relative contributions of feedforward and feedback to CNS control remain to be determined, which will be the subject of future studies.

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Appendix

Biomechanical model and optimization of feedback parameters

The model's equations of motion are of the form (Kuo and Zajac 1993):

$$M(\theta)\ddot{\theta} = V(\theta, \dot{\theta}) + G(\theta) + T + W(a) \quad (1)$$

where θ is a vector of joint angles, M is the mass matrix, V is a vector of velocity-dependent terms, G is a vector of gravity-dependent terms, T is a vector of joint torques, and W is a vector dependent on external perturbation magnitude a . The inertial parameters for the models were found by incorporating a series of 27 anthropometric measurements into a nonlinear regression model of the body segments (Yeadon and Morlock 1989). We used Eq. 1 in inverse dynamics computations to estimate joint torques (Kuo 1998), and also in the feedback control model (Fig. 2). We also developed a 4-segment model, including knee motion, to quantify the advantages of a more complex model (see Discussion).

These equations of motion were incorporated in a feedback control model of postural responses to perturbations of the support surface. We used a linear state feedback control (Barin 1989; Kuo 1995), producing joint torques as a function of the joint angles and velocities to stabilize the body (see Fig. 2). We assumed that the CNS can either directly sense or indirectly estimate the

equivalent of the state information $x = [\theta_{\text{ank}} \ \theta_{\text{hip}} \ \dot{\theta}_{\text{ank}} \ \dot{\theta}_{\text{hip}}]^T$. The control task was to produce joint torques $u \triangleq T$ with the feedback law:

$$u = K(x - x_{\text{ref}}) \quad (2)$$

where K is the (2×4) feedback control gain matrix, and x_{ref} is the state corresponding to the upright reference position. The state equations, linearized about the upright vertical position, are of the form:

$$\dot{x} = Ax + Bu + w \quad (3)$$

where A , and B are system matrices, and w describes perturbation. Combining Eqs. 2 and 3 yields the closed-loop system:

$$\dot{x} = (A - BK)x + w \quad (4)$$

whose stability depends on the quantity $(A - BK)$. For a given subject, A and B are relatively fixed, and the gain (K) is selected by the CNS. The selection of K effectively determines the postural response strategy. The movement resulting from a perturbation can be predicted from initial conditions and the perturbation magnitude (w), resulting in simulated state and torque trajectories over time, x_{sim} and u_{sim} , respectively.

We used optimization to describe the postural response strategy in terms of the feedback parameters. The objective was to minimize the sum-squared, normalized deviations of the model states x_{sim} from the experimental data x_{exp} and the model torques u_{sim} from the data u_{exp} :

$$J(K) = \sum \delta x^T Q \delta x + \delta u^T \delta u \quad (5)$$

where $\delta x \triangleq (x_{\text{exp}} - x_{\text{sim}}) / |x_{\text{exp}}|$, $\delta u \triangleq (u_{\text{exp}} - u_{\text{sim}}) / |u_{\text{exp}}|$ and the summation occurs over samples of recorded data. The Q matrix was used to weight the relative contributions of errors in state and control, and was chosen to be $Q = 0.01I^{4 \times 4}$ where I is the identity matrix. This places equal weighting on all states relative to each other, with the overall scaling factor of 0.01 chosen to place some weighting on matching experimentally-derived joint torques. One constraint was placed on the optimization, requiring a stable closed-loop system, i.e., eigenvalues of the system matrix having nonpositive real parts. Therefore, the constrained optimization problem is written mathematically as follows:

$$\min_K J(K) \text{ subject to } \text{Re}\{\text{eig}(A - BK)\} \leq 0 \quad (6)$$

To perform the optimization, we used a sequential quadratic programming (SQP) algorithm, one of many algorithms that can minimize a quadratic objective subject to nonlinear constraints (Shittowski 1985). We repeated

the optimization multiple times using random initial guesses for K , to check for local minima in the optimization. As a measure of the degree of fit, we calculated R^2 for each fit using the same relative weightings of Eq. 5.

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