Learned changes in the complexity of movement organization during multijoint, standing pulls

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Abstract. This paper tests the hypothesis that the central nervous system (CNS) learns to organize multijoint movements during a multijoint 'bouncing pull' task such that, after practice, motion of the anterior-posterior center of mass (CM_{AP}) more closely resembles that of a conservative, one degree of freedom (DF), inverted pendulum model. The task requires standing human subjects to produce precise peak pulling forces on a handle while maintaining balance – goals that can be easily accomplished if movement is organized as in the model. Ten freely standing subjects practiced making brief, bouncing pulls in the horizontal direction to target forces (20–80% of maximum) for 5 days. Pulling force, body kinematic and force plate data were recorded. An eight-segment analysis determined sagittal-plane CM motion. We compared the effects of practice on the regression-based fit between actual and model-simulated CM_{AP} trajectories, and on measures of CM_{AP} phase plane symmetry and parameter constancy that the model predicts. If the CNS learns to organize movements like the inverted pendulum model, then model fit should improve and all other measures should approach zero after practice. The fit between modeled and actual CM_{AP} motion did not improve significantly with practice, except for moderate force pulls. Nor did practice increase phase plane symmetry or parameter constancy. Specifically, practice did not decrease the differences between the pre-impact and rebound positions or speeds of the CM_{AP}, although speed difference increased with pulling force. CM_{AP} at the end of the movement was anterior to its initial position; the anterior shift increased after practice. Differences between the pre-pull and balance-recovery ankle torque (T_A) impulses were greater on day 5 and correlated with the anterior shift in CM_{AP}. These results suggest that practice separately influenced the force production and balance recovery phases. A modified model with damping could not explain the observed behaviors. A modified model using the actual time-varying T_A profiles improved fit at lower force levels, but did not explain the increased postural shift after practice. We conclude that the CNS does not learn to organize movements like the conservative, inverted pendulum model, but rather learned a more complex form of organization that capitalized on more time-varying controls and more intersegmental dynamics. We hypothesize that at least one additional DF and at least one time-varying parameter will be needed to explain fully how the CNS learns to organize multijoint, bouncing pulls made while standing.

1 Introduction

1.1 Problem

The production of precise contact forces against the environment is a difficult problem for both biological and robotic systems. Biological systems, including humans, often have the additional challenge of coordinating force production with the maintenance of balance, since many contact force tasks (catching, hitting, pushing or pulling objects) are performed while the subject is standing freely. In robotics this problem is solved expediently by bolting one end of the robot arm to a wall or floor, simultaneously reducing the number of degrees of freedom (DFs) that must be controlled and eliminating the need to balance the robot. The central nervous system (CNS) cannot resort to this strategy, but must learn to organize multijoint actions so that freely standing subjects can perform contact tasks without losing balance. How the CNS learns this kind of organization is unknown.

The broad aim of this paper was to evaluate how the CNS learns to organize a particular multijoint action with dual force-production and balance-recovery goals, specifically 'bouncing' pulls made by freely standing subjects to peak force targets, where motion is restricted to

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the sagittal plane (Lee et al. 1990; Michaels et al. 1993). We hypothesized that practice on bouncing pulls would lead subjects to learn a single coordinative structure or function (Kugler et al. 1980; Newell and McDonald 1992) which organizes movements to mimic a second-order mass-spring system that readily achieves the task's dual goals (Lee 1995). We tested this hypothesis by evaluating whether, after 5 days of practice on the bouncing pull task, subjects' global behavior (defined in terms of the body's anterior-posterior CM motion, CM_{AP}) increasingly resembled that of a second-order system. The alternative hypothesis was that the CNS would learn a more complex form of organization, perhaps involving more effective use of the system's DFs or time-varying control parameters.

1.2 Background

1.2.1 Bouncing pull task and model. A subject performing the bouncing pull task (Fig. 1a) typically develops posterior-directed CM momentum before starting to pull. During the pull, the CM_{AP} velocity is reversed. As the person stops pulling, the body rebounds, the forward-directed CM_{AP} momentum is reduced and upright balance is recovered. The amplitude of CM_{AP} motion increases with pulling force. Well-practiced subjects' CM_{AP} phase planes are approximately symmetrical about the zero velocity axis for pulls with peak forces ranging from 20% to 95% of the person's estimated maximum pull (Michaels and Lee 1996; see also Figs. 2 and 4 in the present paper). The symmetry means that backward motion before force production is mirrored by anterior motion during recovery of balance back to the initial starting posture.
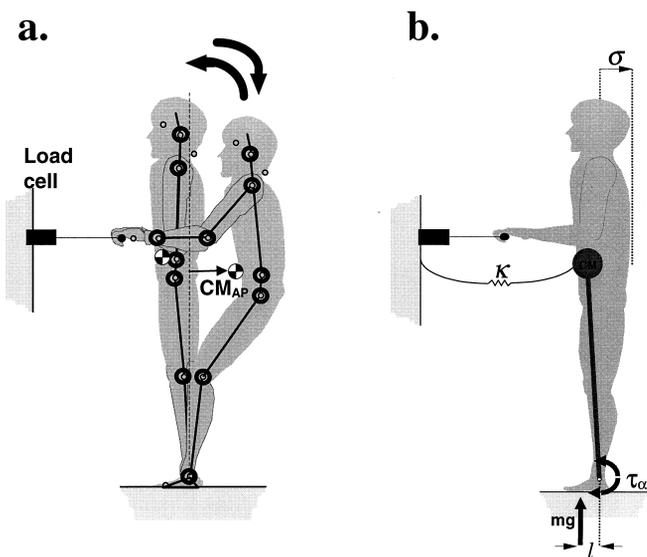
Historically, mass-spring models have been used to characterize CM motion in tasks with a bouncing component. These include animal and human locomotion and hopping (Dawson and Taylor 1973; McMahon 1990; Farley et al. 1991, 1993; Full and Tu 1991), rhythmic lateral weight shifts that resemble ski-slalom movements (Vereijken et al. 1992) and infants' bouncing in a jumper seat (Goldfield et al. 1993). The bouncing pull task is more complex in the sense that movement organization must satisfy two goals: a contact (pulling) force and balance maintenance. Nevertheless, the shape of the bouncing pull task's CM_{AP} phase planes suggests that the dynamics of this action resemble a mass-spring system. That observation led Michaels et al. (1993) to model subjects' behavior as an inverted pendulum connected by a unidirectional spring (elastic cord) to the environment (Fig. 1b). This model accounted for more than 90% of CM_{AP} motion in skilled subjects (Michaels et al., 1993; Michaels and Lee 1996). The model has three constant parameters: σ (slack or threshold length of the elastic cord), κ (stiffness of the elastic cord) and τ_α (torque that drives the pendulum about its axis).[1] Motion of the pendulum is initiated by a step change in τ_α, which causes a change in axial torque, which in turn rotates the pendulum backward about its axis until slack σ is taken out of the cord. The elastic cord generates the pull until slack returns, and then rebound momentum carries the pendulum back to the initial position, at which point a downward step change in τ_α terminates motion. This model is conservative (has constant total energy) because it has one mechanical DF, a purely elastic spring, and constant parameters. Consequently, it accomplishes the task's dual goals of producing an impulse-like pull and maintaining balance by presetting appropriate values of σ, κ and τ_α.

1.2.2 Learning of multijoint pulls. Evidence is inconclusive that subjects learn the simple form of organization represented by the inverted pendulum model. A single study on five subjects found that regression-based fits of the model to subjects' movements improved after 3 days' practice in making moderate force pulls (Lee 1995). Those findings supported the idea that subjects learn the simplifying organization represented by the model. However, some asymmetries were observed in the CM_{AP} phase planes, such as empirical estimates of the σ and τ_α parameters showing time-variation between the start and end of the pull. A reliable increase in phase plane asymmetries after practice would suggest that subjects learn a different and potentially more complex form of organization than is represented by the 1-DF model. Other studies of multijoint actions have yielded conflicting findings concerning whether practice leads to simpler or more complex movement organization (e.g., Arutyunyan et al. 1969; Lee and Russo 1994; Vereijken

Fig. 1. a Exemplary postures seen during the bouncing pull, overlaid by the eight-segment anthropometric scheme used for determining the center of mass (CM) trajectory. A *line* indicates each link, and a *large circle* indicates each joint. A *small circle* indicates each retroreflective marker used in motion analysis. **b** The inverted pendulum model superimposed on the body

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[1] The parameter τ_α was presented previously as *CP* or *l*, the center of pressure location. Here we refer to τ_α, which is estimated by ankle torque T_A. See Appendix A, equation (A2), for the simple relation between τ_α and *l*.

et al. 1992). Those studies' conclusions were based upon changes in movement variability or cross-correlations between segmental trajectories, however, rather than upon predictions tested by explicit models of movement organization. The present study, in contrast, tests model-based hypotheses about how practice alters movement organization.

1.3 Hypotheses and rationale

We adopted a threefold approach to evaluating whether subjects who practice the bouncing pull task over 5 days learn to organize their movements to resemble those predicted by the inverted pendulum model. First, we tested the hypothesis that practice would improve the regression-based fit of this model to subjects' CM_{AP} motion. This regression approach, while answering the overall question about model fit, could be insensitive to subtle but systematic practice-related deviations of subjects' behavior from the model's predictions.

Second, we evaluated predictions derived from the hypothesis that subjects learn to organize their movements like the conservative inverted pendulum model. The model's assumption of energy conservation implies that CM_{AP} phase planes should be more symmetric after practice. Specifically, CM_{AP} velocities at the beginning and end of the pull, and differences between initial and final CM_{AP} posture, should decrease after practice. Moreover, model parameters should be more constant after practice. Alternatively, subjects might learn to increasingly time-vary parameters, signifying greater complexity in system controls. We tested these hypotheses by comparing empirical estimates of the model's parameters made at different times within the pull, before and after practice.

Third, we modified the model in two ways which might accommodate observed discrepancies between predicted and observed behaviors. We added damping to the spring, which changes the structure of the model. We also altered the model's kinetic inputs by using actual ankle torque T_A(which results showed was time-varying) in model simulations, rather than the constant values estimated through the regression approach. If these modifications could explain practice-related changes in behavior, it would suggest that increased complexity occurs within the framework of the 1-DF inverted pendulum model. A failure of such modifications to explain practice effects would suggest that movement organization becomes complex in other ways, for example, by greater use of additional DFs.

2 Methods

2.1 Sample and protocol

Ten healthy adult volunteers (age 23–49 years; 8 female, 2 male) with no history of orthopedic or neurological disorders trained for five separate days on the standing horizontal pulling task. Subjects stood freely on a force platform, holding a handle with both hands (Fig. 1a).

They were required to keep their feet flat on the floor at all times. They were told to generate impulse-like pulls straight back, with the arms parallel to the floor, to peak force targets equaling 20%, 40%, or 80% of their estimated maximum, which was defined as height (m) × mass (kg) × 8 (Lee et al. 1990). Visual feedback was used to control the position of the center of pressure before the start of the trial. Blanking the center of pressure (COP) display signaled the subject to initiate one pull, at a self-determined time. Subjects were told to return to an upright and quiet posture, but it did not have to be the position from which they started. They were given verbal feedback about their actual peak force, using a 'fading' feedback schedule (100% on day 1, decreasing to no feedback on day 5). Subjects made 36 pulls to each target on the first 4 days; on day 5 they also produced pulls to 10%, 50%, 60% and 95% targets.

2.2 Data collection and processing

Ground reaction forces and moments were recorded with an AMTI force plate and pulling force with an 1100 N Sensotec load cell (200 Hz) on all days. On days 1 and 5, sagittal plane motion was also recorded at 50 Hz using an ELITE system (resolution 1 mm). Reflective hemispheric markers were located over the fifth metatarsal, lateral malleolus, knee, head of the greater trochanter, superior iliac crest, neck, ear, temple, humeral head, lateral epicondyle of the elbow, and the lateral bony prominence of the wrist (Fig. 1a). Marker trajectories were conditioned using a linear phase FIR filter (D'Amico and Ferrigno 1990). Motion data were interpolated using a natural cubic spline algorithm to match the 200 Hz sampling frequency of the force plate and load cell data.

An eight-segment rigid body analysis (foot, shank, thigh, pelvis, trunk, head, upper arm and forearm) was used to estimate CM motion, as the vector sum of the contributions of segmental mass distributions (Dempster et al. 1959; Dempster 1955 via Plagenhoef 1971; Winter 1990). This analysis produced a more accurate estimate of CM motion than the five-segment analysis (rigid trunk; no head) used previously (e.g., Michaels et al. 1993).

2.3 Analyses of model-subject differences

2.3.1 Overall model-subject fit. Numerical integration and a hybrid nonlinear optimizer were used to adjust the model's σ, κ and τ_α parameters to obtain the best fit of the model to each trial's kinematic and kinetic trajectories (see Appendices A and B). The squared product-moment correlation coefficient (r^2) between model-simulated and empirical CM_{AP} accelerations was used to quantify how well the model matched the subject's behavior on each trial.

2.3.2 Measures of conservative behavior. (1) *Phase plane symmetry.* The hypothesis that the CNS learns to organize movements during bouncing pulls to conserve net mechanical energy implies that CM_{AP} phase planes should become more symmetric about the zero velocity
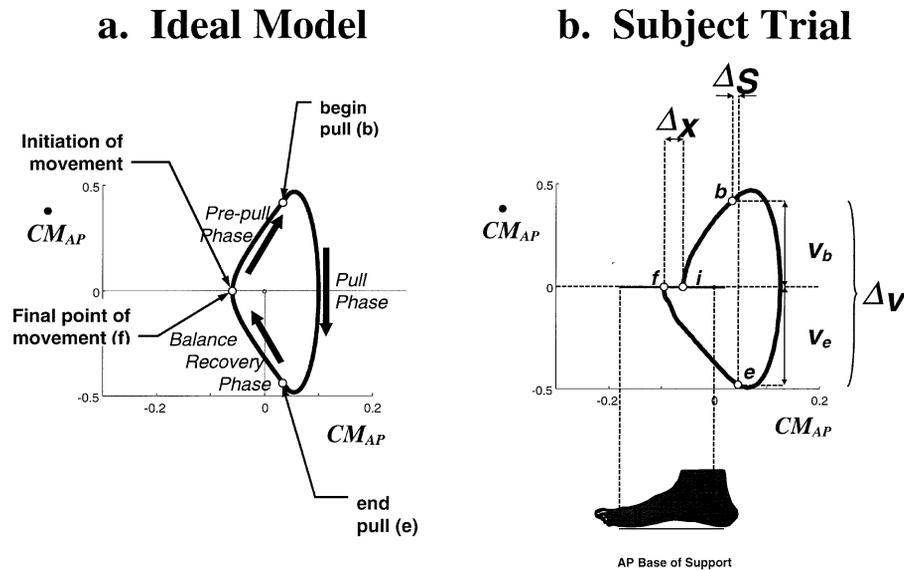
a. Ideal Model   # b. Subject Trial

Fig. 2a, b Model and subject anterior-posterior CM (CM_{AP}) trajectories in the phase (velocity vs position) plane. a Model trajectory, showing the three phases of the task. b Subject trajectory, showing the measures of phase plane asymmetry

axis, with equal and opposite pre-impact and rebound velocities; and motion should be initiated from and return to the same upright posture. These hypotheses were tested by evaluating whether practice reduced (a) the difference between the absolute magnitudes of CM_{AP} velocity at the beginning and end of pulling, Δv, or *speed change*; or (b) the difference between the person's initial and final standing CM_{AP} position, Δx, or *postural shift* (Fig. 2b).

(2) *Time-invariance of parameters.* The conservation assumption implies that σ, τ_α and κ should become constant after practice.[2] We tested this hypothesis by determining whether differences between empirical estimates of the parameters that were obtained at different times in the pull (Fig. 2b) were smaller on day 5 than day 1. We estimated the constancy of σ as the difference between CM_{AP} position at the beginning and end of the pull (*slack change*, Δs), and the constancy of τ_α as the difference between T_A impulses measured during the pre-pull and balance-recovery phases (*torque change*, ΔT_A). The hypothesis that κ is time-invariant was not tested, because changes in κ cannot be disambiguated from changes in σ without perturbations; unmodeled effects of damping would confound estimates of κ (cf. Latash and Zatsiorsky 1993).

2.4 Statistical analysis

Peak force was normalized with respect to estimated maximum and used to group trials into seven force blocks, each spanning a 10% range (from 15–25% through 75–85% of maximum). Each subject's means of the dependent variables were computed for each force block on day 1 and day 5. Those means were used in repeated measures analyses of variance (10 subjects, 2 days, and 7 force levels) to test for the effects of practice and force. The Huynh-Feldt adjusted degrees of freedom were used to test hypotheses about the effects of force and day by force interactions because some conditions showed non-normal distributions (Huynh and Feldt 1976).

3 Results

3.1 General description of task performance

The duration, peak displacement and peak velocity of CM motion increased with pulling force (Fig. 3a). CM motion was always larger in the anterior-posterior than the vertical direction. Larger pulling forces were generated by placing the slack point more posterior, which increased the duration of the pre-pull phase and provided the time to develop more momentum. Pulling force (Fig. 3b) had a relatively fast rise time (mean 210 ms) and slightly slower relaxation time; these times did not vary with practice or pulling force. Peak pulling forces were more accurate on day 5 [$F(4, 36) = 5.49$, $P < 0.001$], showing that practice improved performance on the task's primary goal. T_A trajectories approximated smoothed, constant-amplitude pulses lasting from the beginning to the end of movement (Fig. 3c). As predicted by the inverted pendulum model, the CM_{AP} phase planes generally had a lenticular shape on both days, with approximate symmetry about the zero-velocity line (Fig. 4).

3.2 Overall model fit

The fit of the inverted pendulum model to subjects' behavior was moderate to excellent, with subject mean

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[2] These measures provide further tests of the hypotheses that phase planes were asymmetrical, and that asymmetry did not decrease with practice.
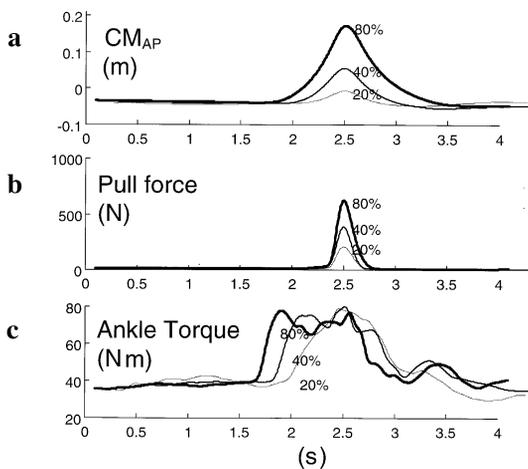
Fig. 3a–c. Overlaid time series for 20%, 40% and 80% pulls by a typical subject, on one day. **a** CM$_{AP}$; **b** pull force; **c** ankle torque
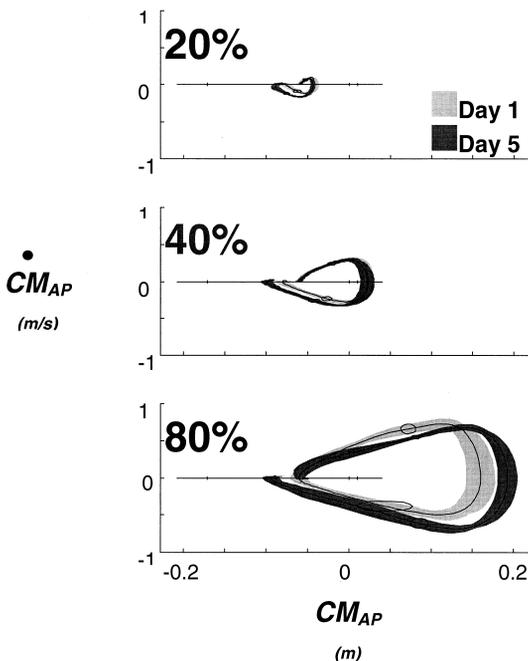

Fig. 4. CM$_{AP}$ phase planes for a typical subject at the three force levels. Day 1 data are surrounded by *light shading*, indicating 95% confidence interval; day 5 data are surrounded by *darker shading*. *Ellipses* indicate the variance in the position and velocity dimensions at the beginning and end of the pulling phase. The *horizontal line* represents the length of the foot. *Cross hairs* on this line indicate the position of the ankle and estimated edges of the base of support (Lee and Deming 1988)

r^2 ranging from 0.71 to 0.90 (Fig. 5a). The effect of practice on model fit was inconsistent for pulls of different peak force. Specifically, r^2 was significantly higher on day 5 for 35 to 45% pulls [day by force interaction, $F(4.93, 44.35) = 4.56$, $P < 0.005$]. In contrast, model fit did not change significantly for the remaining force blocks. Many subjects had a very high r^2 fit (>0.85) even on day 1, leaving little room for improvement with prac-

tice. Finally, model fit increased with pulling force [$F(2.66, 23.98) = 13.21$; $P < 0.001$].

3.3 Effects of practice on conservative behaviors

3.3.1 Phase plane symmetry. The Δv and Δx measures of CM$_{AP}$ phase plane symmetry were inconsistent with the hypothesis that subjects learned to organize their movements more like the conservative, inverted pendulum model. Specifically, Δv was not significantly lower after practice (Fig. 5b), alone or in interaction with force ($P > 0.05$). Force had a significant effect on Δv [$F(1.79, 16.09) = 7.68$, $P < 0.006$]. For pulling forces $< 35\%$, Δv was zero or even positive, indicating a gain in kinetic energy during the pull. For pulls above 35% Δv varied with pulling force, showing a greater loss in kinetic energy as pulling force (and CM$_{AP}$ velocity) increased. Postural shift, Δx, was significantly greater than zero overall [$F(1, 9) = 24.85$, $P < 0.001$; Fig. 5c], which means that subjects finished their movements by leaning significantly more anterior than they started. The anterior postural shift was significantly larger on day 5 (mean $\Delta x = -0.011$ m) than day 1 [mean $\Delta x - 0.024$ m; $F(1, 9) = 8.99$, $P < 0.02$], suggesting an organization that was less like the model after practice. Pulling force did not influence Δx.

3.3.2 Parameter time-variation. Both Δs and ΔT_A were time-varying before and after practice; and time-variations in ΔT_A increased with practice. Analysis of individual Δs plots (not shown) showed substantial variation in the sign of Δs. Consequently, the absolute values of Δs (Fig. 5d) were used to test the hypothesis that practice would reduce Δs to zero. Absolute Δs differed significantly from zero before and after practice [$F(1, 9) = 141.02$; $P = 0.0000$]. Practice did not decrease time-variations in Δs, either alone or in interaction with force.

On both days, the T_A impulse was significantly larger during the balance recovery than pre-pull phase [$F(1, 9) = 13.39$, $P < 0.006$], indicating that the T_A impulse was time-varying. Moreover, ΔT_A was greater on day 5 than day 1 [$F(1, 9) = 5.66$, $P < 0.05$], indicating greater time-variation after practice. These effects were due to longer durations or higher average amplitudes of the T_A impulses during balance recovery; subjects differed in the extent to which they changed impulse duration, impulse amplitude, or both. Pulling force did not influence ΔT_A. For all subjects, ΔT_A was significantly correlated with Δx ($r = -0.57$, $P < 0.05$). The increased balance-recovery T_A impulse thus may have contributed to the greater anterior shift in CM$_{AP}$ after practice.

3.4 Model modifications

We ran two further simulations to investigate whether the practice-related increase in Δx might be explained within the 1-DF model. First, we changed the structure of the model by adding a viscous element to the model's spring (damping modification). Second, we changed the kinetic inputs to the system, for the balance-recovery phase, by substituting the experimentally measured,
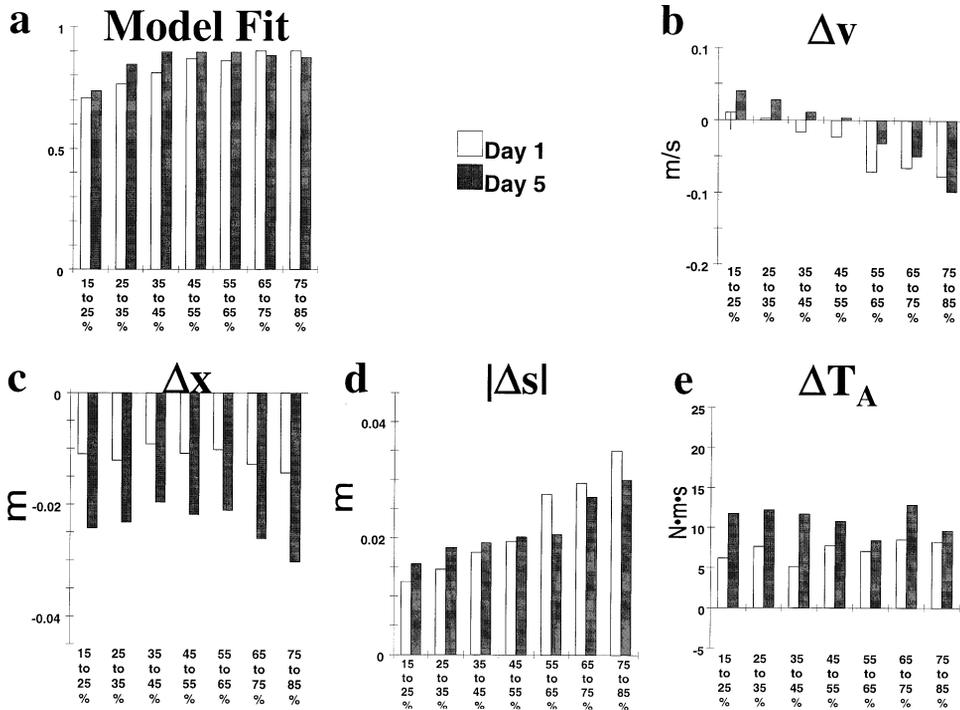
Fig. 5a–e. Group means, by force and day, for measures of model fit, symmetry and time-invariance of parameters. **a** Model fit, r^2, between simulated and experimental CM_{AP} accelerations. **b** Speed change, Δv: $\Delta v < 0$ signifies lower speeds at rebound. **c** Postural shift, Δx; $\Delta x < 0$ signifies an anterior shift in final CM_{AP}. **d** Slack change, $|\Delta s|$; $|\Delta s| = 0$ signifies no difference in CM_{AP} location at the beginning and end of the pull. **e** ΔT_A impulse between the pre-pull and balance-recovery phases; $\Delta T_A > 0$ implies a greater impulse in balance-recovery
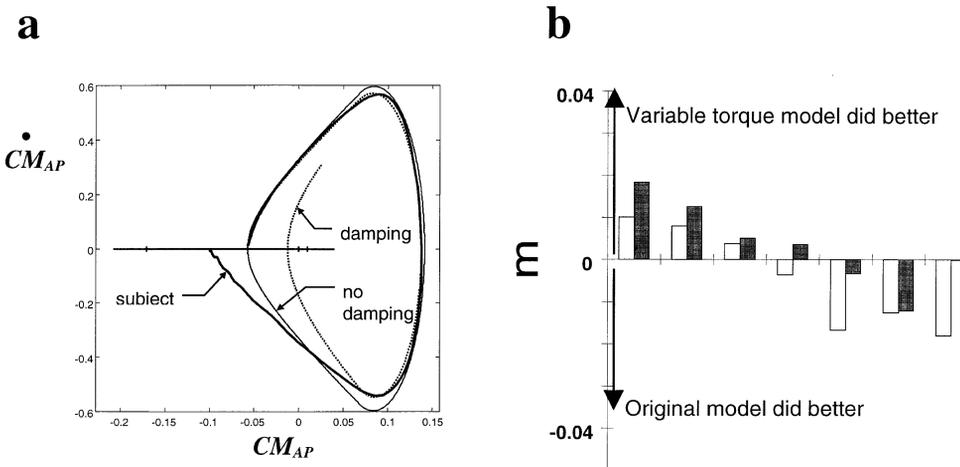

Fig. 6. **a** Phase plane trajectories for the undamped (original) model and the damped (modified) model, superimposed on one trial of typical subject data. The damped model follows the trajectory until the balance-recovery phase begins. **b** Group mean differences in the postural shift error for the variable torque (VT) and original constant torque (CT) models, by day and force. Positive differences mean that the VT model did a better job of reaching the final position, while a negative value means that the original CT model did a better job; zero means the two models did equally well

time-varying values of T_A for the constant estimate of τ_α obtained by regression-optimization methods (variable torque modification). Simulation results from these modified models were compared with the empirical CM_{AP} data.

3.4.1 Damping modification. The simulations demonstrated that just adding damping cannot explain the observed postural shift before or after practice. Figure 6a shows one empirical trial overlaid with simulated CM_{AP} motions predicted from the original (undamped) and damped models. The optimization routine obtained a best value for spring damping during the pulling phase (Appendix B). The damping modification resulted in energy loss during the pull, as occurred on many trials ($\Delta v < 0$, Fig. 5b). We did not run simulations for all forces, but energy dissipation and speed loss would in-

crease with pulling force (and, higher CM_{AP} velocities), consistent with the empirical findings. Adding damping cannot, however, explain trials where speed increased during the pull ($\Delta v > 0$, Fig. 5b). More crucially, damping resulted in a posterior postural shift, which is opposite to the experimental observations ($\Delta x < 0$, Fig. 5c). The final CM_{AP} position in the damped model actually falls behind the base of support, implying a backward fall for a subject. Thus, no matter what (positive) values viscosity takes on or how it changes with practice, adding damping cannot explain the anterior shift in CM_{AP} or the increased postural shift on day 5.

3.4.2 Variable torque modification. Allowing T_A to time-vary reduced but did not eliminate the discrepancy between the model-predicted and actual final CM_{AP}. Overall, the variable torque model predicted final CM_{AP}

postures that were significantly posterior to subjects' final CM_{AP}, just like the original (constant torque) model [$F(1,9) = 9.56$; $P = 0.0129$]. Figure 6b compares the agreement between observed final CM_{AP} position, and simulated CM_{AP} position predicted from the variable torque and original forms of the model. The variable torque model matched the anterior shift in CM_{AP} better for low force pulls, but both models did equally well for moderate force pulls, and the original model had a slight advantage for higher force pulls [force main effect: $F(3.76, 33.85) = 8.7$; $P = 0.0001$]. These effects did not differ between day 1 and day 5.

4 Discussion

4.1 Practice increased the complexity of movement organization

This study investigated whether 5 days' practice on the bouncing pull task simplified or complicated movement organization. This task requires the CNS to organize the multijoint action to satisfy two goals: pulling force and balance maintenance. The results indicated that the CNS learns to accomplish those goals by complicating movement organization, supporting Bernstein's model of skill acquisition (1967). Changes in organization were related primarily to the balance-recovery phase. Practice effects appear to involve two types of complexity: greater time-variation of control parameters, and greater use of dynamics associated with DFs that were neglected in the 1-DF model.

Consistent with previous studies (Michaels et al. 1993; Michaels and Lee 1996), the 1-DF model generally fit subjects' CM_{AP} behavior quite well, and improved with practice for moderate force pulls (Lee 1995). Nonetheless, three lines of evidence suggest that movement organization becomes more complex after practice. First, model fit overall did not change with practice. Second, practice led to larger postural shifts and T_A changes, which indicates an increased departure of subjects' behavior from the symmetrical phase planes predicted by the model. Third, neither incorporating viscous damping in the spring nor permitting ankle torque to time-vary during balance recovery reliably enhanced the agreement between the modeled and actual anterior shift in CM_{AP}. An alternative to our conclusion that practice results in a more complex form of organization is that the CNS learns some form of organization that differs completely from that of an inverted pendulum system. This alternative seems unlikely, however, given the overall fit of even the 1-DF model to subjects' movements. It seems more probable that the learned deviations in subjects' behavior from the conservative model reflect greater complexity of organization, specifically increased time-variation of parameters or additional DFs after practice.

4.2 Time-variation in parameters

Time-variations were observed in Δs and ΔT_A, the empirical measures of the σ and τ_α parameters, before as well as after practice[3]. Because the direction of Δs was inconsistent, its variations could represent noise in empirical measures rather than time-variation in σ. In contrast, the T_A impulse was consistently greater in the balance recovery than pre-pull phase, a difference that increased on day 5. From the time-variation in ΔT_A, we infer that subjects learned to use a more complex τ_α signal to control movement, especially during balance-recovery.

The increased time-variation in the T_A trajectories could relate to subjects learning to improve dynamic aspects of balance control. To evaluate that possibility, we computed the closest distance that the COP came to the heel or toe during balance recovery (minimal COP). On day 1, the minimal COP distance was closer to the edges of the foot for larger than for smaller pulls. On day 5, the minimal COP distance was similar for all pulls; that is, it never approached the edges of the feet as closely as on day 1. Recent studies have elucidated the mechanical constraints on T_A that are required to keep the foot flat on the floor in quiet standing (Gordon 1991; Kuo and Zajac 1993; Patton and Pai 1995; Pai and Patton 1997). The pulling task requires subjects to transiently move the CM_{AP} into kinematic regions that are outside the boundaries of quiet standing, but the constraints on T_A must be met for balance to be recovered after the pull. Further research should determine whether this explanation is correct, or whether learned time-variations in T_A occur for some other reason, for example, reduced energy expenditure, jerk or joint torque cost (Nelson 1983).

4.3 Evidence for a model of pulling with more DFs

Two aspects of the data provide indirect evidence that a model with more kinematic DFs will be needed to characterize how the CNS learns to organize bouncing pulls. First, the 1-DF model did not adequately characterize CM_{AP} motion even after adding a viscous element to the spring and allowing ankle torque to time-vary. Second, model-subject discrepancies were greater after practice. The human system has dynamics which the 1-DF model fails to represent. One obvious source of these 'missing dynamics' is intersegmental torques and forces, which implies a model with more kinematic DFs. We speculate that simply adding a second DF to the model might adequately characterize subject behavior, because a previous analysis showed that task constraints reduce the system to two kinematic DFs (Michaels et al. 1993). If two DFs suffice to describe CM motion both days, then the practice effect on postural shift might be due to an increased utilization of intersegmental dynamics (Schneider et al. 1989). Alternatively, subjects might learn to use even more DFs after practice (Bernstein 1967). Future research should determine whether a model with two DFs will suffice to characterize how the CNS learns bouncing pulls, or whether a more complex segmental model is required.

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[3] As noted under Methods, time-variations in the stiffness parameter κ could not be accurately assessed under the conditions of the pulling task.

4.4 Limitation of the conservation assumption

Several observations suggest that a conservative model, even one with more DFs, is unlikely to explain how the CNS learns to control movements in the bouncing pull task. First, CM_{AP} phase planes were asymmetrical. Second, T_A impulses changed from the pre-pull to the balance-recovery phase of the action. Third, speed gains were sometimes observed during the pulling phase, especially for small force pulls on day 5, indicating an input of energy to the system. Fourth, the increased speed loss at higher pulling forces implies a velocity-dependent dissipation of energy during the pulling phase. Finally, the results of simulations with the damped spring model support a role for dissipative elements in movement organization during the pulling phase. It is noteworthy that the greatest changes in speed during the pulling phase occurred for the highest and lowest forces, suggesting that non-conservative behaviors were most pronounced for those extreme conditions. This observation is consistent with reports that non-conservative behavior in other bouncing actions is greatest during extreme conditions (Farley et al. 1991). Such findings support the importance of parametric studies that explicitly test the conservation assumption, which is often made in research on bouncing, multijoint actions (cf. McMahon 1990).

Finally, while the data in our study cannot resolve what mechanisms underlie non-conservative behaviors, we hypothesize that neural inputs in the form of time-varying muscle activation, combined with visco-elastic musculoskeletal elements, contribute to energy modulation throughout the entire bouncing pull task. This hypothesis is similar to Ingen Schenau's proposal that the elastic characteristics of leg muscle and tendon are insufficient to counter the dissipative effects of damping during countermovement jumps, necessitating a transient energy input via muscle contraction beyond that needed to stiffen the joints (Ingen Schenau 1984). However, non-conservative behaviors in the bouncing pull task occurred during both the pulling phase (roughly equivalent to the countermovement jump) and the balance-recovery phase, which suggests that the CNS alters energy input during both parts of the task. It appears that energy input during the pulling phase exceeds any dissipative effects of damping during low force pulls (resulting in speed gains) but only partly cancels dissipative effects during higher force pulls (resulting in speed losses). Such hypothesized changes in energy input during contact force production are consistent with findings that leg and arm muscle activation increases immediately before and during the pull (Lee et al. 1990; W.A. Lee and K. Knight, unpublished data). Data on altered muscle activation during the balance recovery phase have not yet been reported. Studies which compare muscle activation throughout the entire task, before and after practice, are therefore needed to elucidate how actively controlled, non-conservative elements contribute to the learning of movement organization in the bouncing pull task.

4.5 Summary

This study has shown that movement organization becomes more complex, not simpler, as subjects practice making multijoint, bouncing pulls. The changes in organization were related primarily to the balance-recovery phase, suggesting that the CNS may learn to control the task's dual goals more independently. Changes in movement complexity appear to be mediated by both the time-variation of active controls and increased use of dynamics associated with DFs that had been neglected in the 1-DF model. We hypothesize that a model which incorporates both types of complexity will be necessary to explain how the CNS learns to control bouncing pulls, or other multijoint actions that involve intermittent contact forces with the environment.

Appendix A. Dynamic equations

The equations of motion for the point-mass, inverted pendulum-and-spring model (Fig. 1b) are:

$$\begin{cases} \ddot{\Theta} = \dfrac{g\sin\Theta}{r} + \dfrac{\tau_\alpha}{mr^2} - \dfrac{\kappa r(r\sin\Theta - \sigma)\cos\Theta}{mr} \\ \quad \text{for } r\sin\Theta - \sigma > 0 \\ \\ \ddot{\Theta} = \dfrac{g\sin\Theta}{r} + \dfrac{\tau_\alpha}{mr^2} \\ \quad \text{for } r\sin\Theta - \sigma \leqslant 0 \end{cases} \tag{A1}$$

where Θ is clockwise rotation from vertical, σ is the slack (equilibrium) point of the elastic cord, κ is the stiffness of the elastic cord, and τ_α is the joint torque. The top expression is used when the slack (σ) is taken out of the spring; otherwise the bottom expression is used. The torque τ_α approximately related to the position of the center of pressure (l) by the following (see Michaels et al. 1993):

$$\tau_\alpha = mgl \tag{A2}$$

Appendix B. Nonlinear regression

The hybrid regression algorithm included local and global non-linear optimization techniques. The goal was to obtain the best possible fit of model to subject data by adjusting the three model parameters τ_α, κ, and σ. Initial conditions were matched with the subjects CM data, and a numerical simulation was performed. A quadratic programming method, BFGS (Broydon 1970; Fletcher 1970; Golfarb 1970; Shanno 1970), was combined with a global simulated annealing algorithm (Metropolis et al. 1953; Kirkpatric et al. 1983) to avoid converging on the local minima caused by small fluctuations in subject data. Once the BFGS optimizer has found a local minimum, the simulated annealing process perturbed the search

away from the solution based on a probability distribution. Once the perturbation was made, the BFGS system again searched for a local minimum. This process alternated at higher accuracy and smaller perturbations until the final global solution was reached, specified by a cost function gradient of less than 0.0001. The cost function was the summed root mean square (RMS) error between the subject and model states (Θ and $\dot{\Theta}$):

$$\text{cost} = [\Sigma(\Theta_{\text{subject}} - \Theta_{\text{model}})^2]^{1/2}/\Theta_r$$
$$+ [\Sigma(\dot{\Theta}_{\text{subject}} - \dot{\Theta}_{\text{model}})^2]^{1/2}/\dot{\Theta}_r \qquad \text{(B1)}$$

where Θ_r and $\dot{\Theta}_r$ represent the range each state spanned for the trial.

A time-resampling was performed on each record before evaluating the cost function, because conventional time series with equal inter-sample intervals biased the more static phases of the motion. A given data point was used only if a sufficient (threshold) change in position or velocity occurred. The position and velocity thresholds were chosen to be the maximum changes observed in each trial at the 200 Hz sampling frequency. This signal conditioning resulted in comparable sampling of the different movement phases, but non-uniform sampling frequencies.

Three parameters were varied to find the best fit of the model to the subject data: the magnitude of the ankle torque, τ_α, the spring slack point, σ, and the spring stiffness, κ. Three fixed constraints, based on physiological, anthropometric and mechanical considerations, were placed on the optimization (although these were never active in the regression solutions). First, the τ_α parameter could only cause center of pressures within a region of stability under the foot, defined as the area between the head of the first metatarsal and the posterior aspect of the lateral malleolus (Lee and Deming 1988). Second, the stiffness κ had to be mechanically sufficient for rebound. Third, the σ parameter, which is equivalent to the location of CM_{AP} at the onset of the pulling force, had to be less than the maximum possible distance the center of mass can reach from the space of all possible joint postures.

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