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Importance of Body Sway Velocity Information in Controlling Ankle Extensor Activities During Quiet Stance

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Masani, Kei, Milos R. Popovic, Kimitaka Nakazawa, Motoki Kouzaki, and Daichi Nozaki. Importance of body sway velocity information in controlling ankle extensor activities during quiet stance. *J Neurophysiol* 90: 3774–3782, 2003. First published August 27, 2003; 10.1152/jn.00730.2002. In literature, it has been suggested that the CNS anticipates spontaneous change in body position during quiet stance and continuously modulates ankle extensor muscle activity to compensate for the change. The purpose of this study was to investigate whether velocity feedback contributes by modulating ankle extensor activities in an anticipatory fashion, facilitating effective control of quiet stance. Both theoretical analysis and experiments were carried out to investigate to what extent velocity feedback contributes to controlling quiet stance. The experiments were carried out with 16 healthy subjects who were asked to stand quietly with their eyes open or closed. During the experiments, the center of pressure (COP) displacement (COPdis), the center of mass (COM) displacement (COMdis), and COM velocity (COMvel) in the anteroposterior direction were measured. Rectified electromyograms (EMGs) were used to measure muscle activity in the right soleus muscle, the medial gastrocnemius muscle, and the lateral gastrocnemius muscle. The simulations were performed using an inverted pendulum model that described the anteroposterior kinematics and dynamics of quiet stance. In the simulations, an assumption was made that the COMdis of the body would be regulated using a proportional-derivative (PD) controller. Two different PD controllers were evaluated in these simulations: *1*) a controller with the high-derivative/velocity gain (HDG) and *2*) a controller with the low-derivative/velocity gain (LDG). Cross-correlation analysis was applied to investigate the relationships between time series obtained in experiments *1*) COMdis and EMGs and *2*) COMvel and EMGs. Identical cross-correlation analysis was applied to investigate the relationships between time series obtained in simulations *3*) COMdis and ankle torque and *4*) COMvel and ankle torque. The results of these analyses showed that the COMdis was positively correlated with all three EMGs and that the EMGs temporally preceded the COMdis. These findings agree with the previously published studies in which it was shown that the lateral gastrocnemius muscle is actively modulated in anticipation of the body's COM position change. The COMvel and all three EMGs were also correlated and the cross-correlation function (CCF) had two peaks: one that was positive and another that was negative. The positive peaks were statistically significant, unlike the negative ones; they were larger than the negative peaks; and their time shifts were much shorter compared with the time shifts of the negative peaks. When these results were compared with the CCF results obtained for simulated time series, it was discovered that the cross-correlation results for the HDG controller closely matched cross-correlation results for the experimental time series. On the other hand, the simulation result obtained for LDG controller did not match the experimental results. These findings suggest that the actual postural control system during quiet stance adopts a control strategy that relies notably on velocity information and that such a controller can modulate muscle activity in anticipatory manner without using a feedforward mechanism.

INTRODUCTION

Human bipedal stance is inherently unstable because a large body mass is kept in erect posture with its center of mass (COM) located high above a relatively small base of support. The mechanism responsible for equilibrium control of quiet stance has attracted the attention of many researchers in the field. However, the nature of the control mechanism is still an object of controversy.

One approach that has proved useful for investigating human equilibrium control is the analysis of the responses of a quietly standing body to various perturbations, such as perturbations to the proprioceptive subsystem (Fitzpatrick et al.1992a,b, 1996; Gurfinkel et al. 1995; Horak and Nashner 1986; Nashner 1976, 1977; Woollacott et al. 1988), perturbations to the visual subsystem (Dijkstra et al. 1994a,b; Peterka and Benolken 1995; Schöner 1991), and perturbations to the vestibular subsystem (Day et al. 1997; Fitzpatrick et al. 1996; Johansson et al. 1995; Pavlik et al. 1999). These studies have played a significant role in elucidating the contribution made by different subsystems to overall equilibrium control (Dietz 1992; Horak and Macpherson 1996).

Another approach to investigating human equilibrium control is to analyze spontaneous body sway: trajectory of the center of pressure (COP) (Collins and DeLuca 1993, 1994, 1995; Day et al. 1993; Gatev et al. 1999; Lacour et al. 1997; Mauritz and Dietz 1980; Panzer et al. 1995), trajectory of the COM (Gatev et al. 1999; Panzer et al. 1995; Winter et al. 1998, 2001), trajectory of the ankle joint angle (Fitzpatrick et al. 1994a,b), and trajectory of other body

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points (Accornero et al. 1997; Aramaki et al. 2001). These studies investigated the quantitative and qualitative properties of the spontaneous body sway by comparing the system's behavior under different physiological conditions, such as aging (Accornero et al. 1997; Panzer et al. 1995), disruption or alteration of proprioception feedback (Fitzpatrick et al. 1994b; Mauritz and Dietz 1980), disruption or obstruction of vision feedback (Accornero et al. 1997; Collins and DeLuca 1995; Fitzpatrick et al. 1994b), loss or alteration of vestibular sense (Lacour et al. 1997), and varying stance width (Day et al. 1993; Winter et al. 1998).

A group of investigators who adopted the latter approach, Gatev et al. (1999) recently reported significant correlation between spontaneous body sway [COM displacement (COMdis) as a representative parameter of body sway] and the activity of the lateral gastrocnemius muscle (LG). They also discovered that the LG activity temporally preceded COMdis. This result could not be interpreted as a linear response of the LG to the positional change of the body. Instead, Gatev et al. (1999) proposed that the CNS applies feed-forward control, which anticipates the body position change and activates the LG in advance to regulate balance during quiet stance, rather than a feedback control. Other experimental (Fitzpatrick et al. 1996) and theoretical (Morasso and Schieppati 1999) studies have also proposed feed-forward control as compensation for the inevitable transmission delay in the neural process, which is adequate to destabilize quiet stance. However, one difficulty with the feed-forward hypothesis is: how does the CNS predict body position?

Over the last 10 years, a number of independent studies have reported that certain postural reactions were adapted according to velocity information (Dijkstra et al. 1994b; Jeka et al. 1998; Schöner 1991). The importance of velocity information in controlling balance during quiet stance was also suggested in simulations carried out by Morasso and Schieppatti in 1999. Velocity feedback can play a significant role in anticipating body position change because it carries information about the subsequent state of the body, i.e., a change in COM velocity (COMvel) indicates the direction and intensity with which the current COMdis will be changed in the following time instant. In general, the velocity feedback in addition to the position feedback, called the proportional + derivative (PD) control, can potentially predict the future condition of the system and can stabilize it more effectively than only a position/proportional controller. Several simulation studies, which applied a single joint inverted pendulum model to simulate human quiet stance, revealed that the PD controller can facilitate stable control of the proposed model (Morasso and Schieppatti 1999). However, there is no experimental study without perturbations that investigates the contribution of velocity information in controlling the body during quiet stance, and the structure of the PD controller, i.e., the ratio of position and velocity information, remains unclear.

The purpose of this study was to investigate whether a velocity feedback mechanism makes a significant contribution in an anticipatory modulation of ankle extensor activities during quiet stance. Therefore theoretical and experimental studies were carried out to test this hypothesis.

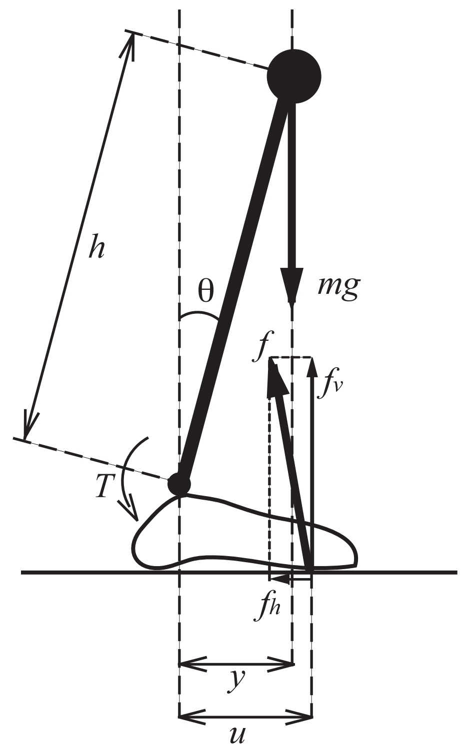

FIG. 1. An inverted pendulum model of quiet stance, where y is the center of mass (COM) position, u is the center of pressure (COP) position, f is the ground reaction force divided with f_h and f_v components, θ is the sway angle, g is the acceleration of gravity, T is the total muscle torque about the ankle, and h is the distance of COM from ankle.

DYNAMICS OF QUIET STANCE

The ankle joint torque needed to stabilize the body during quiet stance can be generated actively and passively.

Passive torque components are the result of tension/stiffness produced by muscle tonus and by the stiffness of the surrounding tissue, such as ligaments and tendons. However, the stabilization of quiet stance by passive torque alone is a very challenging task, and an active component is required to maintain stability (Morasso and Schieppati 1999). The active torque component is produced by the CNS, which modulates/controls muscle contractions based on the overall body kinematics and dynamics of spontaneous body sway that are influenced by external disturbances (Morasso and Schieppati 1999; Winter 1990; Winter et al. 1996). The fact that LG activity was modulated in accordance with COMdis in the study by Gatev et al. (1999) suggests that this active mechanism is operating.

Herein, dynamics of quiet stance is discussed, as well as generation of the active torque component. For the purpose of this analysis, the human body was approximated as a single segment, single joint inverted pendulum (Fig. 1) that rotates about the ankle joint (Morasso and Schieppati 1999; Peterka and Benolken 1995; Winter et al. 1998). The dynamic equation of the inverted pendulum model is

$$I\ddot{\theta} = mgh \sin \theta + T + \epsilon \qquad (1)$$

where θ is the sway angle, $\ddot{\theta}$ is the sway acceleration, m is the mass of the body, I is the moment of inertia of the body (excluding feet), h is the distance of COM from the ankle, g is the gravitational acceleration, T is the total ankle torque, and ϵ is the torque disturbance, which is sufficiently small compared with other torque contributions. Notably, ankle torque dominates body movement in this equation. Because COM is located in front of the ankle joint, backward ankle torque is continuously applied to the body to prevent it from falling forward (Smith 1957). Because ankle flexor activities are rare and ankle extensors are considerably activated (Gatev et al. 1999; Joseph and Nightingale 1952; Loram and Lakie 2002; Panzer et al. 1995), it can be said that ankle extensors contribute the most toward control of the ankle joint torque and therefore the body posture during quiet stance.

The ankle torque should satisfy the following equation concerning to the foot segment

$$T + f_v u \approx 0 \tag{2}$$

where f_v is the vertical component of ground reaction force and u is COP position (COPdis). If we take into account that $f_v \approx mg$ in quiet stance, this equation shows that changes in ankle torque are immediately and linearly translated into changes of COP position. From *Eqs. 1* and *2* one can derive

$$u \approx y - \frac{I}{mg}\ddot{\theta} \tag{3}$$

where y is the COM position. The COP position and COM position must coincide ($u = y$) under the static equilibrium condition (the inertial term = 0). However, due to excess ankle torque, the COP frequently departs from this instant equilibrium point (Zatsiorsky and Duarte 2000) ($u \neq y$) and the excess ankle torque generates COM acceleration ($\ddot{\theta} \neq 0$). Thus reduction of excess ankle torque to facilitate alignment of the COP position and the COM projection on the standing surface represents the active mechanism for controlling quiet stance.

The high correlation between COPdis and muscle activity (Gatev et al. 1999; Schieppati et al. 1994) can be accounted for by *Eq. 2*, which shows a direct relationship between COPdis and the torque generated by muscles. On the other hand, the high correlation between COMdis and LG (Gatev et al. 1999) suggests that the ankle torque generated by ankle extensors are almost equal to the gravity torque of the body ($mgh \sin\theta \approx T$, in *Eq. 1*), and that the active mechanism stabilizes the body well.

METHODS

To investigate the impact of velocity information on balance control during quiet stance, the following approach was adopted. At first, we obtained kinematic parameters, such as COPdis, COMdis, and COMvel, in the anterioposterior direction and individual EMGs of the ankle extensors during quiet stance. Cross-correlation analysis was applied to investigate the relationship between kinematic parameters and rectified EMGs. We then conducted a theoretical analysis of quiet stance with an inverted pendulum model. In this study, an assumption was made that the COMdis of the pendulum is regulated using a PD controller. Two PD controllers were evaluated in these simulations: *1*) a controller with the high-derivative/velocity gain (HDG) and *2*) a controller with very low-derivative/velocity gain (LDG). We also obtained the relationship between the kinematic parameters of the inverted pendulum and ankle torque using the cross-correlation analysis. Finally, cross-correlation results of both studies were compared with examination of the hypothesis that the velocity information contributed significantly to the control of quiet standing.

Experiments

Sixteen healthy men (mean ± SD age, 23.8 ± 3.9 yr; mean ± SD height, 169 ± 6.6 cm) participated in this study. All subjects gave informed consent, which was approved by the ethical committee of our research institute.

Each subject was requested to keep a quiet stance posture standing barefoot on a force platform (type 9281B, Kistler, Zürich, Switzerland) with their eyes open (EO condition) or closed (EC condition). The subjects had their arms hanging along the sides of their body, their feet were parallel, and the distance between their heels was 15 cm. The duration of each trial was approximately 40 s, and data from the latter 30 s were subjected to the subsequent analyses. Five trials were conducted for each condition, and sufficient resting time was allowed between trials. In this paper, we have only focused on the anteroposterior body sway, because the ankle extensor muscles are the main contributors to stabilizing body sway in this direction.

The COPdis was obtained using a force platform measurement. The horizontal position of the waist point was measured as an approximation of the COMdis using a CCD (charge coupled device) laser displacement sensor (1 μm resolution; LK-2500, Keyence, Osaka, Japan). This parameter was used to represent body sway. The COMvel was calculated by numerically differentiating the COMdis as a function of time. Electromyograms (EMGs) were recorded by Ag/AgCl surface electrodes with a diameter of 5 mm, which were connected to a preamplifier and a differential amplifier having a bandwidth of 5 Hz to 1 kHz (1253A, NEC Medical Systems, Tokyo, Japan). After careful abrasion of the skin, the electrodes were placed longitudinally over the right soleus muscle (SOL), medial gastrocnemius muscle (MG), LG, and tibialis anterior muscle, with an interelectrode distance of 20 mm. A 16-bit A/D converter with 1-kHz sampling frequency was used to measure the above data. The measured data were stored on a personal computer.

Measured EMGs were numerically rectified. Both rectified EMGs and the kinematic data were low-pass filtered using the fourth-ordered, zero-phase-lag Butterworth filter (Winter 1990). Since this study mainly addressed the concordance of low-frequency body movements (a major part of the signal was in the frequency range below 1 Hz (Fitzpatrick et al. 1992b; Gurfinkel 1973; Masani et al. 2001), the cutoff frequency of the Butterworth filter was set to 4 Hz. The rectified and smoothed EMGs were considered to represent the level of muscle activity during quiet stance. Since the activity of the tibialis anterior muscle during the experiments was marginal, a decision was made not to consider it further in our analysis. These filtered time series were used in the following cross-correlation analysis.

Theoretical analysis

Figure 2 shows the closed-loop controller and the plant/body regulated by the PD controller adapted from Peterka (2000). The body dynamics and kinematics during quiet stance were described using an inverted pendulum model with parameters set to values of the typical adult male (m = 76 kg, I = 66 kgm^2, and h = 0.87 m; as shown in Fig. 1). The input to the body model was the torque exerted about the ankle joint, which consisted of two components. One was due to a random disturbance torque (Td) that generated body sway patterns similar to those observed experimentally, and the other one was due to the command torque (Tc) generated by the CNS in response to body motion and disturbances. The "sensory" time delay (τ_1 = 0.05 s), which represents cumulative time loss due to neural transmission from the ankle proprioceptors to the CNS and the sensory information processing by the CNS, was introduced. The "command" time delay (τ_2 = 0.05 s), which represents cumulative time loss due to the CNS decision-making process and the neural transmission from the CNS to the ankle extensors, was introduced. The simulations were performed using Simulink software (MathWorks). A Gaussian noise time series with zero mean and unit variance was used to model Td. This noise

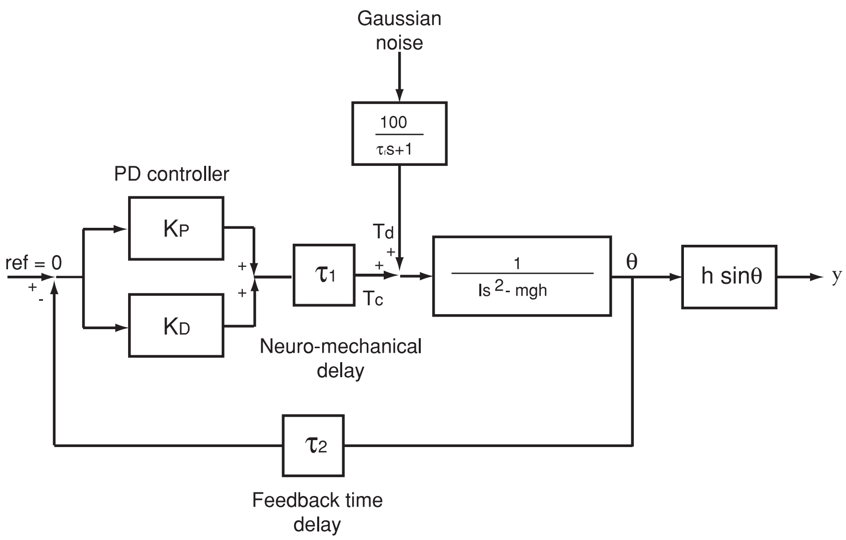

FIG. 2. Close-loop control scheme of quiet stance used in the theoretical analysis.

was first-order, low-pass filtered with a time constant of $\tau_f = 1$ s, which produced waveforms with sway characteristics similar to those seen in experiments. The system's dynamics was typically simulated no longer than 40 s and the sampling frequency was 100 Hz.

As discussed above, a PD controller that used COMdis and COMvel as feedback variables was applied in simulations. The PD controller was defined with proportional and derivative gain factors, K_P and K_D, respectively. The command torque was then calculated according to the following equation

$$Tc = -K_P\theta - K_D\dot{\theta} \tag{4}$$

In our simulations, two PD controllers were considered. One was the LDG controller, and the other one was the HDG controller. In the LDG case, K_P was arbitrarily set to $20N \cdot m \cdot \text{deg}^{-1}$ and K_D was set to $4N \cdot m \cdot \text{deg}^{-1}$, where ratio K_D/K_P was 0.2. In the HDG case, K_P was set to $20N \cdot m \cdot \text{deg}^{-1}$, the same as in the LDG case and the K_D was set to $10N \cdot m \cdot \text{deg}^{-1}$, where ratio K_D/K_P was 0.5. It should be noted that the pure proportional controller ($K_D = 0$ or $K_D \ll K_P$) applied to the inverted pendulum system was found to be unstable.

Before the simulations with the proposed model were carried out, a Nyquist analysis was performed to demonstrate that both the LDG and HDG controllers generated stable behavior of the given system and that they were both able to compensate for Td disturbances despite time delays τ_1 and τ_2. Following that, 50 simulations were carried out for each of the proposed controllers. The cross-correlation analysis was applied to the simulation outputs as discussed in the following text.

Cross-correlation analysis

Cross-correlation was applied to the following time series: *1*) COPdis and each EMG, *2*) COMdis and each EMG, *3*) COMvel and each EMG, *4*) COMdis and Tc, and 5) COMvel and Tc. Please note that an assumption was made that the measured EMG signals in experiments and the Tc obtained in simulations represent the control command of the CNS in response to system's perturbations.

To evaluate the cross-correlation and time shift between two time series x and y that had zero means, the CCF ($R_{xy}(\tau)$) was applied. $R_{xy}(\tau)$ was defined as follows

$$R_{xy}(\tau) = \frac{\overline{x(t+\tau)y(t)}}{\sqrt{\overline{x^2}\,\overline{y^2}}} \tag{5}$$

where τ denotes the time lag of y with respect to x, and the overbar denotes an average over time t. Since the direct calculation of *Eq. 5* needs considerable time, the fast Fourier transform (FFT) was used instead (Bloomfield 2000). First, the cross-power spectral density between $x(t)$ and $y(t)$ was calculated using a 2^{13}-point FFT. The $\overline{x(t+\tau)y(t)}$ was then obtained by applying the inverse FFT to this cross-power spectral density function (Bloomfield 2000).

The following is the actual procedure that was applied to calculate the CCFs. The 30-s-long data sets were first divided into seven segments that were 2^{13} points long, i.e., 8.192 s long. Please note that

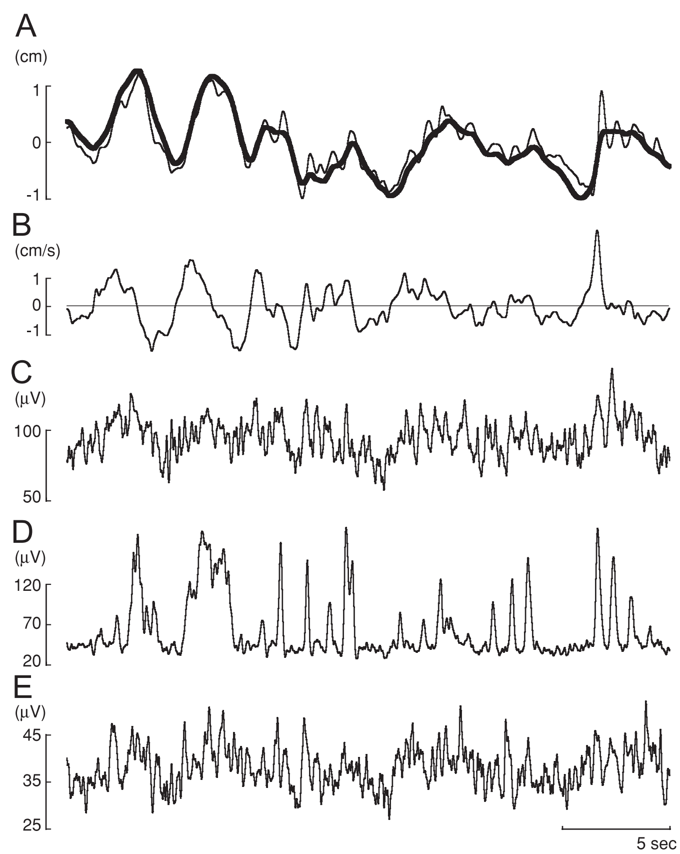

FIG. 3. Representative examples of time series for a single trial in one subject during EC condition: *A*: COP displacement (COPdis; thin line) and COM diplacement (COMdis; bold line); *B*: COM velocity (COMvel); *C*: soleus (SOL) electromyogram (EMG); *D*: medial gastrocnemius (MG) EMG; *E*: lateral gastrocnemius (LG) EMG.

almost half of the selected 8.192-s-long segments were overlapped with the adjacent segments. Then, 13-bit FFT algorithm was applied to these segments to generate segments' periodograms. Next, an ensemble-averaged CCF of these periodograms was calculated as a CCF for each trial. Therefore the cross-correlation coefficients were calculated for 8.192-s-long time segments, and the CCF time resolution was 0.002 s (Nyquist criterion for sampling period of 0.001 s). The value and time shift of the highest peaks of the ensemble-averaged CCF of five trials for each eye condition (EO and EC) were calculated for each subject individually. Later, the group mean value was obtained for each eye condition. For theoretical data, the group mean value of 50 simulations was obtained.

The peak value of CCF and the time shift were used as variables of interest in the Results and the Discussion. Fisher's *Z*-transform was applied to each peak CCF value to normalize the data for subsequent statistical analysis. However, the graphs presented in the document are provided in the original form, i.e., before the *Z*-transform was applied, for the reader's convenience. The significance of the group mean peak CCF value and the difference of the group mean time shift with respect to zero value were tested by *t*-test. $P < 0.05$ was used as a level of significance to prevent excessive false-positive results.

RESULTS

Cross-correlation analysis for position parameters and muscle activities

Figure 3 illustrates a typical time series of the COPdis, COMdis, and COMvel, and EMG time series for SOL, MG, and LG, for the EC condition. The slow component of COPdis coincides with COMdis, while the faster component of COPdis oscillates around the COMdis. Figure 4, *A* and *B* show the CCF between COPdis and EMGs and between COMdis and EMGs, respectively, for EC condition for the same subject as in Fig. 3. The horizontal broken line indicates the r value of ± 0.195 at which r is statistically different from zero ($P < 0.05$, $n = \infty$). There is a clear positive significant peak for each EMG, which-has a negative time shift in both figures. A positive correlation indicates that, as EMG increased (decreased), the COPdis and COMdis moved forward (backward). A negative time shift indicates that the position parameters (COPdis and COMdis) lagged behind the EMGs.

Figure 5 summarizes the peak values and time shifts of CCFs between position parameters and EMGs. Figure 5, *A* and *B* show peak values and time shifts of CCF between COPdis and EMGs, respectively. Figure 5, *C* and *D* show peak values and time shifts of CCF between COMdis and EMGs, respectively. All peak values were significant, and time shifts were significantly different from zero. These results indicate that changes of position parameters occurred with considerably long time shift, 0.147 to 0.198 s, after the corresponding muscle activities. In other words, forward displacements of COP and COM followed increasing muscle activity, and backward displacements of COP and COM followed decreasing muscle activity.

Cross-correlation analysis for COMvel and muscle activities

Figure 4*C* shows the CCF between COMvel and EMGs during the EC condition for the subject discussed in Fig. 3. There were two clear peaks for each EMG; one had a positive value and the other one had a negative value. The time shifts of the positive peaks were close to zero, while those of the negative peaks had larger negative values.

Figures 6*A* and 5*B* summarize the peak values and time shifts of CCFs between COMvel and EMGs, respectively. The group means of the positive peak correlations of *1*) MG for

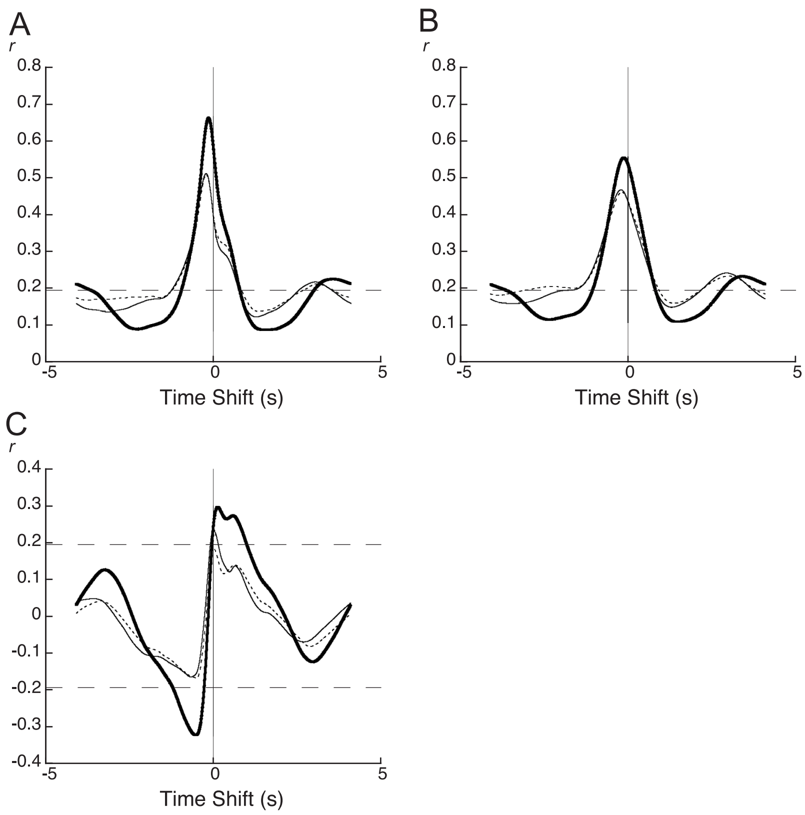

FIG. 4. Examples of the normalized cross-correlation function (CCF) ensemble averaged for 5 trials during eye closed (EC) condition for the same subject as shown in Fig. 3: *A*: CCF between COPdis and EMGs; *B*: CCF between COMdis and EMGs; *C*: CCF between COMvel and EMGs. In all 3 figures the thin line indicates CCF for SOL, the bold line indicates CCF for MG, and the dashed line indicates CCF for LG. The horizontal broken line indicates an r value of ± 0.195 at which r is different from zero ($P < 0.05$, $n = \infty$).

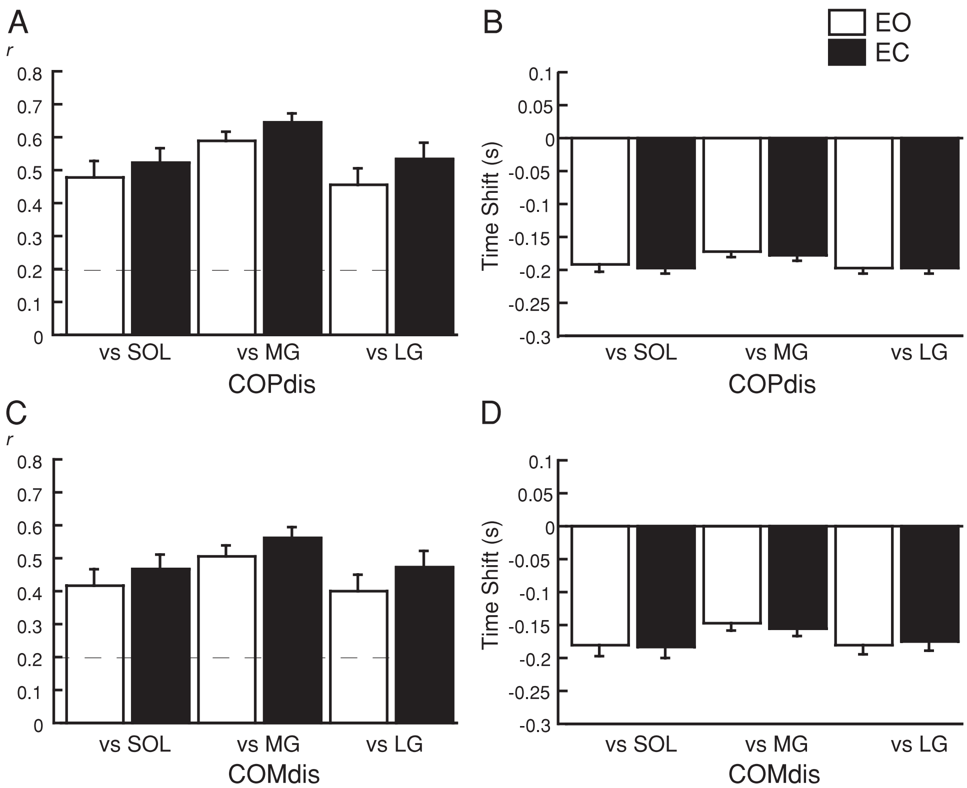

FIG. 5. Group means of the cross-correlation analysis between COP and COM measurements and EMGs: *A*: peak CCF values between the COPdis and EMGs; *B*: time shifts between the COPdis and EMGs at peak CCF values; *C*: peak CCF values between the COMdis and EMGs; and *D*: time shifts between the COMdis and EMGs at peak CCF values. For each graph, vs. SOL, vs.MG, and vs. LG indicate CCFs with muscle activity for the respective muscles. Open bar indicates CCF in eye open (EO) condition, and closed bar indicates CCF in EC condition. Data are group means ± SE (n = 16). The horizontal broken line indicates an r value of ±0.195 at which r is different from zero (P < 0.05, $n = \infty$).

both eye conditions, *2*) SOL for EC condition, and *3*) LG for EC condition were all significant. All group means of peak correlations for negative peaks were not significant. It is important to note that the positive peaks were significantly larger than the negative peaks for all muscles and for both eye conditions. In addition to this, we should note that the time shifts for positive peaks were much shorter than those for the negative peaks. Although all group means of time shifts for positive peaks were positive, only group means of time shifts of MG in both conditions were significantly different from zero. All group means of time shifts for negative peaks were significantly negative.

Cross-correlation analysis for simulation study

The typical simulated time series of Tc and COMdis in the case of HDG are shown in Fig. 7*A*. One can observe that the system was stabilized by this simple controller and that the obtained COMdis time series had similar properties compared with measured COMdis time series. The CCF between COMdis and Tc was also bell-shaped and appeared to be similar to the CCF between COMdis and EMGs. Peak values of CCF between COMdis and Tc were 0.938 and 0.994 for the HDG and LDG controllers, respectively.

Figure 7*B* shows the time shift of these CCFs. In the LDG case, the time shift was 0.059 s, which was much smaller than the actual measured value (from 0.147 to 0.198 s). However, in the HDG case, the time shift was 0.121 s, which was close to the actual measured values. Figure 7*C* shows peak values of CCF between COMvel and Tc, which had a two-peaks shape similar to the experimentally obtained data. In the LDG case, its positive and negative peaks had almost the same values. However, in the HDG case, the positive peak was larger than the negative peak, similar to the experimental results (see Fig. 6*A*). In addition, the time shift result of HDG was also similar

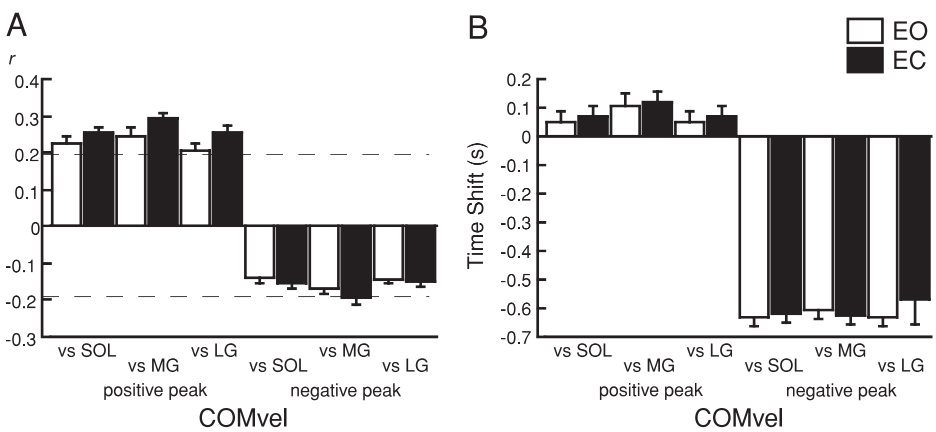

FIG. 6. Group means of the cross-correlation analysis between COMvel measurements and EMGs: *A*: peak CCF values between the COMvel and EMGs; *B*: time shifts between the COMvel and EMGs at peak CCF values. For CCF between COMvel and muscle activities, there were two peaks. One was a positive peak and the other was a negative peak. The graphs show these two peaks, respectively. For each graph, vs. SOL, vs. MG, and vs. LG indicate CCFs with muscle activity for the respective muscles. Open bar indicates CCF in EO condition, and closed bar indicates CCF in EC condition. Data are group means ± SE (n = 16). The horizontal broken line indicates an r value of ±0.195 at which r is different from zero ($P < 0.05$, $n = \infty$).

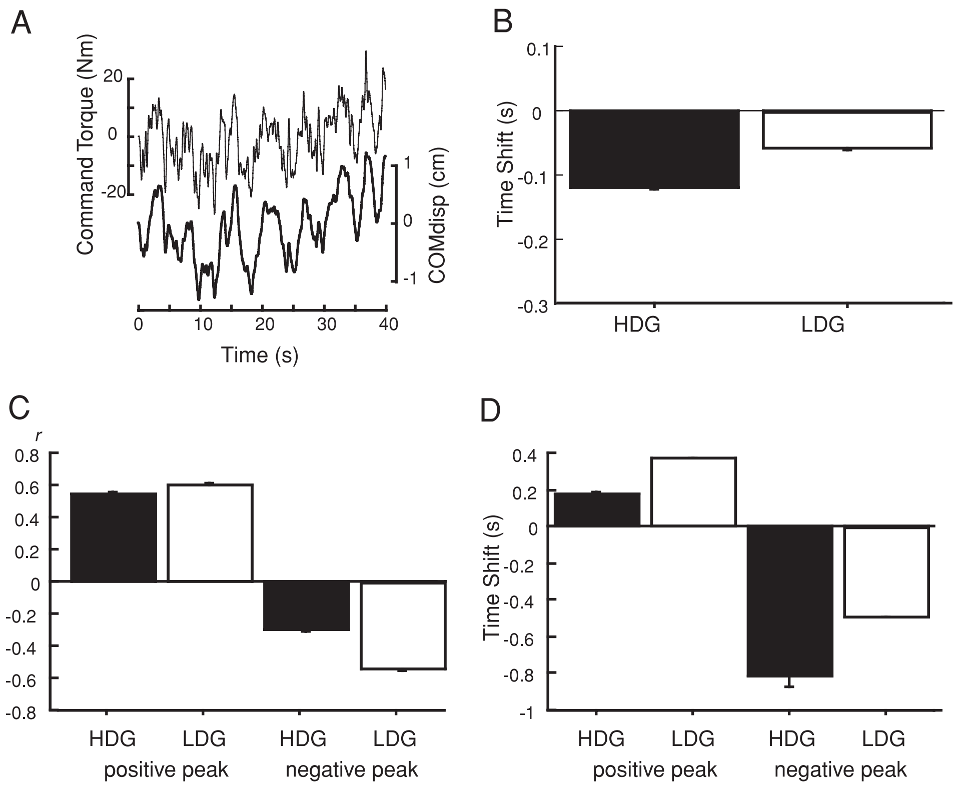

FIG. 7. Results of the numerical simulation experiment: *A*: representative examples of time series of the command torque from the controller (Tc) and the COMdis in the high-derivative gain (HDG) case; *B*: time shift at peak of the normalized CCF between COMdis and Tc; *C*: peak value of CCF between COMvel and Tc; and *D*: time shift at peak of CCF between COMvel and Tc. In *B–D*, the closed bar indicates CCF in the HDG case, and the open bar indicates CCF in the low-derivative gain (LDG) case. In *C* and *D*, the graphs are shown for the positive and the negative peaks, respectively.

to the experimentally obtained time shift results (see Fig. 6*B*). Figure 7*D* shows the time shifts of CCF between COMvel and Tc. In the LDG case, the time shifts of the positive and negative peaks were similar in value. However, in the HDG case, the time shift of the positive peak had a value similar to the one obtained in experiments, and the time shift of the negative peak was significantly larger compared with the positive peak.

DISCUSSION

Anticipatory modulation of muscle activities to COMdis

The ankle extensor activities were positively correlated with, and temporally preceded, both COPdis and COMdis. Since the finding regarding the COPdis can be accounted for by *Eq. 2*, only the findings pertaining to COMdis will be discussed.

The cross-correlations between COMdis and EMGs indicate that the body sway is closely related to muscle activities, meaning that the body sway reflects certain aspects of the active control mechanism of posture control (Morasso and Schieppati 1999). The time shift results indicate that the ankle extensors are controlled in anticipation of the change in the COMdis, which confirms findings reported by Gatev et al. (1999). Morasso and Schieppati (1999) in their theoretical analysis suggested the necessity of an anticipatory activity in the calf muscle with respect to COM position change to compensate for the neural transmission delay. Fitzpatrick et al. (1996) demonstrated experimentally that anticipatory action is necessary to counteract body position change. Our result and the results of Gatev et al. (1999) present additional evidence for these two findings. However, until now, the mechanism of how the CNS anticipates future COM position remained unclear.

Contribution of velocity information to controlling quiet stance

The numerical simulations carried out with a single joint inverted pendulum model, the balance of which was regulated with a PD controller, generated similar time shift results between COMdis and Tc as the time shift between COMdis and EMGs measured during quiet stance experiments. In particular, similar time shift results were obtained for the HDG type of controller. In the case of the LDG controller, the time shift was very different from the one observed in the experiments. This indicates that a feed-forward mechanism is not needed to regulate balance control and that the velocity provides sufficient information to anticipate the COM position change. In addition, the parameters of the CCF for COMvel and Tc time series obtained in simulations using the HDG controller were similar to the ones obtained during quiet standing experiments (Figs. 6, *A* and *B* and 7, *C* and *D*). The CCF between COMvel and EMGs showed that the positive peaks were larger than the negative ones and that the time shifts for positive peaks were much shorter compared with the negative ones. Similar CCF parameters were also achieved in simulation with the HDG controller, while the results obtained with the LDG controller substantially differed from the ones observed in experiments. These results indicate that the actual postural control system adopts a control strategy that relies notably on velocity information and that such a controller can modulate the muscle activity in an anticipatory manner similar to the one observed in quiet standing experiments. Furthermore, this finding shows that a feed-forward mechanism for controlling balance is not needed and that the CNS may be able to anticipate changes in COMdis if it is provided with sufficient velocity information.

Change in COMvel indicates the direction and intensity with which the current COM position will be changed in the next time instant. Thus the COMvel information is critical for anticipating how COM position will change and what corrective measures need to be taken by the CNS to compensate for these disturbances. Morasso and Schieppati (1999) suggested that the process in the CNS that integrates multisensory information to obtain position and velocity information of the COM (state vector) is needed to stabilize the body. In their computational simulation, the state vector was used as a feedback variable to control an inverted pendulum. Peterka (2000) also reported that a simple PID (proportional + integral + derivative) control, which uses the velocity information as a feedback variable, could stabilize an inverted pendulum and simulate the random walk property of the COP trajectory. These theoretical studies predicted that velocity information, in addition to position information, would contribute to the control of quiet stance. The results of this study present evidence that velocity information makes a crucial contribution to the control of quiet stance.

Because there is no sensory system that directly measures the COMvel, it is speculated that integrating multisensory information at the CNS (Horak and Macpherson 1996) could contribute to the velocity feedback mechanism. The strong coupling of visual information with body sway has been previously reported (Dijkstra et al. 1994a,b; Peterka and Benolken 1995; Schöner 1991). Although visual sensation is sensitive to the velocity of the visual stimulus (Dijkstra et al. 1994b; Schöner 1991), it would not be a main sensory source in the velocity feedback mechanism because it was equally observed in the EC condition. Proprioceptive sensation (Fitzpatrick and McCloskey 1994), as in group I (Griffin et al. 1990; Weiss and White 1986) and group II (Schieppati and Nardone 1997), is conceivable as a contributor to the velocity feedback mechanism because it plays a significant role in controlling quiet stance. Several studies reported the significant contribution of plantar cutaneous receptors in the control of quiet stance (Kavounoudias et al. 1998; Magnusson et al. 1990). Morasso and Schieppati (1999) pointed out the potential crucial role of these receptors in the estimation of state vector. These receptors are adequate to detect vertical and horizontal components of ground reaction force and COP position. This kinetic and kinematic information is important in calculating COM position and COMvel (Morasso and Schieppati 1999). Thus integrating this multisensory information, especially proprioceptive and plantar cutaneous sensations, would play a significant role in the velocity feedback mechanism. However, further investigation is needed to clarify the source and process of this mechanism.

In conclusion, we confirm the previously reported finding that activities of ankle extensors are actively modulated in anticipation of the body's position changes. By comparing the experimental results with the simulation results, we conclude that the actual postural control system during quiet stance adopts a control strategy that relies notably on velocity information and that such a controller can modulate muscle activity in an anticipatory manner without using a feed-forward mechanism.

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DISCLOSURES

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