Human standing: does the control strategy preprogram a rigid knee?

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Human standing: does the control strategy preprogram a rigid knee? J Appl Physiol 114: 1717–1729, 2013. First published April 25, 2013; doi:10.1152/japplphysiol.01299.2012.—Human standing requires control of multisegmental configuration. Does the postural system normally allow flexible adjustment of configuration, or does it minimize degrees of freedom at the ankle, knee, and hip joints? Gentle, external, unpredictable, sagittal, mechanical perturbations (randomized force, 1–10 N; duration, 0.2–2 s; and leg) were applied to either knee of 24 healthy participants who stood symmetrically for 200 s. The translation of knee perturbation force to ankle, knee, and hip joint rotations in the perturbed and unperturbed legs was studied. We assessed whether consequent joint rotations indicated a stiff configuration-conserving or viscous energy-absorbing relationship to the knee perturbation. Two distinctive response patterns were observed. Twenty-two participants showed limited knee flexion and high ankle stiffness, whereas two participants showed substantial knee flexion, low ankle stiffness, measurable internal rotation of the unperturbed hip (0.4 ± 0.3 vs. 3.0 ± 1°, 5.7 ± 17 vs. 0.5 ± 0.3 N°/0.1 ± 0.4°, respectively, mean ± SD), and a viscou relationship between perturbation force and subsequent ankle flexion, knee flexion, and perturbed and unperturbed hip internal rotation. The size of knee-flexion response to knee perturbations was uncorrelated with the extent of unperturbed standing sway. Normal standing conceals a large inter-individual range in leg control strategies, indicating adaptive potential to progress with development and skill acquisition and decline with age, disease, injury, and fear. Commonly, leg configuration was maintained stiffly. Less commonly, a bilateral, low-stiffness, energy-absorbing strategy utilizing the available degrees of freedom was shown. We propose that identification of individual coordination strategy has diagnostic and prognostic potential in relation to perceptive-posture-movement-fall interactions.

knee control; posture; control strategy in standing

Asymmetric Knee Perturbations Can Reveal Multijoint Leg Coordination in Relation to Center Of Mass Regulation

Many experiments have been performed using ankle (3, 9, 36) and hip perturbations (13, 18, 24, 27) and interpreted using the ankle and hip strategies. A knee strategy makes little difference to horizontal motion of the whole body CoM (2); thus the knee joint has been considered unimportant in the control of standing (28). To our knowledge, the knee has not been tested with perturbations. The knee is commonly believed to be locked during standing (15), implying that a perturbation would not change the leg configuration. However, small angular displacements of this joint are observed even in upright standing (10, 15, 21, 39), allowing the possibility that the knee joint might have either high or low stiffness.
An open question is whether neuromuscular mechanisms allow selective stiffening of the joints within the leg (29). This possibility would fit well within the hypothesis that degrees of freedom that influence CoM position, such as ankle flexion, are restricted, whereas those that do not influence CoM position, such as hip internal rotation and knee flexion, are unconstrained (40, 41).

Perturbations applied at the knee strongly test the extent to which the leg degrees of freedom are mobilized. Collective immobilization of ankle, knee, and hip predicts that the whole body would move forward, approximating a single-segment inverted pendulum (19) (Fig. 1, top). Collective mobilization would allow substantial ankle, knee, and hip joint movement (44) (Fig. 1, bottom). We applied perturbations randomly to one knee at a time rather than both knees simultaneously. This asymmetric approach was more informative regarding normal standing because of the following: 1) it disturbed the sagittal position of the CoM; 2) it allowed us to investigate axial rotation of the contralateral (unperturbed) hip and thus investigate mobilization-stiffening in dimensions that are unrelated to sagittal control of CoM position; and 3) it prevented participants from predicting which knee would be pulled.

The response to mechanical perturbation reveals whether the control strategy achieving minimal unperturbed joint movement during unperturbed standing aims to conserve the joint angles or to absorb the perturbation energy and allow the joint angles to evolve. If the control strategy for the whole leg is configuration conserving, i.e., to resist the perturbation in a springlike manner, then, when the force is applied, the joints rotate. When the force is removed, the body returns to the initial configuration. The joint angle is proportional to the applied perturbing force. If the stiffness is high, the leg will remain relatively straight, and the whole body will move, approximating a single segment.

If the control strategy for the whole leg is to absorb the perturbation in a viscous manner and maintain low stiffness, then when the force is applied, the joints rotate, and when the force is removed, the rotation stops, and the initial angle is not restored. In this case, the joint rotation velocity is proportional to the applied perturbing force.

Biological control systems normally exploit redundancy to provide flexibility, reliability, and robustness of control (23). Consequently, during development of motor control and skill acquisition, there is normally a progression to utilize degrees of freedom more fully (6). Likewise, reduced utilization of degrees of freedom can be a symptom of declining ability through age (20), disease (37, 38), or fear (1). Thus our secondary question concerns the range of leg control strategies in healthy participants standing normally, to understand the potential for adaptation through development. If it can be identified, the individual coordination and control strategy potentially has diagnostic value relating posture-movement-falls functionality to factors of progression and decline.

Knee Perturbation Predicts Two Main Possible Responses

To summarize, when applying gentle perturbations at the knee, according to the control strategy, a spectrum of responses might be observed. We postulate two extremes: 1) the knee does not flex and the body moves as a single segment (Fig. 1, top); or 2) the knee flexes and the body utilizes the multi-segmental degrees of freedom (Fig. 1, bottom).

Using gentle perturbations, the aim of this paper is to investigate the control strategy used in normal unperturbed standing regarding the utilization of the degrees of freedom of the leg joints.

1) Are the leg joints fixed in standing, or can they be easily mobilized by small perturbations?

2) Is the perturbation energy absorbed by the leg, or is the leg configuration controlled to resist the perturbation and elastically return the perturbation energy?

METHODS

Ethical Approval

These experiments were approved by the ethics committee of the Institute for Biomedical Research into Human Movement and Health, Manchester Metropolitan University. Participants gave written, informed consent to these experiments, which conformed to the standards set by the latest revision of the Declaration of Helsinki.

Participants and Procedure

Twenty-four healthy participants (nine women), aged 41 ± 14 yr (mean ± SD), stood symmetrically on two force plates for 200 s with their eyes open. Each of their knees was strapped with a band connected via Kevlar string to a custom-made servo motor (Fig. 2A).
Fig. 2. Apparatus for knee perturbation. A: every participant was sagittally pulled at the knee level through two custom-made knee puller apparatus (puller 1 and 2). One apparatus was applied at each knee. The apparatus consisted of a servomotor (SM) that generated a force that was proportional to the current (from the current generator, PS), and that force was transferred to the lever arm. A Kevlar string was knotted to the distal end of each lever arm and transmitted the force applied to each knee. A cotton band was placed around each knee, and the Kevlar string was knotted to this band. B: example of a sequence of pulls from the two pullers. Each puller was controlled by a Matlab program (The MathWorks), and they produced randomized pulls of different sizes (1, 1.80, 3.10, 5.6, and 10 N) and durations (0.2, 0.6, and 2 s) for a total of 15 pulls each. This case shows a series of pulses in which the product force by time (impulse) was increasing with time, which was used in preliminary trials.

This cotton band was secured around the knee with Velcro and did not constrain knee motion. The band was positioned distally to the femoral epicondyles markers (medial and lateral) and proximally to the tibial condyles markers (medial and lateral). It was confirmed that the participant could not feel any force pulling at their knees. Participants were reassured that the pulls would be very gentle and they would not lose equilibrium. They were asked to stand normally, as if they were waiting at the bus stop, looking, without fixating, at the eye level, visual view, 8 m away. A randomized series of gentle sagittal pulls of variable force (step profile up to 1, 1.80, 3.10, 5.6, and 10 N) and duration (0.2, 0.6, and 2 s) were applied unpredictably to either knee (Fig. 2B). In each 200-s trial, the five forces were applied for the three durations, making 15 pulls applied at each knee for a total of 30 pulls. The maximum and minimum interval between two subsequent pulls was 21.24 and 1.09 s, respectively. The purpose of randomizing the onset, magnitude, duration, and perturbed leg was to make each perturbation unpredictable for the participant. All participants performed at least two trials.

All participants performed an unperturbed standing trial with the knee band removed following the same instructions as above. Ten participants performed this trial before the knee perturbation experiment; the remaining participants, after the perturbation experiment.

**Apparatus and Measurements**

The participants stood with their feet on two force platforms (AMTI, OR6–7, Watertown, MA). The ground reaction force and its point of application (PoA) were obtained from the force platforms. A 10-camera motion analysis system (VICON 612, Oxford Metrics) was used to measure the body kinematics: retro reflective markers were placed on the second metatarsal head, the lateral and medial malleoli, the heel, the midpoint on the side of the tibia for the definition of the shank segment, the lateral and medial tibial condyles, the lateral and medial femoral epicondyles, the tibial tuberosity, the midpoint on the side of the femur for the definition of the thigh segment, and the pelvis (anterior/posterior, left and right, and sacrum). Both kinematic and force plate data were sampled at 60 Hz.

The sagittal plane gentle pulls were generated by two custom-made knee-pulling apparatus, one for each knee (Fig. 2). The apparatus allowed unimpeded movement while standing quietly and to generate a sudden gentle force when required. Each system used a servomotor (Servalco) producing a pulling force proportional to the current. The motor had a lever arm to which the Kevlar string was knotted. This lever arm contained a strain gauge to measure the force applied by the pull, and this sensor was calibrated. When a current was applied, a gentle force was applied sagittally at the knee joint through the Kevlar string. Kevlar was used as it is very light, but inextensible. The motor-to-participant distance was 2.5 m. When perturbations were not applied, a constant, imperceptible force (<1 × 10⁻³ N) was applied to take the slack out of the string while allowing the participant to move freely. When a perturbation was applied, there was minimal acceleration and initial transient in the force recorded, which was over long before the knee moved (see Fig. 4A).

Having shaved and cleaned the skin, surface EMG (Bagnoli, Delsys, Boston, MA) data were recorded from gastrocnemius, tibialis anterior, biceps femoris, vastus lateralis, and rectus femoris of the left and right leg (sampling rate 1 kHz), amplified (×1,000), and band-pass filtered at 20–450 Hz. The EMG signals were digitally rectified, low-pass filtered (first-order transfer function, time constant 0.2 s), and subsequently downsampled to 60 Hz.
Data Analysis

Analysis of perturbation postural state. To assess whether there was any change in postural state during the 200-s trial, for all muscles, the mean low-pass-filtered EMG activity between 1 s before and perturbation onset of each of the 30 perturbations was calculated and compared with the other perturbations. To assess whether the experimental setup altered the postural state, for all muscles, the mean low-pass-filtered EMG recorded in normal standing was compared with the muscle activation recorded in the 1 s before all of the 30 perturbations.

Quantities calculated for analysis. ANTERIOR/POSTERIOR COORDINATE OF THE CENTER OF GRAVITY. This was calculated by low-pass filtering the PoA (sagittal component) with a frequency cutoff of 0.5 Hz (32). For each participant, for unperturbed trials, the center of gravity (CoG) standard deviation was calculated.

ANTERIOR/POSTERIOR COORDINATES OF THE KNEES AND SACRUM. See Figs. 3B and 4B. These were calculated by averaging the knee (lateral and medial tibial condyles, lateral and medial femoral epicondyle, tibial tuberosity) and pelvic (anterior/posterior, left and right) markers, respectively. In preliminary tests using the same camera setup, the spatial resolution of the Vicon system was established. A 14-mm marker was recorded while oscillating sinusoidally on an externally controlled loud speaker using both the Vicon and a laser system. The Vicon system could track marker movements between 0 and 5 Hz for any peak-to-peak displacement $\geq 0.084$ mm.

ANKLE, KNEE, AND HIP JOINT CENTERS, FLEXION-EXTENSION, AND INTERNAL-EXTERNAL ROTATION ANGLES. See Figs. 3, C and D, and 4, C and D. The ankle joint center was calculated relative to the lateral malleolus using the individually measured ankle width (43). The knee joint center was calculated as the center of a line joining markers on lateral and medial femoral epicondyle. The hip joint center was calculated using three markers (sacrum, left and right anterior superior iliac spines) and anthropometric measures taken from each participant (43). All angles were calculated using the GaitLab algorithm (43) and

Fig. 3. Example responses to knee perturbations. Changes are shown in sagittal marker positions, joint angles, and muscular activity during a 4-s trial portion for a participant who allowed the knee to flex. A: force trace for the two pullers (solid line for right and dashed line for left) showing different amplitudes and durations of the pulls. B: sagittal position of line of gravity (CoG) (black dashed line), and markers placed on the sacrum (black solid line) and the right (blue solid line) and left knees (blue dashed line). C: flexion-extension angles for ankle (green line), knee (blue line), and hip (red line) joint. Positive angles mean extension for the ankle and flexion for knee and hip. D: internal rotation angles for ankle (green line), knee (blue line), and hip (red line) joint. Positive angles mean internal rotation for ankle, knee, and hip. Muscular activation for the following muscles is shown: gastrocnemius (Gas; blue line; E), tibialis anterior (TA; red; E), rectus femoris (RF; blue; F), vastus lateralis (VL; red; F), and biceps femoris (BF; green; F). Solid and dashed lines show, for each quantity, right and left, respectively. To facilitate the identification of the instant in which the pulls were generated, vertical lines (solid and dashed as a reference to the side perturbed) were imposed onto all the panels.
Fig. 4. Responses to perturbations. Averaged responses are shown to pulls of changes in marker sagittal position and joint angles for two representative participants averaging all of the pulls applied to the perturbed knee. Column Straight Knee is a representative trial showing the strategy of keeping the knee straight. Column Flexing Knee is a representative trial of the strategy of allowing the knee to move. A: force trace of the knee perturbation averaged over all pulls, combining both legs as perturbed and unperturbed. B: sagittal displacements of line of gravity (black dashed line), and markers placed on the sacrum (black solid line) and the right (blue solid line) and left knee (blue dashed line). C: flexion-extension angles for ankle (green line), knee (blue line), and hip (red line) joint. Positive angles mean internal rotation for ankle, knee, and hip. Solid and dashed lines show, for each quantity, perturbed and unperturbed side, respectively. 0 N in A is the mean zero force. 0 mm in B is the value at the onset of the perturbation for each quantity shown. 0° in C and D is the mean angle measured over the trial. In the “straight knee” case, the knee flexion was restricted (B), the body moved as a whole (B), and no large changes of the joints angles were shown (C and D). In the “flexing knee” case, not only the knee, but also the ankle and the hip showed a clear flexion (C). The knee and both hips (also the contralateral side) showed an internal rotation, while the ankle rotated externally (D). The vertical scales for the two panels are not the same, to facilitate the visualization of the main features described in the text.

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Analysis Following Perturbation and Response Averaging

Using averaged quantities calculated (above), the following were quantified for each trial.

1) The maximum change following perturbation onset.
2) Sagittal displacement of body at knee height according to the rigid leg/inverted pendulum model (IP). To quantify the extent to which the knee would move if the leg/body were a rigid single segment, the sagittal displacement of the sacrum was calculated and rescaled to knee height using

\[ IP = \frac{S \times a}{a + b} \]

where \( S \) is the maximum, averaged, sacral sagittal displacement; \( a \) is the length of the perturbed lower leg; and \( b \) is the length of the perturbed upper leg.

3) Knee flexion, deviating from inverted pendulum prediction (non-IP). To quantify the extent to which participants flexed the knee in deviation from the rigid leg configuration, we used

\[ \text{non-IP} = K - IP \]

where \( K \) is maximum, averaged, sagittal displacement of the knee.

Parametric Regression Analysis Following Perturbation and Response Averaging

The experimental model used regards the whole body neuromuscular system as a black box to which a single input is applied (force perturbation to knee) and from which multiple outputs (e.g., changes in leg joint angles) are produced (Fig. 1). A priori one cannot assume the multiple outputs covary equally. For example, in response to knee

Linear Analysis of Response to Perturbations Producing Single-trial Measures for Statistical Analysis

Perturbation and response averaging. Preliminary regression analysis between perturbation force and quantities calculated for analysis (above) showed that relationships between individual responses and perturbations were rarely significant. This is consistent with the small size of the perturbation-evoked responses compared with variation associated with the normal unperturbed process of maintaining standing. Even where significant individual relationships occurred, allowing calculation of regression coefficients, there was no evidence of a consistent, systematic variation according to perturbation amplitude, duration, or amplitude multiplied by duration (impulse). Moreover, analysis of the EMG levels preceding each of the 30 knee pulls reported in the RESULTS (below) showed no significant variation with time between the beginning and end of the trial for any muscle. Thus, for each trial, all perturbations of all amplitude, duration, and leg, and all quantities calculated for analysis (above) were averaged within the temporal window 0.1 s before to 5 s after perturbation onset, having subtracted the mean value within that window. This linear-averaging process produced nonparametric estimates of the multiple outputs to the single-perturbation input (Fig. 1). Averaging preserved the temporal-amplitude structure of the multiple signal pairs’ perturbation-response, but by averaging the variation unrelated to the perturbations to a small remnant was reduced (Fig. 4).
perturbation, the perturbed knee joint may flex, but the unperturbed hip joint may not rotate.

The aim was to know whether the relation between the force perturbation stimulus and the various response variables could be described as springlike or dampinglike. For each perturbation-response signal pair, a second-order linear regression model was constructed relating applied force to the response variable and its first and second derivative. Differentiation was performed using a Savitzky-Golay filter with a low-pass corner frequency of 2 Hz (30). The model coefficients indicate the numerical values of the stiffness, viscous damping, and inertia for that perturbation-response pair (Fig. 1). The second derivative was included in the model to separate the inertial component, if present, from the damping and stiffness components. To assess the extent to which the relationship is a stiffness or damping one, a partial $R^2$ was calculated in which only that variable (or the first derivative) and a constant was included in the regression model.

In modeling these relationships using second-order linear regression, it is convenient to name the stiffness and damping coefficients according to the output quantity, e.g., knee stiffness. However, it should be stressed that the model coefficients (e.g., knee stiffness) represent behavior of the complete neuromuscular system in controlling that quantity (knee angle) in response to the knee perturbation. The model coefficient does not represent the biomechanical property of the part itself (knee joint) or the muscles around it.

When stiffness and damping coefficients from the regression analysis were not significantly different from zero, they were assigned a value of NaN (not a number). This approach of assigning NaN would avoid biasing against participants with immeasurably low stiffness or damping: both approaches gave almost identical results.

Analysis of the Involuntary Response to Perturbation

Following perturbation and response averaging, for each trial, and for all recorded muscles, the mean, averaged, low-pass-filtered EMG of the perturbed and unperturbed leg were quantified in the following time windows: before the perturbation, 1–50 ms after the perturbation (short latency involuntary response), 51–100 ms after perturbation (medium latency involuntary response), 101–150 ms after perturbation (medium-long latency involuntary response), and 151–200 ms after the perturbation (long latency response). These windows were used to test for possible passive or involuntary responses to the perturbation.

Statistical Analysis

Classification of responses. Since participants appeared to respond according to two distinct groups (high non-IP coefficient, allowing the leg to flex, and low non-IP coefficient, keeping the knee straight), a cluster analysis of cases was applied to all of the trials collected. Each case was attributed single values of the IP and non-IP measures (maximum change following perturbation and response averaging), and cases were clustered using Euclidean distance and median linkage. Cases were classified according to the primary distinction. This approach facilitated analysis of the differences across the range.

Discrimination of differences. Discriminant analysis was used to test whether the classification was significant and to assess the extent to which quantities of interest could account for differences between the two groups. The following quantities defined above were included in the analysis: CoG, flexion, and internal rotations of the perturbed ankle and knee, internal rotation of the unperturbed hip, hip, and unperturbed hip (maximum change following perturbation and response averaging); stiffness and damping coefficients and their partial $R^2$ for CoG and joint rotations. These quantities were entered stepwise using the confidence levels of $P = 0.05$ and $P = 0.1$ for entry and removal respectively (Table 1).

More generally, to identify significant differences between groups, nonparametric tests were used to account for outliers. For comparing two groups, the Mann-Whitney U-test was used (see Fig. 6). For comparing more than two groups, the Kruskal-Wallis test was used (see Figs. 5 and 7). Generally, $P$ values are shown for results that are statistically significant at 95% confidence or better. Unless otherwise stated, the results are reported as means ± SD.

To identify differences between EMG recorded in unperturbed trials and during the perturbed trials recorded in the 1 s before each perturbation, a Kruskal-Wallis test was used. To identify differences between EMG recorded in the 1 s before every pull during each perturbation trial, a Kruskal-Wallis test was used.

RESULTS

Typical Trial of a Series of Knee Perturbations With Responses Measured

Each participant was perturbed at each knee with randomized, gentle sagittal pulls of five different amplitudes and three durations (Fig. 2B). Figure 3 represents a portion of a trial in which a participant showed relatively large knee flexion. For this trial, the pulled knee moved according to the size and duration of the perturbation, with the first pull showing knee peak displacement of 80.3 mm (Fig. 3B), while the whole body (sacrum marker and CoG trace) moved forward much less than the perturbed joint, with peak CoG displacement of 32.7 mm for the same pull (Fig. 3B). After the onset of the same pull, the perturbed ankle, knee, and hip flexed by 8.4, 16, and 6.3°, respectively (Fig. 3C). In association with these large flexions, the perturbed ankle and knee internally rotated by 1.7 and 9°, respectively, and the hip externally rotated by 1.7° (Fig. 3D).

About 1 s after the perturbation onset, the perturbed and unperturbed rectus femoris were activated (Fig. 3F).

Leg Configuration: Inverted Pendulum (Straight Knee) vs. Noninverted Pendulum (Flexing Knee) Behavior

Did participants respond to a knee perturbation by defending or not defending the straight leg configuration? By averaging all of the pulls from both legs (Fig. 4) for two representative

<table>
<thead>
<tr>
<th>Quantity of Interest</th>
<th>Correlation Coefficient With Discriminant Function</th>
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<tbody>
<tr>
<td>Ankle $R^2$ viscosity</td>
<td>0.915</td>
</tr>
<tr>
<td>Knee flexion angle</td>
<td>0.668</td>
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<tr>
<td>Ankle flexion angle</td>
<td>0.614</td>
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<tr>
<td>Unperturbed hip $R^2$ viscosity</td>
<td>0.476</td>
</tr>
<tr>
<td>Knee viscosity</td>
<td>0.372</td>
</tr>
<tr>
<td>Ankle viscosity</td>
<td>0.371</td>
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<tr>
<td>Unperturbed hip internal angle</td>
<td>0.228</td>
</tr>
<tr>
<td>Perturbed hip $R^2$ viscosity</td>
<td>0.224</td>
</tr>
<tr>
<td>CoG displacement</td>
<td>0.161</td>
</tr>
<tr>
<td>Perturbed hip stiffness</td>
<td>0.161</td>
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<tr>
<td>Knee internal rotation angle</td>
<td>0.151</td>
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<tr>
<td>Perturbed hip flexion angle</td>
<td>0.151</td>
</tr>
<tr>
<td>CoG displacement viscosity</td>
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</tr>
<tr>
<td>CoG displacement stiffness</td>
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</tr>
<tr>
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<tr>
<td>Ankle stiffness</td>
<td>−0.028</td>
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</table>

A linear discriminant function best classifies trials into two groups, previously identified as straight knee and flexing knee. This table reports the correlation coefficient between quantities of interest and the discriminant function. The quantities included as terms in the discriminant function are in bold. CoG, sagittal component of the center of gravity.
participants, the main kinematics representing two possible behaviours are shown.

In Fig. 4 “straight knee” column, the individual moved as one whole segment rotating at the ankle joint as the inverted pendulum model would suggest, even though the knee was perturbed. Furthermore, no movement in the leg and the body was registered for the first 0.8 s after the perturbations. Then a minimal but sudden knee displacement was shown (peak displacement 2.8 mm) with a marginally larger whole body displacement (4 mm in CoG and 3.4 mm at the sacrum level) (Fig. 4B, “straight knee”). The leg joints flexed with similar delay and again with a sudden change, and the average maximal flexion after the perturbations at the knee, hip, and ankle were, respectively, 0.3, 0.1, and 0.2° (Fig. 4C, “straight knee”). The knee and hip internally rotated by 0.2 and 0.1°, respectively, and ankle externally rotated by 0.2° (Fig. 4D, “straight knee”). The jerky knee flexion was visually checked for all the trials and was observed in 21 trials.

By contrast, in Fig. 4, “flexing knee” column, another participant allowed the knee to move when perturbed; also the other joint positions evolved instantly in response to the perturbation. The averaged knee marker displacement recorded was large (12.4 mm), and the whole body movement (6 mm in CoG and 5.2 mm at the sacrum level) (Fig. 4B, “flexing knee”) was smaller than the knee movement, although larger than the whole body movement of the preceding inverted pendulum-like example (Fig. 4, “straight knee”). The knee flexed by 2.4°, but also the hip and the ankle flexed by 0.7 and 1.6°, respectively (Fig. 4C, “flexing knee”). The knee and the hip internally rotated by 0.4 and 0.5°, and the ankle externally rotated by 0.5° (Fig. 4D, “flexing knee”). Interestingly, while in the case that the body behaved as one single segment (Fig. 4, “straight knee”), the hip belonging to the nonperturbed leg did not show any rotations; in the case that segmental movement was allowed, it internally rotated by 1.1°, which is the direction required by axial rotation of the pelvis in accordance with the perturbation to the opposite knee (Fig. 4D, “flexing knee”).

Pulls applied to the knee disturb configuration in two important ways. These pulls can cause flexion of the leg at the knee, or they cause forward body movement of the body. Both of these effects were quantified: extent to which the leg is flexed (Fig. 5A, abscissa) and whole body forward movement (Fig. 5A, ordinate). These measures (Fig. 5A) show, in comparative fashion, movement of the whole body about the ankle joint, but scaled to the height of the knee, assuming an inverted pendulum (IP) configuration, and flexion of the leg, calculated as displacement of the knee from the inverted pendulum trajectory (non-IP). Most of the trials (x’s) were clustered in the bottom left corner and showed little body movement, i.e., IP component < 2.5 mm, and small knee movement, i.e., non-IP component < 6 mm. In these trials, the participants minimized body movement, including keeping their leg straight. A smaller number of trials showed that the individuals allowed their knees to flex (non-IP > 6 mm) in response to the perturbation (open circles). All of these trials, except one, showed also a larger body movement (IP > 2.5 mm). Large knee flexion and body movement were associated (Pearson, \( r = 0.57, n = 64, P < 0.001 \)), although a few outliers can be seen (Fig. 5A).

Since differences in response to the knee perturbation appeared to reflect substantially different strategies, cluster analysis was used to separate the cases (trials) according to their leg flexion and whole body movement. The dendrogram in Fig. 5B shows the similarity among all the cases, where similarity between two clusters i and j is defined as \( s(i,j) = 100 \times [1 - d(ij)/d(max)] \), where \( d(max) \) is the maximum value in the original distance matrix. Figure 5B shows that the primary distinction lies between trials 5, 13, 7, 6, 8, 16, and 14 as one group (open circles in Fig. 5A) and all of the other trials.

Standing Asymmetry Does Not Explain the Knee Flexion Response

Human standing is usually slightly asymmetric, and that was equally true for both groups, with the center of gravity typically one-tenth of the distance from the midline to either ankle joint (Fig. 5C). Participants did not shift weight between perturbations. Within trials, there was no significant effect of leg (perturbations applied to left or right) on weight asymmetry \( \left( n = 1.920, F_{(1,1855)} = 2.4, P = 0.12, \text{ANOVA, using factors “leg” and “trial”} \right) \). The knee flexion response was not related to the extent to which the perturbed knee was supporting body weight (Fig. 5C). There is no correlation between trial averaged asymmetry and knee flexion (non-IP) (Pearson, \( n = 64, r = 0.04, P = 0.75 \)).

Compared With Allowing the Knee to Move, Does the Straight Leg Strategy Ensure More CoM Stability in Unperturbed Standing?

The two groups of trials identified by the cluster analysis (Fig. 5, A and B) corresponded to two groups of participants: 2 individuals showed large knee flexion, the remaining 22 did not. Thus the differences between participants were investigated in unperturbed standing sway: no significant correlation (Pearson, \( r = 0.21, n = 24, P = 0.33 \)) was found between perturbed knee flexion in deviation from the rigid leg (non-IP) and unperturbed, normal standing sway (Fig. 5D). Furthermore, the two participants who showed a higher perturbed knee flexion than the others (Kruskal-Wallis, \( P < 0.001, n = 24 \)) (open circles) showed no significant difference in normal standing sway from other participants (Tukey’s least significance difference procedure, post hoc multiple comparison, \( P > 0.05, n = 24 \)).

Results of the regression analysis show that differences in the resulting damping rather than stiffness best account for the two strategies (straight knee, flexing knee), and that joint rotations of the perturbed ankle and knee and unperturbed hip were related (Fig. 6). Entering stepwise all joint rotation, stiffness, and viscous damping variables, standardized canonical discriminant analysis shows the two groups (straight knee, flexing knee) were significantly different (Wilk’s \( \lambda = 0.245, P < 0.001, \chi^2 = 81.505, \text{degrees of freedom} = 2 \)) and were best separated by a linear function with two terms: the partial \( R^2 \) relating ankle flexion velocity to trial averaged perturbation force (Wilk’s \( \lambda = 0.407 \) and knee flexion angle (Wilk’s \( \lambda = 0.279 \)) with canonical coefficients 0.771 and 0.428, respectively. Using “leave one out” validation, this function correctly classified 98.4% of the trials. Examination of the structure matrix (Table 1) shows the variables that correlate most highly with the discriminant function were the two variables in the discriminant function (correlations of 0.915 and 0.618, respectively), followed by ankle flexion angle (correlation = 0.614), partial
compared with when it did (R), the flexing knee showed lower and negative knee damping (R = 0.4°, P = 0.09, 0.5 vs. 0.4, P < 0.001), and internal rotation of the unperturbed hip was slightly lower (0.01 ± 0.03 vs. 0.12 ± 0.09, P < 0.001). The same was true for the unperturbed hip ones (0.01 ± 0.03 vs. 0.12 ± 0.09, P < 0.001) (Fig. 6B). The group with little knee flexion (straight knee) showed lower and negative knee damping (−0.2 ± 0.5 vs. 0.4 ± 0.1 N·s·°⁻¹, P < 0.01). For the group that showed small knee flexion (straight knee), the perturbed hip internal rotation damping coefficient was negative and lower than when the knee flexed (−0.4 ± 0.9 vs. 0.5 ± 0.1 N·s·°⁻¹, P = 0.001) (Fig. 6C). The group that showed little knee movement (straight knee) showed much higher absolute stiffness coefficient calculated for the ankle flexion angle (5.7 ± 17.4 vs. 0.5 ± 0.3 N/°, P < 0.001), and perturbed knee and ankle flexion velocity (0.372 and 0.371, respectively).

Figure 6 summarizes the mean and SD of variables significantly different between the groups (straight knee vs. flexing knee). For the group showing very little knee flexion (straight knee) compared with the other one (flexing knee), ankle flexion was greatly reduced (0.3 ± 0.3 vs. 1.8 ± 0.5°, P < 0.001), knee flexion was greatly reduced (0.4 ± 0.3 vs. 3.0 ± 1.4°, P < 0.001), and the internal rotation of the unperturbed hip was slightly reduced (0.6 ± 0.7 vs. 1.1 ± 0.4°, P < 0.01) (Fig. 6A). For the trials in which the knee did not flex (straight knee) compared with when it did (flexing knee), the R² of the damping coefficients for the ankle was extremely lower (0.02 ± 0.03 vs. 0.43 ± 0.08, P < 0.001). The same trend was true for the knee ones (0.03 ± 0.04 vs. 0.43 ± 0.03, P < 0.001), the perturbed hip ones were slightly lower (0.03 ± 0.06 vs. 0.12 ± 0.09, P < 0.01), and the same for the unperturbed hip ones (0.01 ± 0.03 vs. 0.12 ± 0.09, P < 0.001) (Fig. 6B). The group with little knee flexion (straight knee) showed lower and negative knee damping (−0.2 ± 0.5 vs. 0.4 ± 0.1 N·s·°⁻¹, P < 0.01). For the group that showed small knee flexion (straight knee), the perturbed hip internal rotation damping coefficient was negative and lower than when the knee flexed (−0.4 ± 0.9 vs. 0.5 ± 0.1 N·s·°⁻¹, P = 0.001) (Fig. 6C). The group that showed little knee movement (straight knee) showed much higher absolute stiffness coefficient calculated for the ankle flexion angle (5.7 ± 17.4 vs. 0.5 ± 0.3 N/°, P < 0.001) (Fig. 6D).
The perturbations used were gentle to produce joint rotations of unpredictable size, timing, duration, and leg in a population of 24 individuals were studied.

The perturbations used were gentle to produce joint rotations (and moments) that are physiologically relevant. Participants were asked to stand normally and soon learned that the perturbations were not threatening. Normal standing sway was not unpredictable, and weight-bearing symmetry did not change between perturbations. Indeed, the operator could not see any difference in the standing pose assumed by the participants compared with their usual one. The background EMG in the perturbation trials compared very closely to that in normal standing, with no significant difference in most muscles. The

DISCUSSION

As a test of the strategies to control the leg joints in conditions as close as possible to normal standing, the responses to gentle, sagittal knee perturbations of unpredictable size, timing, duration, and leg in a population of 24 individuals were studied.

The perturbations used were gentle to produce joint rotations and straight leg strategies. Trials were classified as knee kept straight (straight knee) and allowed to flex (flexing knee), shown in left and right bars, respectively. The quantities presented here are those significantly different between the groups. Columns refer to ankle flexion of perturbed leg, knee flexion of perturbed leg, and internal rotation of perturbed and unperturbed hip. A: trial mean rotations following knee perturbation. B: partial R² relating trial averaged force to averaged joint rotation velocity and a constant. C: “viscous” coefficient relating trial averaged perturbation force (cf., Figs. 3 and 4) to averaged joint rotation velocity. D: “stiffness” coefficient relating trial averaged perturbation force to averaged joint rotation.

Perturbed Standing Was Representative of Normal Standing

For each trial, the EMG level preceding each of the 30 knee pulls was tested, and no difference was found for any muscle (Kruskal-Wallis, P > 0.78). Thus the state of postural muscle activity was consistent throughout perturbation trials.

There was no consistent difference between EMG in normal standing and the mean EMG in the perturbation trials recorded in the 1 s preceding each perturbation. Seven of the ten muscles studied showed no difference (Kruskal-Wallis, right vastus lateralis P = 0.083, the other six muscles were all P > 0.23). The three muscles that showed a slight difference were inconsistent in direction. While muscle activity was slightly higher in the unperturbed standing trials for right tibialis anterior and biceps femoris (difference of 0.74 ± 2.48 μV, P < 0.05, and 3.80 ± 2.37 μV, P < 0.001, respectively), left vastus lateralis showed slightly higher activity when the band was strapped around the knees (difference of 0.60 ± 0.26 μV, P < 0.05). Thus EMG levels were not elevated on account of the perturbation procedure.

The Contribution of Passive and Involuntary Reflex Mechanisms

For the two groups (straight and flexing knee), the level of muscular activity in the involuntary period (up to 200 ms) after the perturbation is reported in Fig. 7. The participants who maintained a straight leg during knee pulls (straight knee) did so without any involuntary change in muscle activity during the first 200 ms (n = 10, P > 0.05 for each muscle). For the participants who allowed the knee to flex (flexing knee), tibialis anterior in the unperturbed leg was the only muscle that showed increased activity after 150 ms from the perturbation (P < 0.05). For all of the other muscles, all of the participants showed no change in muscle activity in the first 200 ms (n = 10, P > 0.05 for each muscle in flexing knee group and for every muscle in the straight knee group). Thus preset triggered responses to these gentle pulls are discounted, and intrinsic joint stiffness, i.e., resistance unassociated with changes in muscle activity, accounts for the “stiff” leg, at least for the first 200 ms.

0.01) (Fig. 6D). To summarize, in response to knee perturbation, the straight knee group maintained high ankle stiffness, preserving CoM position and a straight leg configuration. On the contrary, the flexing knee group allowed the perturbed leg to flex, the pelvis to rotate internally on the unperturbed hip, and the CoM to move forward in accordance with the size and duration of the perturbation, allowing joint rotation to cease when the perturbation stopped.
Fig. 7. Average muscular activity in relation to the perturbation onset. Rows show the mean muscle activity recorded during the following intervals: 50 ms before the perturbation; 1–50 ms, 51–100 ms, 101–150 ms, and 151–200 ms after perturbation onset. All of the perturbations within one trial were grouped into perturbed and unperturbed leg and averaged. The two groups, knee kept straight (straight knee) and knee allowed to flex (flexing knee), are presented separately. Mean and SD values are shown for following muscles: gastrocnemius (A), TA (B), VL (C), BF (D), and RF (E).

Inconsistent small differences in activity in three muscles indicate that standing in the perturbation trials was less rather than more active than normal unperturbed standing. If these differences represent anything other than drift in the background noise of low-activity muscles, then perhaps knee movement caused by the mechanical pulls allowed the participants to relax their muscles from a slightly stiffer “normal” standing. If so, the perturbation procedure underestimated rather than overestimated the system stiffness relative to normal standing. Therefore, we predict that these results reflect normal control of standing and would be replicated in other experimental settings.

From the present experiment, the following results were established clearly and unambiguously.

1) In response to gentle knee perturbation, the majority of participants (22) maintained a “straight leg configuration” with minimal knee flexion, (0.4 ± 0.3°), minimal ankle flexion (0.3 ± 0.3°), and small internal rotation of unperturbed hip (0.6 ± 0.7°) (Figs. 4–6).

2) A small number of participants (2) allowed the perturbed knee to flex passively with large flexion at the knee (3.0 ± 1.4°) and ankle (1.8 ± 0.5°), moderate internal rotation of the unperturbed hip (1.1 ± 0.4°), and a “viscous damping” relationship between perturbation force and ankle, knee, perturbed hip, and unperturbed hip rotation (Figs. 4–6).

3) There was no significant difference in muscle activity levels between unperturbed and perturbed standing or between successive perturbations in perturbed standing.

4) There was no correlation between the extent of unperturbed standing sway and the size of knee flexion in response to knee perturbation (Fig. 5D).

5) The knee flexion response was not related to asymmetric weight bearing (Fig. 5C).

On the basis of these results, the following questions are discussed. 1) Is the knee locked in normal standing? 2) Are leg joints mobilized collectively or differentially according to functional relevance? 3) Is the control strategy configuration conserving or energy absorbing? 4) Is leg stiffness maintained by passive mechanisms or active, delayed feedback? 5) What is the functional relevance of the findings of the study?

Is The Knee Locked in Normal Standing?

The knee has hardly been studied in standing because its movement and its regulation have been thought to contribute very little to the control of the CoM position in standing (2, 26, 31, 33) and because the knee is assumed to be locked in standing (17).

The locking mechanism of the knee is a consequence of the anatomy of the joint and its movement, consisting of a combination of extension and internal rotation of the femur on the tibia (17). The range near close packing is functionally important in quiet symmetric standing because, according to how far forward relative to the knee the line of gravity falls (17), the joint can be more or less close packed. The locking mechanism of the knee is understood to promote economical passive stabilization of the knee joint in human standing (17, 35). However, knee locking may be enhanced by active internal rotation of the femur relative to the pelvis and tibia caused by the muscles crossing the knee and hip joint (adductor magnus and longus, biceps femoris, semimembranosus and semitendinosus). In this case, the hip might also be more locked.

Stability in standing is possible without knee hyperextension and locking (21, 40). In fact, the cartilage compression, the menisci action, and the tibial plates shape stabilize the knee joint (35), and standing is also possible without muscle activity (25). Furthermore, knee motion in standing was shown in several experiments (5, 16, 22, 33, 42). This literature argues against the concept that the knee is necessarily locked to ensure stability and efficiency. However, the minimal motion usually
identified at the knee has been related to a high knee stiffness (15), or could be compatible with accurate control of position without requiring joint locking by coactivation or intrinsic stiffness mechanisms (31). In the present paper, when the knee was perturbed, even though the whole body was pulled forward, for most participants the knee was hardly flexed at all (Fig. 5A), and this broadly confirms the accepted modeling and anatomical assumptions of close packing mechanism in normal standing (17, 35). However, in seven trials, two participants showed an instantaneous knee flexion, which is consistent with the experiments that found knee motion in standing (10, 12, 21). Because popliteus contraction is required to unlock the knee (17), a delay in the knee flexion recordings would be measured due to the onset of this activation (11); this was not observed for these seven trials, which indicates no knee locking. This shows that alternative mechanisms need to be considered, and standing is possible with low leg stiffness, without locking the knee.

Are Leg Joints Mobilized Collectively or Differentially According to Functional Relevance?

Our results support the idea of bilateral, multijoint mobilization or stiffening. Participants who allowed knee flexion showed simultaneous ankle flexion and internal rotation of the contralateral hip (Fig. 6). While the former is almost inevitable, the latter is not. Many leg muscles are biarticular; thus excess activation requires compensatory coactivation crossing multiple joints. Hence, selective mobilization or stiffening would be difficult (29). Our results do not provide additional support for the hypothesis of selective mobilization of degrees of freedom, which are irrelevant to the main controlled variable (21, 40, 41), in this case presumably the CoM position. Selective, differentiated control is probably best facilitated by strategies that minimize activation.

Is the Control Strategy Configuration Conserving or Energy Absorbing?

By fitting a regression model between the perturbation force and joint angle responses, the behaviors were classified as springlike or dampinglike, by a linear relationship between force and angle, or force and angular velocity, respectively. If the relationship were springlike, the control strategy for the whole leg would be configuration-conserving, the leg would remain relatively straight, and the whole body will move approximating a single stiff segment. If the relationship were dampinglike, the control strategy for the whole leg would allow the joints to rotate, absorbing the perturbation energy in a viscous manner.

The two groups of trials were robustly identified by clear differences in the mechanisms responsible to react to the perturbation (Figs. 4–6). The two behaviors were clearly discriminated by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did not flex were characterized by an order of magnitude higher response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6). Stiffness implies that joint position not flex were characterized by an order of magnitude higher response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1). Trials in which the knee did discriminate by the “viscous damping” vs. “stiffness” response strategies (Fig. 6, Table 1).

Unlike the stiffness control strategy, in which the mechanical energy of the perturbation is returned, the positive damping coefficient reveals that the mechanical energy of the perturbation is absorbed into the system. The group that did not allow the knee to flex showed negative damping coefficients; paradoxically, these participants extended their knees in response to the perturbation. By inference, they were defending their configuration strongly and actively in opposition to the perturbation.

Is Leg Configuration Maintained by Passive Mechanisms or Active, Delayed Feedback?

For the perturbed leg, no significant, systematic change in muscular activity was observed in the first 200 ms after the perturbations (Fig. 7). The lack of change in the observed muscle activity indicates that the observed movements were initially passive. For the fixed leg group, the knee may be locked by purely passive hyperextension, but tonic active rotation or muscular coactivation may have been involved in keeping the knee locked. For the knee flexion group, the absence of change in muscle activity for at least 200 ms accompanied by the knee flexion are indicative of a passive biomechanical response initially.

Since perturbation duration lasted up to 2 s, well into the voluntary period of responses, the later response from both groups must have been voluntarily sanctioned (Figs. 3 and 4). Within the fixed leg group, the negative damping coefficients (Fig. 6) imply that they moved their knees backwards in response to the forward pull. Because involuntary responses up to 200 ms were excluded, on account of the unchanging EMG signals, this knee retraction most likely reflects a preprogrammed voluntary action to oppose the perturbation. This represents a functional immobilization of knee joint degrees of freedom.

What is the Relevance of the Findings of the Study?

During pilot tests, we applied the perturbation to both knees simultaneously. The same basic result was observed in that some participants responded in an inverted pendulum-like manner, as if they had no knee joint, and some participants allowed flexion of the knee.

An important result is the observed range of viable leg control strategies in normal standing. A consequence of redundancy in kinematic and control strategies is that individual variation is highly likely. Normally exploitation of degrees of freedom increases with development and skill acquisition to provide flexibility, reliability, and robustness of control (23). Bernstein (6) was among the firsts to study joint immobilization when learning a new task, such as playing a musical instrument, and showed that, as individuals progressively learn, they release the joint immobilization that is typical of the first lessons. Bernstein found the initial joint immobilization unnecessary and detrimental for the more skilled control of the movement. By comparison of the groups, our results showed a most common association of relatively high stiffness, reduced damping, delayed knee flexion, and reduced body sway in response to perturbation (Figs. 4 and 5A). Since it reflects common behavior, the result may be considered unsurprising. However, we suggest the common behavior requires explanation. The leg joints confer functional advantages in allowing...
more possibilities of adjustment. This adds robustness to control of balance. Why should the joints be effectively immobilized when their mobility is not threatening to balance? This stiffening strategy implies cost without functional benefit. This strategy might protect unnecessarily against small perturbations; however, the associated cognitive (i.e., attention shift) and biomechanical delays required to change control strategy to mobilize the legs when needed is a motor detriment, not an asset. This increases rather than decreases the risk of falling. Possibly the explanation lies in the tendency of the motor system to incorporate control choices informed culturally through learning and development and to use automatized solutions, even when they are not wholly appropriate.

Reduced utilization of degrees of freedom can be a symptom of declining ability through age, disease (37, 38), fear, or unfamiliarity (1). Age-related changes in joint coordination reduce flexibility of balance (20). A reduction in degrees of freedom resulting from joint immobilization is a common defense mechanism during fear. Paradoxically, this behavior increases the risk of a fall (7).

Our results leave open the question why the majority of participants controlled standing using a stiff leg configuration during the perturbed standing task. The reader may conclude this result reflects the unfamiliarity of the task. However, the method used was sensitive to this possibility and was implemented to reveal normal standing control. We suggest our results reflect normal postural control and that the method is diagnostic of individual variation, and we invite other laboratories to replicate the experiment. In our opinion, psychological-perceptual state, efficiency of movement, and efficiency of manual control are all related to the underlying, general control of configuration (posture). Thus individual characterization of general control-coordination strategy is predicted to have diagnostic value. Further research is needed to resolve the developmental, disease, age, and cognitive-perceptual dimensions to individual variations in postural and movement control and the possibilities of adaptation.

Conclusions

In this experiment, gentle, unpredictable, mechanical perturbations were applied to the knee joint during normal standing to reveal whether the leg control strategy mobilizes the joint degrees of freedom. Two response patterns were identified for difference analysis. The majority showed small knee flexion and body sway when perturbed, while two participants showed larger knee flexion, larger body sway, and a viscous damping relationship between perturbation force and leg flexion. Both groups showed similar CoM sway in unperturbed standing. Different strategies to maintain standing are, therefore, possible. Quiet standing is possible with bilateral, low-leg stiffness and absorption of energy from external perturbations, although more commonly the joint configuration is immobilized and associated with relatively rigid legs. Regarding mobilization of joints as an indicator, the majority illustrated postural control that may be less developed or more declined than what is possible. Identification of individual coordination strategy has diagnostic potential for functional implications, including posture-movement-fall interactions.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: I.D.G. and I.D.L. conception and design of research; I.D.G. performed experiments; I.D.G. and I.D.L. analyzed data; I.D.G. and I.D.L. interpreted results of experiments; I.D.G. prepared figures; I.D.G. drafted manuscript; I.D.G., V.B., C.N.M., and I.D.L. edited and revised manuscript; I.D.G., V.B., C.N.M., and I.D.L. approved final version of manuscript.

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