Incorporating Voluntary Knee Flexion Into Nonanticipatory Balance Corrections

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Oude Nijhuis LB, Bloem BR, Carpenter MG, Allum JHJ. Incorporating voluntary knee flexion into nonanticipatory balance corrections. J Neurophysiol 98: 3047–3059, 2007. First published September 26, 2007; doi:10.1152/jn.01303.2006. Knee movements play a critical role in most balance corrections. Loss of knee flexibility may cause postural instability. Conversely, trained voluntary knee flexions executed during balance corrections might help to overcome balance deficits. We examined whether bilateral knee flexion could be added to automatic balance corrections generated by sudden balance perturbations. We investigated how this could be achieved and whether it improved or worsened balance control. Twenty-four healthy subjects participated in three different test conditions, in which they had to flex their knees following an auditory cue (VOLUNTARY condition), had to restore their balance in response to multidirectional rotations of a support surface (REACTIVE condition), or the combination of these two (COMBINED condition). A new variable set (PREDICTED), calculated as the mathematical sum of VOLUNTARY and REACTIVE, was compared with the COMBINED variable set. COMBINED responses following forward rotations were close to PREDICTED, or greater, suggesting adequate integration of knee flexion into the automatic balance reactions. For backward rotations, the COMBINED condition resulted in several near-falls, and this was generally associated with smaller knee flexion and smaller EMG responses. Subjects compensated by using greater trunk flexion and arm movements. Activity in several muscles displayed earlier onset for the COMBINED condition following backward rotations. We conclude that healthy adults can incorporate voluntary knee flexion into their automatic balance corrections and that this depends on the direction of the postural perturbation. These findings highlight the flexibility of the human balance repertoire and underscore both the advantages and limitations of using trained voluntary movements to aid balance corrections in man.

INTRODUCTION

When healthy humans are perturbed, while standing on a movable platform, a cascade of balance-correcting muscle reactions occurs. Some balance corrections have latencies close to 90 ms and have been termed “automatic,” whereas others have longer latencies around 150 ms, which approximates voluntary reactions (Allum et al. 1993; Carpenter et al. 1999; Horak et al. 1990). These reactions are probably chosen from a continuum of balance-correcting synergies: specific preprogrammed muscle response patterns that are embedded within higher-level balance control centers within the CNS. In turn, balance-correcting synergies generate multilink strategies: specific patterns of segmental movements that include variable combinations of hip, knee, and ankle movements to correct instability (Allum and Honegger1993, 1998; Rietdyk et al. 1999; Runge et al. 1999). This multilink action is in accordance with the theory of axial kinematic synergies, where action in one segment or muscle evokes reactions in other segments or muscles close to it (Alexandrov et al. 1998a,b; Crenna et al. 1987).

The question arises whether the knees play a critical role in these multilink strategies. There are two ways in which knee movements could contribute to balance corrections: a sensory contribution (by registering movements induced by the stimulus) or as part of the correcting strategy itself. It remains unclear whether proprioceptive feedback from the knees contributes to the triggering of balance corrections (Allum et al. 1995; Gruneberg et al. 2005). However, loss of knee proprioception is associated with severe delays in balance-correcting responses and marked postural instability (Bloem et al. 2002; Brunetti et al. 2006). Knee movements as part of the balance-correcting strategy have been largely ignored in the literature, despite evidence to the contrary. Significant knee movements occur in response to both translations and rotations of the support surface (Allum and Honegger 1998; Bakker et al. 2006; Creath et al. 2005). Even quiet stance appears to involve knee and hip movements (Hsu et al. 2007). The main action of knee movements in response to sudden support-surface perturbations could be to absorb its impact, thereby reducing tilt of the trunk. For example, sudden lateral tilts of a support surface are largely absorbed by flexion of the uphill knee and extension of the downhill knee (Allum et al. 2003; Carpenter et al. 1999). The importance of this “absorption function” is underscored by the marked instability that ensues when normal knee flexion movements are pathologically reduced, as occurs in patients with cerebellar ataxia, Parkinson’s disease, or peripheral vestibular loss (Allum et al. 2003; Bakker et al. 2006; Horak et al. 2005). Thus it appears that active voluntary knee flexion could contribute to enhanced stability after support-surface perturbations.

Previous research has not examined the effect of voluntary knee movements on balance-correcting strategies. Specifically, we were interested to see whether healthy subjects alter or even delay preprogrammed balance-correcting strategies, when implementing a voluntary movement that may or may not fit their automatic balance-correcting strategy. We posed two main questions. First, can standing subjects implement voluntary
knee flexion movements when their balance is simultaneously perturbed by a moving support surface? Second, would incorporating such voluntary knee flexion into the postural strategy alter the intersegmental shaping of automatic balance corrections? One possible outcome is that voluntary knee flexion would be purely added to the directional sensitivity of automatic balance corrections. Alternatively, voluntary knee movements might suppress the initial automatic responses and thereby also alter the preprogrammed balance-correcting synergy in latency or directional sensitivity. This may cause a disruption of the kinematic strategy, thus leading to postural instability (Alexandrov et al. 1998b; Hughey and Fung 2005).

From a rehabilitation viewpoint, we wondered whether knee flexion could represent a possible defensive strategy to avoid a fall or to reduce its impact. One advantage would be lowering the center of mass (CoM), thereby reducing the force of the impact in case of an actual fall and diminishing the risk of fall-related injuries (Nevitt and Cummings 1993; Tinetti et al. 1995). Supplementary knee movements might also help to induce appropriate knee reactions. For example, when the support surface tilts forward, extra knee flexion would shift the CoM in a more appropriate direction and thereby stabilize posture. We hypothesized that knee flexion would be biomechanically advantageous for forward and laterally directed platform tilts, but possibly not for backward directed tilts where the knees are first extended (Carpenter et al. 1999). Answers to these questions might have implications for the future implementation of specific fall-prevention strategies, e.g., in subjects with pathologically reduced knee flexibility such as patients with cerebellar ataxia (Bakker et al. 2006).

To answer these questions, we studied the kinematic and electromyographic (EMG) responses of healthy subjects who were instructed to rapidly flex their knees in response to an auditory tone alone or to the combination of a tone plus simultaneously delivered multidirectional postural perturbations. We compared these responses to those when no voluntary knee flexion was requested after a support-surface perturbation.

METH ODS

Participants

Twenty-four healthy subjects (12 men; mean age 23 yr, range 18–28) participated. Average height was 175 cm (range 156–188). Exclusion criteria included neurological, balance, or musculoskeletal disorders. All participants gave prior written informed consent. We conducted the experiments in conformance with the standards of the Declaration of Helsinki. The Institutional Review Board of the University Hospital Basel approved the study.

Procedure

We assessed balance control as described previously (Allum et al. 2002; Carpenter et al. 1999). Briefly, participants stood on a servo-controlled dual-axis rotating platform with their feet lightly strapped into heel guides fixed to the platform surface to prevent stepping reactions. Platform tilts occurred in different directions at a constant amplitude of 7.5° and velocity of 60°/s.

The experiment consisted of three different conditions, delivered in blocks without practice trials. Ordering of the three blocks was counterbalanced across subjects. The cued VOLUNTARY condition consisted of 11 trials of voluntary knee flexion only, without concurrent platform perturbation. The auditory cue (1,000-Hz tone; 50 dB) was produced by loudspeakers, positioned at knee height. This cue sounded until it was automatically switched off when movement sensors (light barriers) detected 30° of knee flexion. The instruction was to flex both knees as rapidly as possible in response to the auditory cue, with the specific goal to switch off the sound and keep the knees flexed for ≥2 s. We chose 30° after pilot experiments showed that this was the maximum flexion subjects could achieve comfortably. The condition termed REACTIVE consisted of 49 multidirectional support-surface tilts, without additional cued voluntary knee flexion. For consistency, the same auditory cue as in the VOLUNTARY condition sounded at the onset of platform movement, but now the specific instruction was to respond naturally to the balance perturbation, without additional knee flexion. The remaining condition was termed COMBINED and included 49 trials with concurrent support-surface tilts and auditory-cued voluntary knee flexion. The same auditory cue as in the VOLUNTARY condition was used. The specific instruction was the same as for the VOLUNTARY condition, but also included the instruction to regain a stable balance.

The REACTIVE and COMBINED conditions contained perturbations that were randomly delivered in six different directions (eight trials each): pitch forward (toes down or 0°); pitch backward (toes up or 180°); and four combinations of pitch and roll stimuli: forward left (315°), forward right (45°), backward left (225°), and backward right (135°). These randomly delivered multidirectional perturbations helped to reduce stimulus predictability (Allum et al. 2002). Handrails adjusted to the height of the participants’ wrist were present 40 cm to the sides. Subjects were instructed to grasp the handrails only when needed. One assistant was present behind the subject to lend support in case of a fall. We defined a response as a near-fall if the subject needed to grab the handrails or receive assistance to prevent a fall.

Outcome measures

We instrumented participants with 18 infrared emitting diodes (IREDs) to collect full body kinematics. The IREDs were placed on the following anatomical landmarks: frontally at the level of the malleoli, at the center of the patellae; frontally at the level of the greater trochanters; anterior superior iliac spines; elbow axes; acromions; processus styloideus radii; and both temples, one at the chin and one at the sternal angulus. Three additional IREDs, placed at the front corners and center of the rotational surface, were used to trace pitch and roll movements. An OPTOTRAK motion analysis system (Northern Digital Canada, Waterloo, Canada) tracked the IREDs at 64 Hz. We also calculated anterior–posterior (AP) and mediolateral (ML) ankle torques at 1,024 Hz from support-surface reaction forces measured with strain gauges embedded in the rotating platform.

To record surface EMG signals, pairs of silver–silver chloride electrodes were placed about 3 cm apart along the following muscle bellies on the left side of the body: tibialis anterior, soleus, rectus femoris, biceps femoris, gluteus medius, external oblique, paraspinal muscles (L1–L2 spine level), biceps brachii, and medial deltoid. We recorded on one side of the body for practical reasons, having previously identified the absence of left–right asymmetries (Carpenter et al. 1999; 2004b; Grin et al. 2007). EMG recordings were band-pass analogue filtered between 60 and 600 Hz, full-wave rectified, and low-pass filtered at 100 Hz with a third-order Paynter filter before sampling at 1 kHz.

Data analysis

Biomechanical and EMG recordings were initiated 100 ms before stimulus onset and had a sampling duration of 1 s. Following analogue to digital conversion, all recordings were averaged off-line across
each perturbation direction. The first recording under each condition was discarded to reduce habituation effects (Keshner et al. 1987).

For all outcome measures (kinematics, ankle torques, EMG), we summed the values for the VOLUNTARY and REACTIVE conditions and named this the PREDICTED variable (gray lines and columns in Fig. 1). We compared this PREDICTED value with the value for the COMBINED condition. COMBINED values equal to PREDICTED values would point to a simple addition of voluntary knee flexion on REACTIVE alone responses. If COMBINED response values were significantly different from PREDICTED, this would imply that voluntary knee flexion was not integrated into COMBINED response through a simple addition, but in a more complex interactive way.

To estimate effects of voluntary knee flexion on “overall” postural performance, we calculated total body CoM displacement in the AP, ML, and vertical (V) directions using a 12 body segment adaptation (Grin et al. 2007) of a 14 body segment model (Winter et al. 1998). We calculated the area under the curve (AUC) of the CoM displacements and velocities in each direction, using trapezoid integration between 100 and 800 ms from stimulus onset. Before integration, values were full-wave rectified to avoid having negative areas given the biphasic pattern of some responses.

We measured the AP CoM velocity and knee velocity at 300 ms when this variable peaked to demonstrate correlations between CoM and knee flexion velocity.

Onset latencies of AP ankle dorsiflexion torque were calculated using a threshold of 2 Nm with respect to prestimulus values. Responses for the downhill leg and uphill leg were now pooled separately to obtain four diagonal values: forward uphill, forward downhill, backward uphill, and backward downhill (i.e., forward uphill was calculated as the right leg for forward right perturbations, pooled with the left leg for forward left perturbations). Onset latencies of knee flexion velocities were calculated and pooled in the same manner as for ankle dorsiflexion torque. The threshold used was 50°/s flexion velocity because this was the average peak velocity plus 2 SD for knee flexion during forward tilts in the reactive condition.

Angle changes between segments were calculated over a 150- to 550-ms interval (see Statistical analyses for justification). For axial segments (i.e., pelvis and trunk) the four directions used were pitch forward, forward left, backward left, and pitch backward, instead of the pooled diagonal directions, to be consistent with the analysis and laterality of the EMG recordings (left side). For the limbs, where no differences other than sign were expected, we averaged the right-sided

**Knee angle**

**A** Pitch Forward

- VOLUNTARY
- REACTIVE
- COMBINED
- PREDICTED
- AUC 150-550 ms

**B** Pitch Backward

- VOLUNTARY
- REACTIVE
- COMBINED
- PREDICTED
- AUC 150-550 ms

**C** Knee angle (AUC 150-550 ms)

- PREDICTED
- COMBINED

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![Graph A](image1)

*Figure 1.* A: average population traces of knee movements in the pitch forward direction (toes down; 0°) for the 3 different conditions and the calculated PREDICTED variable. B: same for the pitch backward direction (toes up; 180°). C: columns showing the averages of the calculated PREDICTED variable compared with the COMBINED condition of the change in knee angle ± 1 SE in 6 (pooled) directions. Interval used was 150–550 ms (see boxes in A and B). Asterisks indicate significant differences (post hoc t-test, *P* < 0.01).
responses for backward left with the left-sided responses for backward right and vice versa.

EMG areas were calculated using trapezoid integration. First, the level of background activity (measured over a period of 90 ms terminating 10 ms before stimulus onset) was subtracted from the muscle response. The time intervals used for response areas were 120–220 ms in leg muscles, 90–180 ms in trunk muscles, and 80–220 ms in the arms. These intervals were based on calculations of intervals spanning the peak of the difference between the COMBINED and PREDICTED responses (Grin et al. 2007). In addition, we used a second interval (300–500 ms) determined using a second peak in the response traces (Grin et al. 2007).

EMG onset latencies were calculated across each trial and muscle. We used a semiautomatic computer algorithm that searched for the response peak and subsequently went backward in time and determined when the individual EMG trace first fell below the mean plus 2.5 SD of background muscle activity. The algorithm first identified the peak response amplitude in each individual trial within predefined intervals (tibialis anterior, soleus, rectus femoris, and biceps femoris: 100–250 ms; rectus femoris, biceps femoris, and gluteus medius: 60–300 ms; paraspinals: 100–200 ms; arm muscles: 20–240 ms). All peaks and latencies were visually inspected and discarded if necessary.

Statistical analyses

To provide a rational basis for the comparison of the various kinematic variables across test conditions, we first performed a multivariate analysis (Condition × Direction × Plane) on the CoM velocity across the entire recording interval (between 100- and 800-ms poststimulus onset), for all three planes of motion (AP, ML, and vertical). This was followed by another multivariate analysis (done separately for each of the three planes). For this purpose, we divided the traces into consecutive 50-ms bins and examined when the divergence between population traces for the different test conditions divided the traces into consecutive 50-ms bins and examined when the divergence between population traces for the different test conditions revealed significant differences between the COMBINED and PREDICTED conditions in the four directions of platform tilt for the 150- to 550-ms poststimulus interval in AP and vertical planes, but not for the ML plane. Therefore further analyses were restricted to the AP and vertical planes and to the time interval of 150–550 ms.

Cued voluntary knee flexion

All subjects were always able to achieve the required minimum of 30° knee flexion in the COMBINED condition. This is shown for pure pitch perturbations (backward and forward) in Fig. 1, A and B. Subjects could easily flex the knees when rotated forward, where we observed a greater amount of knee flexion in COMBINED compared with PREDICTED (Fig. 1A). However, when rotated backward, subjects had more difficulty flexing the knees in the COMBINED condition because flexion was less than PREDICTED (Fig. 1B). Similar effects were observed for the other directions, with always greater than expected knee flexion for pitch perturbations with a forward component and vice versa (Fig. 1C). This was confirmed statistically, showing that knee flexion was influenced by a Condition (COMBINED vs. PREDICTED) × Direction interaction effect [$F_{(5,12)} = 45.28; P < 0.01$].

Vertical displacement of the CoM

There was no downward CoM displacement during the REACTIVE condition for backward pitch perturbations and negligible downward CoM displacement for forward pitch perturbations (Fig. 2, A and B). In contrast, knee flexion led to a lowering of CoM in all directions, in both the VOLUNTARY and the COMBINED conditions. These effects were observed for all perturbation directions (Fig. 2C), and statistical analyses showed a significant Condition × Direction interaction effect for vertical CoM displacement [$F_{(3,66)} = 144.88; P < 0.01$]. Post hoc analyses showed that for pitch perturbations with a forward component, the COMBINED condition elicited greater downward CoM displacements than PREDICTED ($P < 0.01$). In contrast, for pitch perturbations with a backward component, COMBINED responses were smaller than PREDICTED ($P < 0.01$).

Anterior–posterior CoM

Figure 3, A and B shows the AP displacement of the CoM for pure pitch perturbations (backward and forward). The VOLUNTARY condition showed a forward displacement of the CoM, whereas the REACTIVE condition showed a CoM displacement that was initially in the same direction as the platform perturbation. For forward pitch perturbations, AP CoM displacement during the COMBINED condition equaled the PREDICTED condition and both were greater than the REACTIVE condition alone. In contrast, for pitch backward perturbations, COMBINED AP CoM movements were smaller than the PREDICTED responses. Similar effects were observed for the other directions, with always equal or slightly greater than expected AP CoM movement for pitch perturbations with a forward component versus significantly smaller COMBINED responses for the backward pitch perturbations. 

RESULTS

Identification of intervals for analysis

The MANOVA showed a significant Condition (2 levels: COMBINED and PREDICTED) × Direction (4 levels: forward, backward left, backward right, and vertical) × Plane of movement (3 levels: AP, ML, and V) interaction effect for the CoM velocity [$F_{(9,79)} = 21.4; P < 0.001$]. We next examined these three planes separately using univariate analyses, which also resulted in significant Condition × Direction interaction effects for AP [$F_{(3,32)} = 22.9; P ≤ 0.001$], ML [$F_{(3,32)} = 5.1; P = 0.005$], and vertical CoM velocity [$F_{(3,32)} = 13.3; P = 0.001$]. Within each plane, subsequent multivariate analyses using the 50-ms bins across the 100- to 800-ms interval revealed significant differences between the COMBINED and PREDICTED conditions in the four directions of platform tilt for the 150- to 550-ms poststimulus interval in AP and vertical planes, but not for the ML plane. Therefore further analyses were restricted to the AP and vertical planes and to the time interval of 150–550 ms.
This was confirmed statistically, showing that AP CoM was influenced by a Condition × Direction interaction effect \[F(3,66) = 135.72; P < 0.01\]. These changes in CoM position were confirmed by analyses of CoM velocity (population traces shown in Fig. 3, D and E), which revealed that for forward rotations, the peak AP CoM velocity during the VOLUNTARY condition was of a magnitude similar to that of the REACTIVE condition. In contrast, for backward rotations, the REACTIVE and VOLUNTARY responses were of opposite polarity [Condition × Direction interaction effect; \[F(3,66) = 36.63; P < 0.01\]].

Influence of knee velocity on AP CoM velocity

To further explore the observed differences in CoM displacement and knee angle between forward and backward pitch perturbations, we investigated the relationship between knee velocity and AP CoM velocity (at 300 ms, when CoM velocity peaked; Fig. 3, D and E). In the REACTIVE condition, this relationship showed a nonsignificant trend for forward rotations \((r = 0.55; P = 0.09)\) and no relationship for backward rotations \((r = 0.01; P = 0.97; \text{Fig. 4A})\). In the COMBINED condition, the relationship between knee velocity and AP CoM velocity was higher for forward rotations \((r = 0.72; P < 0.01)\) compared with backward rotations \((r = 0.47; P = 0.02; \text{Fig. 4B})\) and had a steeper slope \((t > 200; P < 0.01)\).

Near-falls

We recorded eight near-falls in four different subjects (four near-falls in one subject, two in another; two subjects experienced one near-fall). All near-falls occurred after backward-directed perturbations and in combination with cued voluntary knee flexion (COMBINED). Figure 5 provides the averaged responses recorded during the four near-falls of the subject with the most frequent near-falls, as compared with four averaged no-fall responses. The near-fall responses are characterized after 250 ms by excessive AP CoM velocity, increased knee flexion velocity, decreased arm movements, and greater EMG activity.

Compensating trunk and arm movements

Both trunk and arm movements appeared to partially compensate for the insufficient forward CoM movement during the

(Fig. 3C). This was confirmed statistically, showing that AP CoM was influenced by a Condition × Direction interaction effect \([F(3,66) = 135.72; P < 0.01]\). These changes in CoM position were confirmed by analyses of CoM velocity (population traces shown in Fig. 3, D and E), which revealed that for forward rotations, the peak AP CoM velocity during the VOLUNTARY condition was of a magnitude similar to that of the REACTIVE condition. In contrast, for backward rotations, the REACTIVE and VOLUNTARY responses were of opposite polarity [Condition × Direction interaction effect; \([F(3,66) = 36.63; P < 0.01]\)].

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Compensating trunk and arm movements

Both trunk and arm movements appeared to partially compensate for the insufficient forward CoM movement during the
COMBINED condition after backward perturbations. Trunk flexion is shown for pure backward pitch perturbations in Fig. 6A. During the VOLUNTARY condition, some 5° flexion of the trunk occurred. For pure backward perturbations the REACTIVE condition initially showed approximately 5° of trunk flexion, which subsequently decreased (Fig. 6A). Larger trunk responses in the COMBINED condition than in PREDICTED were present for all perturbations with a backward component and, to a lesser extent, for perturbations with a forward component (Fig. 6B). This difference between forward and backward rotations was significant [Condition × Direction interaction effect; \( F(3,69) = 7.59; p < 0.01 \)]. Post hoc analyses showed that the COMBINED responses were not different from the PREDICTED responses for forward perturbations, but significantly greater for pure backward pitch perturbations (\( p < 0.01 \); Fig. 6D).

Anticipatory postural adjustments

As expected, we observed anticipatory postural reactions before actual knee movement during VOLUNTARY knee flexions, as reflected by increased tibialis anterior and decreased soleus activity (Fig. 7A). This early activity generated an ankle dorsiflexion torque, which preceded voluntary knee flexion. We were interested to see to what extent the reactively generated ankle responses (as induced by platform motion) were supporting or “working against” these anticipatory postural reactions. Important differences between forward and backward platform rotations emerged that may explain why it
is relatively more difficult to incorporate knee flexions for backward directed rotations. Thus for forward rotations in the REACTIVE condition, the platform-induced ankle torque was appropriately directed (i.e., also in dorsiflexion) to support the subsequently requested voluntary knee movement (Fig. 7B). This resulted in rapid knee flexion during the COMBINED condition (Fig. 7C). In contrast, for backward rotations, the platform-induced ankle torque was oppositely (i.e., plantar flexion) directed to the ankle torque generated by voluntary knee flexion (Fig. 7D). Because of this, knee flexion was delayed in onset during the COMBINED condition until the ankle torque had moved into a dorsiflexion direction (Fig. 7E). Furthermore, the pattern of early unloading in soleus and activity in tibialis anterior was lacking. The delayed onset of knee flexion for backward rotations was also confirmed statistically [significant main effect of direction for the COMBINED condition; $F_{(5,12)} = 26.54; P < 0.01$]. Post hoc analyses revealed significant differences between the forward and backward pitch perturbations ($P < 0.01$).

**Muscle response amplitudes**

Figure 8 shows the responses of three different muscles for pure pitch perturbations (backward and forward). During the early EMG intervals (before 200 ms), all muscles showed comparable or mildly increased activity during the COMBINED condition as compared with the PREDICTED condition. A significant increase was observed only for medial deltoid activity for backward pitch perturbations ($P < 0.01$). This was confirmed statistically, showing that activity in the medial deltoid muscle was influenced by a Condition × Direction interaction in medial deltoid [$F_{(3,24)} = 4.34; P < 0.02$], rectus femoris [$F_{(3,57)} = 3.53; P < 0.05$], and external oblique muscles [$F_{(3,66)} = 3.21; P < 0.05$]. Post hoc analysis revealed that these reductions in onset latency were significant only for backward (or, in the case of left external oblique, leftward) rotations. For example, onset latency of the medial deltoid muscle was shortened from $152 \pm 24$ ms (mean ± SD) during the REACTIVE condition to $132 \pm 23$ ms during the COMBINED condition for pitch backward perturbations. Similarly, rectus femoris onset latency was reduced from $161 \pm 32$ to $146 \pm 26$ ms. For backward left rotations, external oblique responses were shortened from $113 \pm 22$ to $96 \pm 17$ ms.

**DISCUSSION**

We studied the ability of young healthy subjects to implement voluntary knee flexion during automatic balance corrections. We hoped to understand whether and how the CNS would change or adjust existing movement strategies and muscle synergies, to create a stable and integrated balance correction. Our key findings were that subjects could incorporate voluntary knee flexion into their balance corrections. When stance was perturbed in a forward direction the forward CoM displacement increased, yet this had no detrimental effect...
on balance corrections. When stance was perturbed backward, a destabilizing effect occurred, and this necessitated compensatory changes in movement strategy (greater trunk flexion, arm elevation, and earlier activation of muscle responses).

Influence of cued voluntary knee flexion on CoM displacements

Many postural perturbations can be corrected for using “in-place” balance corrections, where the feet do not leave their initial position. Larger postural disturbances require additional defensive reactions, most notably corrective steps or protective arm movements (Allum et al. 2002; Jensen et al. 2001; Maki and McIlroy 1997; Marigold et al. 2003). Here, we investigated the extent to which voluntary knee movements could be used to compensate for postural instability.

It has been argued that voluntary movements can be executed as rapidly as balance corrections only when these are well practiced and performed with a single-choice paradigm under conditions of postural stability (Nashner and Cordo 1981). Alternatively, when the perturbation is anticipated, subjects can respond with the same response latency when the goal is to initiate a step or to maintain stance with an “in-place” reaction (Burleigh et al. 1994). However, when responding to sudden balance perturbations, simultaneous voluntary movements could lead to postural instability by disrupting the kinematic strategy that the CNS normally attempts to simplify by avoiding redundancy of limb movements (Alexandrov et al. 1998b; Hughey and Fung 2005). Nonetheless, Grin et al. (2007) showed that a voluntary arm raise following a sudden balance perturbation helped to restore balance by shifting the CoM in a stabilizing direction, without changes in movement strategy or muscle synergy.

Our present results indicate that disruption of the balance-correcting strategy depends on three factors: the similarity of the required postural strategy to the imposed voluntary movement; the direction of the postural perturbation; and the similarity of the COMBINED response to the PREDICTED response. When sub-
jects were perturbed forward, the two separate movement strategies were very similar and this resulted in a substantial forward displacement of the CoM in the COMBINED condition, but without near-falls. Indeed, we found no difference between the observed COMBINED condition and the calculated PREDICTED variable, suggesting an adequate, stable integration of the two concurrent strategies. This explanation is supported by the high correlation between knee flexion velocity and AP CoM velocity when perturbed forward. In contrast, when perturbed backward, cued voluntary knee flexion appears to disrupt the balance-correcting strategy because several near-falls were observed. In addition, we found no correlation between knee flexion velocity and AP CoM velocity when perturbed backward. Furthermore, COMBINED condition values were different from PREDICTED values, suggesting that both strategies could not be integrated into one stable strategy and that, instead, a change in strategy was required.

**Changes in strategy**

We explored this strategy change by analyzing displacements of individual body segments. When pitched forward, the movement pattern was not changed in the COMBINED condition compared with the VOLUNTARY condition because all segments remained oriented in the same direction. When perturbed backward, the normal strategy (as observed in the REACTIVE condition) was changed both temporally and spatially when cued voluntary knee flexion was enforced. Specifically, although the required amount of voluntary knee flexion in the COMBINED condition was reached, the automatic plantar flexion torque that normally accompanies backward platform tilts had to be overcome first. Therefore onset of knee flexion velocity occurred later in the COMBINED condition than in PREDICTED.
Compensatory strategies

One of our aims was to determine whether voluntary knee flexion might serve as a compensatory strategy for specific fall directions. After forward platform tilts, extra voluntary knee flexion produced no instability. We did observe a lowering of the CoM, which could be interpreted as beneficial in that a lower CoM might reduce the impact of a fall. However, CoM was lowered only modestly and our study was not designed to evaluate changes in contact forces after a fall.

After backward platform tilts, voluntary knee flexion was again associated with a lowering of the CoM, which could be interpreted as beneficial in that a lower CoM might reduce the impact of a fall. However, CoM was lowered only modestly and our study was not designed to evaluate changes in contact forces after a fall.

Changes in synergies

Previous studies have shown that voluntary modifications of the natural response to balance perturbations can be associated with changes in postural synergies (Burleigh et al. 1994). For example, subjects who were instructed not to resist sudden postural perturbations were able to appreciably modify amplitudes of their balance-correcting responses (Bloem et al. 1995). We also recorded surface EMG to explore possible changes in postural synergies. Later occurring muscle activity (300 to 500 ms after the perturbation) was increased in rectus femoris,
which helped to stabilize the already accomplished degree of knee flexion.

Analysis of EMG activity in ankle, trunk, and arm muscles underscored the compensatory changes in movement strategies. For example, EMG activity between 300 and 500 ms from stimulus onset in ankle and paraspinal muscles was increased for the COMBINED condition after backward tilts, and this helped to compensate for the negative effect of voluntary knee flexion by generating greater stabilizing movements of the ankle and trunk. However, this activity did not compensate sufficiently to place the CoM in the predicted stable position.

**Changed muscle response onset latencies**

Cued knee flexion also changed the timing of muscle responses in the postural synergy. Thus for backward directed perturbations, onset latencies in medial deltoid and rectus femoris muscles were reduced as part of the changed synergy. This finding was somewhat surprising because the order of the perturbation directions was randomized. Therefore we assumed that subjects would be unable to adopt specific anticipatory postural adjustments. Such context-dependent modulation of onset latencies was described earlier. For example, earlier muscle activation has been...
demonstrated when voluntary arm abductions were combined with laterally directed balance perturbations (Grin et al. 2007). We assume that these earlier onsets represent an attempt by the CNS to counter the inherent instability of the COMBINED condition for backward perturbations. Regardless of the mechanism involved, the general shift toward earlier onset latencies in the COMBINED condition provides further evidence that the voluntary responses were incorporated into the balance correction.

Another explanation for early muscle response onsets in the COMBINED condition when perturbed backward could be the occurrence of startle responses. Earlier onset latencies of balance corrections after platform tilts have been described in patients with Parkinson’s disease, possibly because the fall induced a startle-like response (Carpenter et al. 2004a). In this case, the startle response would have been provoked by the somatosensory cue of the platform perturbation and not by an auditory cue (Bisdorff et al. 1995; Gruner 1989; Li et al. 2001). However, this seems unlikely because onsets of such startle responses typically occur earlier, at 75 ms in rectus femoris and at 78 ms in medial deltoid muscles (Bisdorff et al. 1995), than the minimum onset of about 100 ms observed here. A more likely explanation is that the preparatory aspects of the voluntary response interacted with somatosensory reflex activity and thereby released preprogrammed balance responses at earlier onset latencies. The reduction in onset latencies would then result from intersensory facilitation (Rothwell et al. 2002) or a facilitated release of the postural synergy from subcortical structures.

In conclusion, healthy young adults can incorporate voluntary knee flexion into balance-correcting responses. This is achieved through direction-dependent adaptations of postural synergies associated with selective modulation of both amplitudes and onset latencies of muscle activity. Biomechanically, this has negative effects on stability for backward perturbations causing backward tilt of the center of mass. Interestingly, young subjects were able to partially counteract the negative effects on postural stability by engaging compensatory adaptations in trunk flexion and arm movements. As such, the experimental design used in this study may offer a promising avenue to test the adaptive plasticity of the CNS to optimize postural control under variable circumstances.

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Table 1. Summary of data for direction of platform rotation (forward pitch and backward pitch) and condition (COMBINED and PREDICTED)

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Direction</th>
<th>Forward Pitch</th>
<th>Predicted</th>
<th>DIFF</th>
<th>Backward Pitch</th>
<th>Predicted</th>
<th>DIFF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tibialis anterior</td>
<td>Combined</td>
<td>10.21 (12.47)</td>
<td>20.91 (20.58)</td>
<td>ns</td>
<td>59.78 (19.91)</td>
<td>48.02 (32.53)</td>
<td>*</td>
</tr>
<tr>
<td>Soleus</td>
<td>Combined</td>
<td>2.00 (2.05)</td>
<td>2.80 (2.24)</td>
<td></td>
<td>2.08 (3.10)</td>
<td>0.41 (4.43)</td>
<td>*</td>
</tr>
<tr>
<td>Rectus femoris</td>
<td>Combined</td>
<td>5.10 (2.89)</td>
<td>3.98 (2.87)</td>
<td>*</td>
<td>5.00 (3.63)</td>
<td>5.99 (3.13)</td>
<td>ns</td>
</tr>
<tr>
<td>Paraspinals</td>
<td>Combined</td>
<td>1.58 (2.03)</td>
<td>2.27 (2.76)</td>
<td>ns</td>
<td>4.56 (3.48)</td>
<td>2.66 (2.26)</td>
<td>*</td>
</tr>
</tbody>
</table>

Mean EMG amplitudes [area under the curves (AUC, units μV·s)] ± 1 SD in the interval of 300 to 500 ms for each muscle (tibialis anterior, soleus, rectus femoris, and paraspinals). Results of Student’s t-tests are shown (DIFF) for the data as a function of condition. Preceding significant (P < 0.01) ANOVAs, F(3,69) had F values between 9.8 and 24.6. *P < 0.01; ns, not significant.

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