



# The role of anticipatory postural adjustments in compensatory control of posture: 1. Electromyographic analysis

Marcio J. Santos<sup>a</sup>, Neeta Kanekar<sup>a</sup>, Alexander S. Aruin<sup>a,b,\*</sup>

<sup>a</sup> Department of Physical Therapy, University of Illinois at Chicago, IL 60612, United States

<sup>b</sup> Marianjoy Rehabilitation Hospital, Wheaton, IL, United States

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## ABSTRACT

Anticipatory (APAs) and compensatory (CPAs) postural adjustments are the two principal mechanisms that the central nervous system uses to maintain equilibrium while standing. We studied the role of APAs in compensatory postural adjustments. Eight subjects were exposed to external predictable and unpredictable perturbations induced at the shoulder level, while standing with eyes open and closed. Electrical activity of leg and trunk muscles was recorded and analyzed during four epochs representing the time duration typical for anticipatory and compensatory postural control. No anticipatory activity of the trunk and leg muscles was seen in the case of unpredictable perturbations; instead, significant compensatory activation of muscles was observed. When the perturbations were predictable, strong anticipatory activation was seen in all the muscles: such APAs were associated with significantly smaller compensatory activity of muscles and COP displacements after the perturbations.

The outcome of the study highlights the importance of APAs in control of posture and points out the existence of a relationship between the anticipatory and the compensatory components of postural control. It also suggests a possibility to enhance balance control by improving the APAs responses during external perturbations.

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## 1. Introduction

Humans frequently experience two major types of balance perturbations while standing or walking. Perturbations of a first type are induced internally as they are created by self-initiated movements involving the body segments such as fast arm or leg lifts or trunk bends. A second type of body perturbation is induced externally when, for example, an individual is standing on a moving bus, or when hit by another person while walking. Both types of postural perturbations create dynamic, inter-segmental forces that shift the body's center of mass (COM) closer to the boundaries of the base of support (BOS), thus endangering the body's stability. In order to preserve the equilibrium, the central nervous system (CNS) uses two types of alterations in the activity of trunk and leg muscles. The first type has been described in a groundbreaking work by Russian scientists Belen'kii, Gurfinkel, and Pal'tsev (Belen'kii et al., 1967) as anticipatory postural adjustments (APAs). APAs are associated with the activation or inhibition of trunk and leg muscles prior to the actual perturbation of balance; their role is to minimize the negative consequences of a predicted postural

perturbation (Bouisset and Zattara, 1987; Massion, 1992). The second type of adjustment in the activity of postural muscles deals with the actual perturbations of balance, and is termed as compensatory reactions (or compensatory postural adjustments – CPAs). CPAs in general cannot be predicted and are initiated by the sensory feedback signals (Alexandrov et al., 2005; Park et al., 2004). Accordingly there is a clear difference in the functions of APAs and CPAs: CPAs serve as a mechanism of restoration of the position of the COM after a perturbation has already occurred (Henry et al., 1998; Macpherson et al., 1989; Maki and McIlroy, 1996), while the function of APAs is to reduce the effect of the forthcoming body perturbations with anticipatory corrections (Aruin and Latash, 1995; Ito et al., 2004; Massion, 1992).

The individual roles of APAs and CPAs in control of posture were studied extensively. Consequently, it was demonstrated that the magnitude of APAs depends on the direction (Aruin and Latash, 1995; Santos and Aruin, 2008) and magnitude of a perturbation (Aruin and Latash, 1996; Bouisset et al., 2000), as well as body stability (Aruin et al., 1998; Nouillot et al., 1992, 2000). It was also shown that APAs are affected by the characteristics of a motor action used to induce a perturbation (Aruin et al., 2003; Aruin and Latash, 1995; Shiratori and Aruin, 2007), body configuration (Aruin, 2003; van der Fits et al., 1998), and fear of falling (Adkin et al., 2002). Previous literature reports that the CPA response depends on the direction and magnitude of the perturbation and

\* Corresponding author. Address: Department of Physical Therapy (MC 898), University of Illinois at Chicago, 1919 W. Taylor St. (4th floor), Chicago, IL 60612, United States. Tel.: +1 (312) 355 0904; fax: +1 (312) 996 4583.

E-mail address: [aruin@uic.edu](mailto:aruin@uic.edu) (A.S. Aruin).

on the dimensions of the base of support (Dimitrova et al., 2004; Henry et al., 1998; Horak and Nashner, 1986; Jones et al., 2008), predictability of perturbation characteristics (Burleigh and Horak, 1996), instructions (McIlroy and Maki, 1993), and involvement of a secondary task such as holding an object in the hands (Bateni et al., 2004). Moreover, distinct patterns of muscle activation called the ankle or hip strategy were described in the leg and trunk muscles in response to surface translations (Horak and Nashner, 1986).

One of the roles of APAs is to minimize the effects of a forthcoming perturbation (Massion, 1992); the presence of APAs does not rule out the existence of a CPA-based control of posture that involves on-line corrections (Bouisset and Zattara, 1987) and braking activities (Crenna et al., 1987; Friedli et al., 1984). However, it is not completely known how these CPAs interact with APAs to preserve body equilibrium. APAs could reduce the need for large CPAs resulting in better balance control. While such an association between the two components seems intuitive, it needs to be investigated further. This issue becomes all the more important since rehabilitation protocols extensively use perturbations such as throwing or catching a ball in treatment of patients (Duran et al., 2001) and athletes (Blievernicht et al., 2000; Cordasco et al., 1996), as well as in exercise activities of the elderly (Barnett et al., 2003).

Electromyographic (EMG) patterns in the trunk and leg muscles during the APA and CPA intervals were studied in experiments in which body perturbations were induced by voluntary movements and unexpected external perturbations, respectively (Gage et al., 2007; Hughey and Fung, 2005). Since body perturbations in these studies were triggered by either subjects' themselves or by the experimenter, it was difficult to control for the similarity of the magnitudes of disturbances applied to the body. Therefore, the observed differences in the EMG patterns during APAs and CPAs could be attributed to the differences between the two control processes, differences in the perturbation magnitudes, or a combination of both. For that reason, the primary goal of this study was to investigate further the respective contributions of the anticipatory and compensatory processes to postural control using perturbations of the same magnitudes applied at the shoulder level. An additional aim of this study was to examine the differences in the patterns of muscle activation between the anticipatory and compensatory periods of postural control. We hypothesized that anticipatory muscle activation will reduce compensatory muscle activity resulting in smaller COP displacements after the perturbation.

To test this hypothesis, we used an experimental paradigm in which consistent body perturbations were induced by a pendulum released by the experimenter. Throughout the experiments, the availability of information about the forthcoming perturbation was varied, as the subjects were standing with eyes open and with eyes closed while performing the same task of receiving the pendulum impact. Since APA magnitude depends on prediction of the timing and magnitude of a forthcoming perturbation, no APAs would be generated in conditions with eyes closed (when the subjects have no specific information about the timing of the pendulum impact). It is important to note here that utilization of the externally induced perturbation to study APAs is justified by the following. First, the outcome of previous studies that implemented a load catching paradigm revealed that APAs could be seen in conditions with no motor action being performed by the subjects themselves (Aruin et al., 2001; Shiratori and Latash, 2001). Second, it was demonstrated experimentally that when the subjects could see the falling load, APAs were observed with patterns that are adequate for counteracting expected perturbations (Aruin et al., 2001). Third, outcome of recent studies using the pendulum impact as a source of predictable perturbations demonstrated the existence of robust APAs when the timing and magnitude of the impact was known to the subjects (Santos and Aruin, 2008). Finally, the results of our pilot experiments confirmed that pendulum impact

induces CPAs. All these facts provide sufficient support for using the pendulum paradigm to elicit both APAs and CPAs. Thus, the paradigm allows applying the same magnitude of either predictable or unpredictable whole-body perturbation to human upright posture. As a result, the recorded EMG activity in the trunk and leg muscles could indeed be associated with respective contributions of the anticipatory and compensatory processes to postural control.

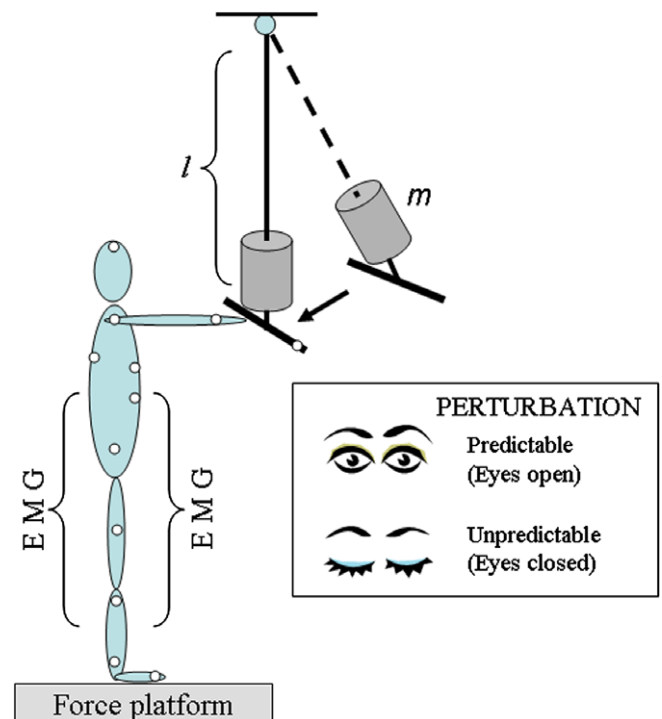
## 2. Methods

### 2.1. Subjects

Eight subjects (4 males and 4 females) without any known neurological or musculoskeletal disorders participated in the experiments. The mean age of the subjects was  $25 \pm 2$  years; mean body mass  $59.1 \pm 6.5$  kg, and mean height  $1.67 \pm 0.08$  m. They all signed a written informed consent approved by the Institutional Review Board of the University of Illinois at Chicago.

### 2.2. Procedure

The subjects were instructed to maintain upright stance while standing barefoot on the force platform with their feet shoulder width apart. They were positioned in front of an aluminum pendulum attached to the ceiling. A load (mass,  $m = 1.36$  kg) was attached to the pendulum next to its distal end and a rope fastened to the pendulum was passed through a pulley system attached to the ceiling (for more details see Santos and Aruin, 2008). Perturbations consisted of unidirectional forces applied to both the subjects' extended arms, using the pendulum that was pulled to a fixed distance away from the subjects' hands (0.8 m). All the trials of the pendulum release were implemented by the same experimenter. The subjects were required to receive each pendulum impact with their hands, while their arms were extended at the shoulder level (Fig. 1), and to maintain their balance after the perturbation. The two experimen-



**Fig. 1.** Schematic diagram of the experimental setup. The subjects stopped the pendulum with their extended arms while standing with eyes open (predictable perturbation) or closed (unpredictable perturbation).  $l$  is the length of the pendulum and  $m$  is an additional mass.

tal conditions were: (1) a series of perturbations were applied with eyes open and as such were predictable in their timing; we call this condition “predictable perturbations” and (2) another series of perturbations were applied with eyes closed; this condition is called “unpredictable perturbations”. No advance warning of the impending perturbation was provided; instead, the subjects wore ear-phones and listened to music delivered via a mini audio player (iPod, Apple Inc.) to prevent them from obtaining auditory information about the moment of the pendulum release during unpredictable perturbations. For safety purposes in all the experiments, the subjects wore a harness with two straps attached to the ceiling. Five trials were performed in each experimental condition and the order of experimental conditions was randomized for each subject. Since the mass of the pendulum and the distance from which it was released remained the same, similar perturbations were induced in both, predictable and unpredictable perturbation conditions. The magnitude of perturbation was large enough to evoke compensatory feet-in-place reactions.

### 2.3. Instrumentation

Electrical activity of muscles (EMG) was recorded from the following right lower limb and trunk muscles: lateral gastrocnemius (GAS), tibialis anterior (TA), rectus femoris (RF), biceps femoris (BF), gluteus medius (GM), external oblique (EO), rectus abdominis (RA), and erector spinae (ES). After the skin area was cleaned with alcohol swipes, disposable electrodes (Red Dot 3M) were attached to the muscle belly of each of the above muscles, based upon recommendations reported in the previous literature (Basmajian, 1980). After similar skin preparations, a ground electrode was attached to the anterior aspect of the leg over the tibial bone. The EMG signals were collected, filtered, and amplified (10–500 Hz, gain 2000) with a commercially available EMG system (Myopac, RUN Technologies, USA).

Ground reaction forces and moments of forces were recorded using a force platform (model OR-5, AMTI, USA). An accelerometer (Model 208C03, PCB Piezotronics Inc, USA) was attached to the pendulum; its signal was used to register the moment of the pendulum impact. The forces, moments of force, EMG and accelerometer signals, were acquired at 1000 Hz by means of a VICON 612 data station (Oxford Metrics).

### 2.4. Data processing

The data were analyzed off-line using MATLAB (MathWorks, Natick, MA) programs. All EMG signals were rectified and viewed on a computer screen and an experienced researcher aligned them according to the first visible onset rise of the accelerometer signal. The alignment time was referred to as time zero ( $T_0 = 0$ ). Then the data were cut off 500 ms before  $T_0$ . Aligned trials within each series were averaged for each subject. Integrals of anticipatory and compensatory EMG activity were derived using average trials for each subject where as the muscle latencies were calculated using individual trials.

The muscle latency was detected in a time window from –450 ms to +200 ms in relation to  $T_0$  by a combination of computer algorithm and visual inspection of the averaged trials. The latency for a specific muscle was defined as the instant lasting for at least 50 ms when its EMG amplitude was greater (activation) or smaller (inhibition) than the mean of its baseline value, measured from –500 to –450 ms, plus 2 SD.

Integrals of the EMG activities ( $Int_{EMGi}$ ) during both tasks were calculated for four different epochs, each of 150 ms duration in relation to  $T_0$ . The time windows for the four epochs were: (1) from –250 ms to –100 ms (anticipatory reactions, APA1); (2) –100 ms to +50 ms (anticipatory reactions, APA2); (3) +50 to 200 ms (com-

pensatory reactions, CPA1); and (4) +200 ms to 350 ms (late compensatory reactions, CPA2). The duration of the APA windows was selected based on the literature data (Shiratori and Latash, 2001), and the results of a pilot study in which onset times of the proximal and distal muscles were observed outside of the typical APA window. The CPA time window was chosen using the literature data on the timing of corrective reactions observed in the trunk and leg muscles in response to external perturbations induced by a platform translation (Henry et al., 1998; Dimitrova et al., 2004). The subsequent division of this interval into two sub-windows was performed to differentiate the reflex responses (CPA1) from the voluntary reactions (CPA2) (Latash, 2008). The  $Int_{EMGi}$  for each of the four epochs was further corrected by the EMG integral of the baseline activity from –500 ms to –450 ms in relation to  $T_0$  as described below:

$$Int_{EMGi} = \int_{tw_i} EMG - 3 \int_{-500}^{-450} EMG \quad (1)$$

where  $Int_{EMGi}$  is the integral of EMG activity of muscles inside each 150 ms epoch  $tw_i$ ,  $i = 1, \dots, 4$ , and  $\int_{-500}^{-450} EMG$  is the 50 ms background muscle activity defined as the integral of EMG signal from –500 ms to –450 ms with respect to  $T_0$  (Aruin and Latash, 1995).

The sum ( $\sum Int_{EMGi}$ ) of the two EMG integrals representing the entire time of anticipatory postural adjustments (APA1 plus APA2) was calculated for predictable tasks. The sum ( $\sum Int_{EMGi}$ ) of EMG integrals reflecting the entire time of compensatory adjustments (CPA1 plus CPA2) was calculated for predictable and unpredictable tasks. These  $\sum Int_{EMGi}$  were calculated for each ventral and dorsal muscle.

Displacements of the center of pressure (COP) in the anterior–posterior direction were calculated using the following approximation (Winter et al., 1996):

$$COP = -\frac{M_y + F_x * d}{F_z} \quad (2)$$

where  $M_y$  is the moment in sagittal plane,  $F_z$  and  $F_x$  are the vertical and anterior–posterior components of the ground reaction force, and  $d$  is the distance from the origin of the force platform to the surface. The average magnitude of the COP displacement for each of the four 150 ms epochs was calculated and corrected by its respective baseline (see below). The time durations for these four different epochs were similar to those calculated for  $Int_{EMGi}$ ; however, they were shifted 50 ms forward for each epoch to account for the electromechanical delay (Cavanagh and Komi, 1979; Howatson et al., 2008). This resulted in the following timing of the four epochs for COP displacement: (1) –200 ms to –50 ms (APA1), (2) –50 ms to +100 ms (APA2), (3) +100 ms to 250 ms (CPA1), and (4) +250 ms to 400 ms (CPA2). The baseline of COP magnitude during the time from –500 ms to –450 ms was also averaged; this baseline was multiplied by 3 and subtracted from each respective COP epoch. As the perturbations were induced symmetrically, only COP displacements in the anterior–posterior direction (Y-axis according to our experimental set-up) will be reported.

It is known that lack of, or distorted visual information may negatively affect postural sway (Black et al., 2008; Hafstrom et al., 2002). Therefore, the generation of compensatory reactions during unpredictable conditions could be influenced by both unpredictability of the perturbation itself and a disturbance in balance control due to a lack of visual information per se. In order to eliminate the latter and attribute the results to unpredictability of the perturbation, a pilot experiment was conducted involving three individuals. They performed the same task of stopping the pendulum released by the experimenter with eyes closed, and with eyes open while wearing transparent glasses. In the later condition, a black tape was attached to the center of the glasses in such a way

that it covered only the pendulum and its trajectory. Thus, in this second condition, while the subjects were not able to see the forthcoming pendulum, their peripheral vision remained unobstructed. The  $Int_{EMGi}$  were compared between these two conditions (eyes closed, and eyes open while wearing glasses). No significant differences were found for either variable between the two conditions – suggesting that closing the eyes in itself did not interfere with the ability of a subject to control balance after unpredictable perturbations. Therefore, the responses obtained in this study with eyes closed were exclusively associated with the unpredictability of the perturbation.

### 2.5. Statistical analysis

Multiple repeated measures ANOVAs with two within-subjects factors (two conditions – predictable, unpredictable – and four epochs) were used to compare the muscular latencies and  $Int_{EMGi}$  for each muscle. A post hoc analysis was used for further comparisons within the four epochs. A *T*-test was used for the comparison of the CPA  $\sum Int_{EMGi}$  for ventral and dorsal muscles between predictable and unpredictable conditions. In all tests, the statistical significance was set at  $p < 0.05$ .

## 3. Results

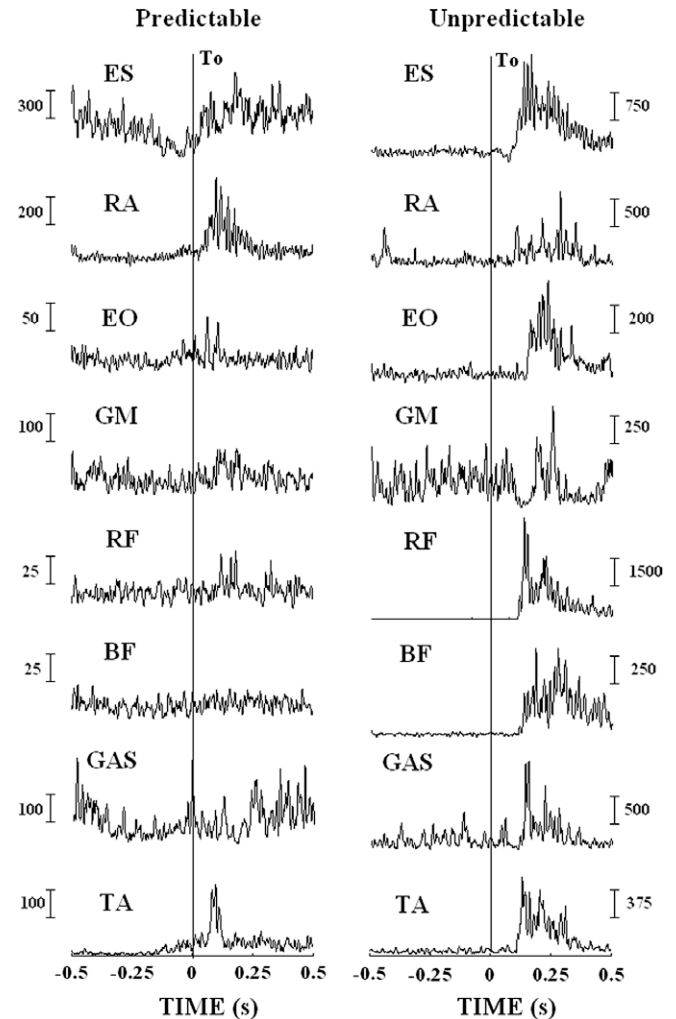
### 3.1. EMG profiles

Fig. 2 displays EMG traces obtained from the ventral, dorsal, and lateral muscles of a representative subject during performance of the task involving predictable and unpredictable perturbations. Anticipatory activity was seen in most of the muscles in the predictable conditions as an increase (rise/activation) or cessation (inhibition) of the background EMG activity. Notice a reciprocal pattern of anticipatory activity of the trunk and leg muscles seen as activation of the ventral muscles (TA, RF, and RA) and inhibition of the dorsal muscles (GAS, BF, and ES) in conditions with the predictable perturbations induced by the pendulum impact. In contrast, no APAs were observed in the experiments with unpredictable body perturbations; instead, a large compensatory EMG activity was seen in most of the trunk and leg muscles after the pendulum impact.

### 3.2. Latency of EMG activity

In conditions with the predictable perturbations onset of EMG activity was seen before the pendulum impact in all the studied muscles (Fig. 3). GAS was the first muscle showing inhibition in the EMG background activity at  $-215 \pm 44$  ms followed by the inhibition of other dorsal muscles, BF at  $-178 \pm 79$  ms and ES at  $-168 \pm 15$  ms before the pendulum impact ( $T_0$ ). Early activation was seen in TA, RF, and RA with latencies at  $-160 \pm 32$  ms,  $-181 \pm 56$  ms, and  $-166 \pm 95$  ms before the impact, respectively. Bursts of EMG activity were observed in lateral muscles as well with latencies of  $-164 \pm 65$  ms for GM and  $-168 \pm 95$  ms for EO before the impact. The order of activation of muscles in the predictable conditions was from distal to proximal.

None of the eight studied muscles showed changes in their background activity before the pendulum impact during the series with the unpredictable perturbations; instead, all the muscles became active after the perturbation impact. The EO, RA, and ES were the first muscles to be activated with latencies at  $60 \pm 25$  ms,  $61 \pm 21$  ms and  $65 \pm 40$  ms after the perturbation, respectively. The onsets of these muscles were followed by the onsets of the RF at  $80 \pm 16$  ms, TA at  $82 \pm 11$  ms, GM at  $85 \pm 29$  ms, GAS at  $88 \pm 14$  ms, and BF at  $91 \pm 36$  ms. The sequence of activation of



**Fig. 2.** A typical EMG pattern (averages of six trials for a representative subject) of the ventral (TA, RF, and RA), dorsal (GAS, BF, and ES), and lateral (EO and GM) muscles recorded in conditions with predictable and unpredictable perturbations. The vertical lines show the moment of body perturbation ( $T_0$ ). Time scales are in seconds and EMG scales are in arbitrary units. Muscles abbreviations: TA – tibialis anterior, GAS – gastrocnemius, BF – biceps femoris, RF – rectus femoris, GM – gluteus medius, EO – external obliques, RA – rectus abdominis, and ES – erector spinae.

muscles was from proximal to distal and it was different than the sequence observed for predictable conditions.

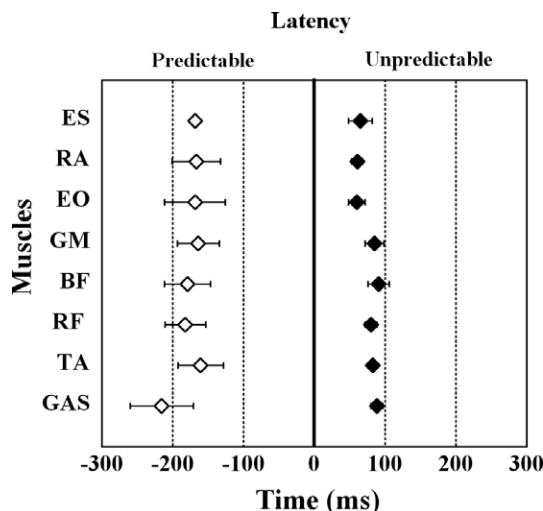
The differences in the latencies of muscles between predictable and unpredictable conditions were statistically significant for all studied muscles ( $p < .05$ ).

## 4. Integrated EMG activity

### 4.1. EMG integrals in ventral muscles

In the series with unpredictable perturbations  $Int_{EMGi}$  in the ventral muscles (TA, RF, and RA) observed prior to the perturbation during both the APA1 and APA2 epochs were negligible. Instead, large  $Int_{EMGi}$  could be seen after the pendulum impact. Fig. 4 shows the temporal evaluations of the  $Int_{EMGi}$  during performance of the tasks with predictable and unpredictable perturbations;  $Int_{EMGi}$  for each of the four epochs are broken into 50 ms blocks for better visualization. Similar representation will be used in Figs. 5 and 6. The results of statistical analysis of differences in  $Int_{EMG}$  between conditions and epochs as well as interactions for each individual





**Fig. 3.** Muscle activity onsets. Note that for predictable perturbations the onset of muscle activity occurred prior to the perturbation and the order of activation of muscles is from distal to proximal. In case of unpredictable perturbations, the muscle onsets occurred after the perturbation ( $T_0$ ) and the order of activation is from proximal to distal. Muscles abbreviations are the same as shown in Fig. 2.

ventral muscle are presented in Table 1. TA, RF, and RA  $Int_{EMG}$  were significantly different between the conditions and epochs. The post hoc analysis demonstrated that for the predictable conditions the RF  $Int_{EMG}$  APA1 epoch was significantly smaller than the CPA1 and CPA2 epochs. For unpredictable perturbations TA, RF, and RA  $Int_{EMG}$  during the CPA1 epoch were significantly greater than  $Int_{EMG}$  calculated for the CPA2 epoch.

#### 4.2. EMG integrals in dorsal muscles

In the experiments with the predictable conditions,  $Int_{EMG}$  in the dorsal muscles (GAS, BF, and ES) were mostly negative suggest-

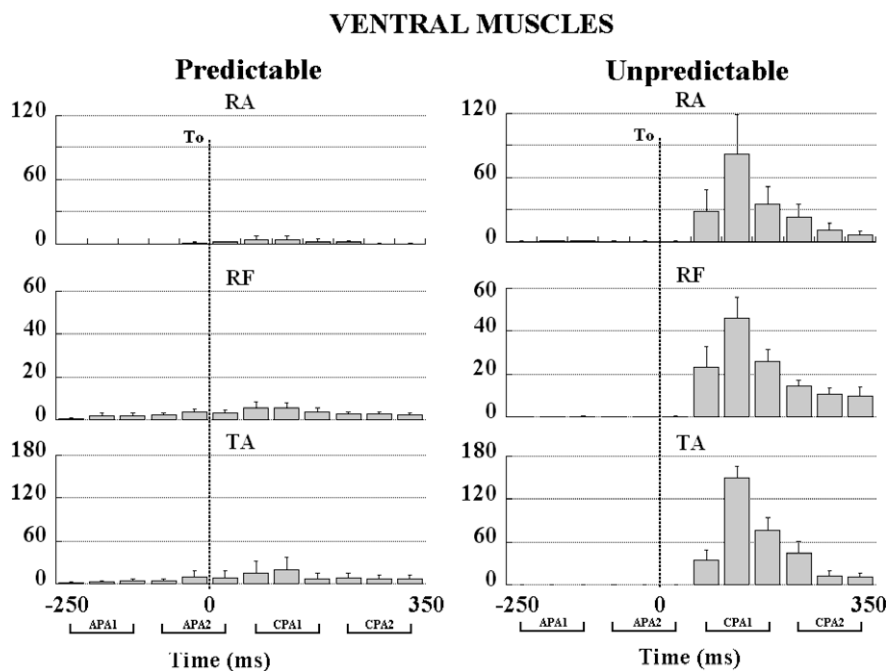
ing that dorsal muscles were inhibited during both the anticipatory and compensatory phases of postural control. In contrast, in conditions with the unpredictable perturbations, small  $Int_{EMG}$  in dorsal muscles during the APA1 and APA2 phases (as compared to predictable conditions) were accompanied by large  $Int_{EMG}$  after the perturbation onset (best of all seen in GAS) (Fig. 5). The effect of condition was significant in GAS and BF (Table 1); in addition, analysis of GAS  $Int_{EMG}$  revealed statistically significant difference among the epochs and interaction between conditions and epochs. The post hoc analysis demonstrated that GAS  $Int_{EMG}$  calculated for CPA1 was significantly greater than the CPA2.

#### 4.3. EMG integrals in lateral muscles

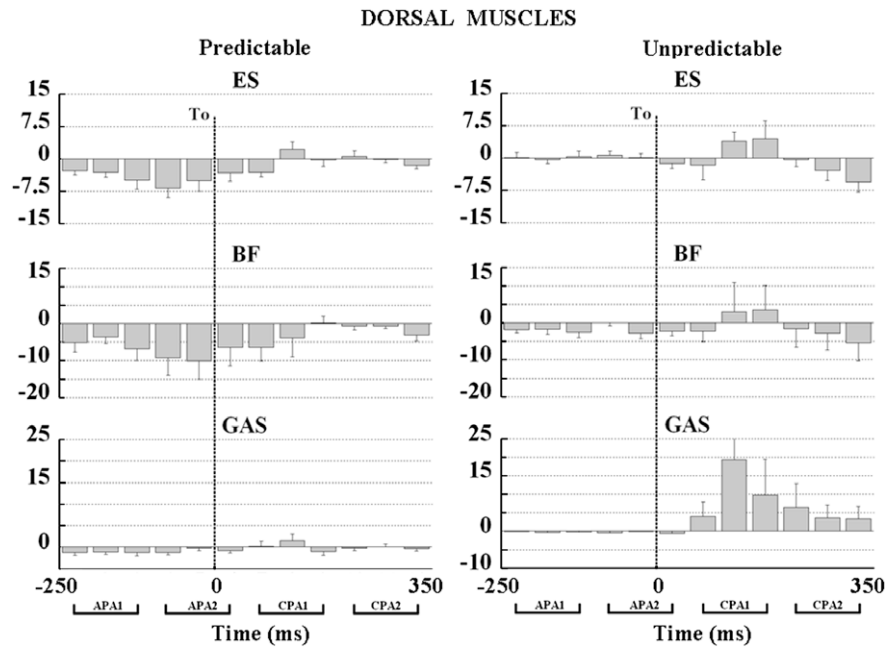
Significant differences in the  $Int_{EMG}$  between the conditions, epochs, as well as conditions-epoch interactions were found in both GM and EO muscles (Fig. 6, Table 1). The post hoc analysis revealed that in the unpredictable condition, the GM and EO  $Int_{EMG}$  during the CPA1 and CPA2 epochs were significantly larger than APA1 and APA2 epochs. Moreover, GM and EO  $Int_{EMG}$  during the CPA1 epoch were significantly greater than  $Int_{EMG}$  calculated for the CPA2 epoch.

#### 4.4. Difference between predictable and unpredictable conditions

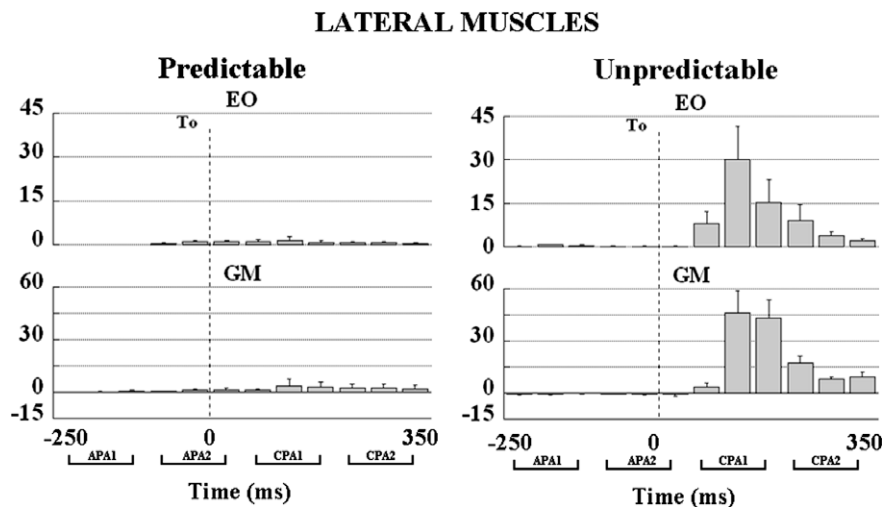
Fig. 7 depicts the sum of  $Int_{EMG}$  of the ventral and dorsal muscles calculated during the anticipatory (APA) and compensatory (CPA) postural adjustments in conditions with predictable and unpredictable perturbations. Notice a considerable inhibition of the dorsal muscles (represented by negative values of the  $\sum Int_{EMG}$ ) during the APA phase in conditions with predictable perturbations. Also notice that  $\sum Int_{EMG}$  calculated for each ventral muscle during the CPA phase in the unpredictable conditions were several times larger than  $\sum Int_{EMG}$  calculated during the CPA phase in the predictable conditions. The TA, RF, and RA  $\sum Int_{EMG}$  during the CPA phase were significantly greater for unpredictable than predictable conditions ( $p < 0.05$ ). In contrast, when  $\sum Int_{EMG}$  of the dorsal



**Fig. 4.** Temporal evaluation (from -250 ms to +350 ms in relation to  $T_0$ ) of the EMG activities of the ventral muscles during predictable and unpredictable conditions. Each point represents the  $Int_{EMG}$  averaged in 50 ms intervals and its standard error across eight subjects. The 4 time epochs of 150 ms used for the analysis are represented by the brackets on the bottom (APA1, APA2, CPA1, and CPA2). The vertical lines show the moment of body perturbation ( $T_0$ ).



**Fig. 5.** Temporal evaluation (from  $-250$  ms to  $+350$  ms in relation to  $T_0$ ) of the EMG activities of the dorsal muscles during predictable and unpredictable conditions. Each point represents the  $Int_{EMG}$  averaged in 50 ms intervals and its standard error across eight subjects. The four time epochs of 150 ms used for the analysis are represented by the brackets on the bottom (APA1, APA2, CPA1, and CPA2). The vertical lines show the moment of body perturbation ( $T_0$ ).



**Fig. 6.** Temporal evaluation (from  $-250$  ms to  $+350$  ms in relation to  $T_0$ ) of the EMG activities of the lateral muscles during predictable and unpredictable conditions. Each point represents the  $Int_{EMG}$  averaged in 50 ms intervals and its standard error across eight subjects. The four time epochs of 150 ms used for the analysis are represented by the brackets on the bottom (APA1, APA2, CPA1, and CPA2). The vertical lines show the moment of body perturbation ( $T_0$ ).

**Table 1**

ANOVA results for  $Int_{EMG}$  between conditions and epochs as well condition/epoch interactions for each muscle

Muscles	Condition (C)		Epochs (E)		Interaction (C×E)	
	<i>F</i> (1, 7)	<i>p</i>	<i>F</i> (3, 21)	<i>p</i>	<i>F</i> (3, 21)	<i>p</i>
ES	1.9	0.22	1.77	0.19	0.96	0.43
RA	5.7	0.04*	4.9	0.01**	3.6	0.02*
EO	8.4	0.02*	6	<0.01**	6.3	<0.01**
GM	29	<0.01**	15.5	<0.01**	15	<0.01**
BF	57.5	<0.01**	1.3	0.30	0.9	0.44
RF	8.7	0.02*	34.4	<0.01**	18.8	<0.01**
TA	102.6	<0.01**	53.7	<0.01**	30.3	<0.01**
GAS	55.5	<0.01**	18.7	<0.01**	14.4	<0.01**

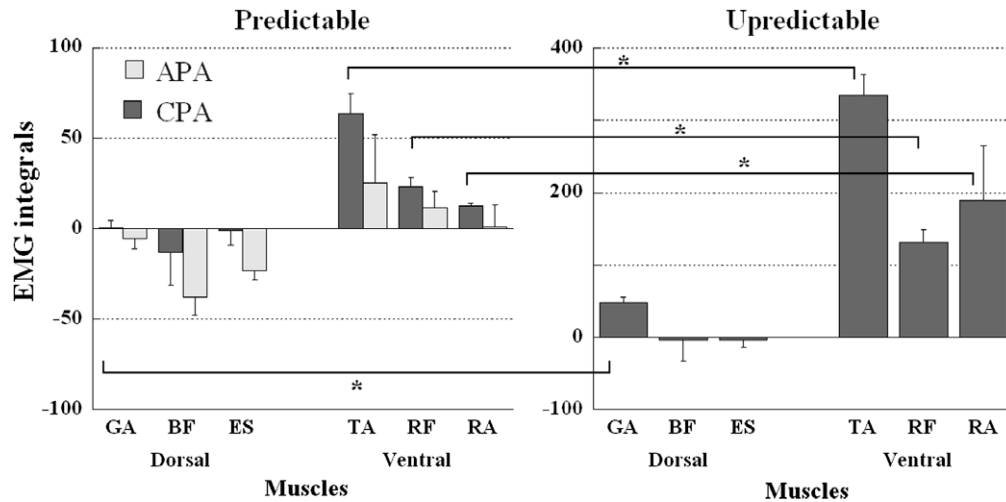
\* Refers to  $p < 0.05$ .

\*\* Refers to  $p < 0.01$ .

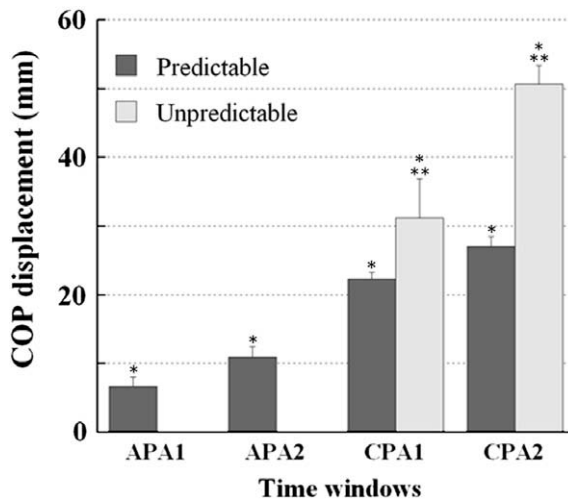
muscles calculated during CPA phase for predictable and unpredictable conditions were compared, the only muscle showing statistically significant difference between the conditions was GAS ( $p < 0.01$ ).

#### 4.4.1. COP displacement

The displacements of the COP in the anterior–posterior direction are shown in Fig. 8. In general, the COP displacements were significantly larger when perturbations were not predictable compared to predictable conditions ( $p < 0.01$ ). For the time period prior to the pendulum impact (APA1 and APA2), considerable displacements in COP were observed when the perturbations were predictable; when they were unpredictable, the COP displacements were negligible. The post hoc tests detected that all COP epochs were



**Fig. 7.** Muscular synergies involving ventral and dorsal muscles represented by the sum of integrals of EMG ( $\sum Int_{EMG}$ ) during APAs and CPAs for predictable tasks and the sum of integrals of EMG during CPAs for unpredictable conditions. \* denotes significant differences in  $\sum Int_{EMG}$  between predictable and unpredictable conditions ( $p < 0.05$ ).



**Fig. 8.** COP displacement (mm) for predictable and unpredictable conditions. Positive values correspond to the displacements of the COP backwards. \* indicates significant differences among the epochs (APA1, APA2, CPA1, and CPA2) and \*\* represents significant differences between conditions (unpredictable and predictable).

significantly different from each other during the predictable condition and that the COP displacement in these epochs increased gradually and significantly from APA1 epoch to CPA2. For unpredictable conditions, the APA1 and APA2 epochs were not significantly different from each other. However, the APA1 and APA2 epochs were significantly smaller than the CPA1 and CPA2 epochs ( $p < 0.01$ ,  $p = 0.01$ ,  $p < 0.01$ , and  $p < 0.01$ ). Moreover, CPA2 was significantly greater than CPA1 epoch ( $p < 0.01$ ). Importantly, during the compensatory phases (CPA1 and CPA2), the COP displacement for the unpredictable condition was significantly greater as compared to the predictable condition ( $p < 0.01$ ).

## 5. Discussion

The hypothesis that the amount of compensatory muscle activation depends on the availability of anticipatory EMG activity was supported.

Larger compensatory reactions were seen during the unpredictable perturbations because these conditions were not associated with any anticipatory corrections. However, when the perturbations were predictable, so that the subjects knew the timing of the perturbation, they generated strong APAs: this resulted in significantly smaller compensatory reactions. The observed changes in the electrical activity of muscles suggest that the CNS assesses the effect of involvement of the APAs and generates or scales down CPAs accordingly. Such assessment and utilization of anticipatory activity resulting in reduced compensatory corrections following a perturbation have also been reported in tasks involving precision grip maintenance in sitting (Kourtis et al., 2008). Thus, it can be suggested that while dealing with perturbations, the general rule applied by the CNS is to optimally use anticipatory corrections if and when possible, resulting in appropriate scaling down of compensatory activity. It is important to note that the way anticipatory and compensatory corrections were used does not resemble “all or nothing” strategy since implementation of APAs prior to the pendulum impact while dealing with predictable perturbations did not exclude completely the generation of CPAs after the perturbations occurred. Moreover, the “all or nothing” strategy is rather a theoretical approach since in a real life there is always some type of compensatory EMG activity used in control of vertical posture. This suggestion could be supported by several observations. First, involvement of EMG activity in the trunk and leg muscles during the CPA could be associated with insufficiency of the APAs that was reported in young children (Hadders-Algra, 2005; van der Heide et al., 2003) and in individuals with neurological disorders (Bazalgette et al., 1987). Second, it was reported that APAs are attenuated in conditions of body instability (Aruin et al., 1998). In such a case, sufficient compensatory muscle activity would be needed to preserve balance. Finally, the existence of continuous muscular activity across both APA through CPA phases during predictable (self-initiated) and unpredictable (externally induced) perturbations has been described in the literature (Hughes and Fung, 2005).

The EMG patterns observed in the current study have several important features.

First, in the case of predictable perturbations, APAs were present during both, APA1 and APA2 intervals. However, the largest anticipatory responses occurred during the APA2 epoch (between  $-100$  ms and  $+50$  ms in relation to  $T_0$ ). The existence of the robust anticipatory adjustments inside this time window are consistent

with the APA literature involving self-initiated (Belen'kii et al., 1967; Cordo and Nashner, 1982; Kanekar et al., 2008; Zattara and Bouisset, 1988) or external predictable perturbations (Aruin et al., 2001; Santos and Aruin, 2008; Shiratori and Latash, 2001). Hence, the observation of largest APAs during the APA2 epoch suggests that the CNS is capable of generating APAs in a time frame that is close to the moment of the perturbation. However, in case the forthcoming perturbations and/or current balance status are more challenging, the CNS might choose generating APAs earlier. The existence of early APAs (between –250 and –100 ms) was described in the experiments involving pointing movements to targets of different size (Bonnetblanc et al., 2004) and the arm-raising task after fatigue (Allison and Henry, 2002).

Second, when no anticipatory corrections were generated (as it happened in the unpredictable conditions), larger EMG responses were seen during the first compensatory phase (CPA1, from 50 ms to 150 ms after the perturbation onset) in almost all studied muscles (TA, RF, GA, GM, and EO) when compared with the second compensatory (CPA2) phase. It suggests that the body perturbations were relatively successfully minimized with the muscular responses generated right after the perturbation that could be attributed to the stretch reflex (Bloem et al., 2002; Cordo and Nashner, 1982; Granata et al., 2004). As a result, a significantly smaller compensatory muscular activity was needed during the second, stabilization (CPA2) phase of the compensatory control of posture. This suggestion is supported by the decreased *Int<sub>EMG</sub>* during the CPA2 phase seen in the TA, RF, GA, GM, and EO muscles. On the other hand, large CPAs observed right after the perturbation onset (CPA1) might generate “too much” compensation which needs to be corrected during the following compensatory activity and such corrections are represented by the EMG activity seen later inside the second (CPA2) epoch.

Third, during predictable perturbations a reciprocal pattern of activation was seen both, before and after  $T_0$ ; dorsal muscles were inhibited whereas ventral and lateral muscles were activated. On the other hand, during unpredictable perturbations a co-activation of the distal leg muscle pair during the second phase of compensatory activity was observed. Co-activation of leg and trunk muscles to increase the stiffness of the joints has been described in the literature during both, the anticipatory (Aruin and Almeida, 1997; Danna-Dos-Santos et al., 2007; Li and Aruin, 2007; Slijper and Latash, 2000) and compensatory (Allum et al., 1989; Berger et al., 1992; Dimitrova et al., 2004) phases of postural control. However, it is important to note that the co-activation of TA-GAS muscles, seen in the current study 200 ms after the perturbation, was accompanied by a reciprocal pattern of muscle activation of the proximal muscles (RA and BF activation and ES and RF inhibition). It appears that by co-activating the distal leg muscle pair the subjects of the current experiment opted to increase the stiffness of the ankle joints in order to generate forces needed for foot-in-place responses. At the same time, in order to restore the upper body position a reciprocal control strategy was used. The fact that the two strategies are used simultaneously suggests that the CNS is capable of implementing multiple strategies while controlling the body position in space.

Finally, it is known that distal to proximal order of anticipatory muscle activation was observed in experiments with self-initiated elbow flexions (Cordo and Nashner, 1982; Friedli et al., 1984). Similar order of early muscle activation (distal to proximal) was seen in the current study even when the perturbations were induced externally but the timing and magnitude of them was known to the subjects. It was advocated previously that distal to proximal sequence of muscle activation relates to the self-initiated perturbation itself as well as to postural requirements or

“postural set” (as coined by Cordo and Nashner (1982)). As such it is employed “to modify the subjects’ balance sway”, making it easy for them to counteract the imminent forces generated by the perturbations to the body (Cordo and Nashner, 1982). However, when the subjects were exposed to unpredictable perturbations as in the current experiment, the sequence of compensatory activation of the muscles was proximal to distal. Similar order of muscle activation starting with the biceps brachii, followed by thoracic muscle and then followed by the low back muscles was observed in experiments with unpredictable external perturbations applied through the upper limbs of standing individuals (Hodges, 2001; Moseley et al., 2003). In the present experiment, the subjects used different strategies to restore the equilibrium according to the perturbation predictability. It appears that when information about the forthcoming perturbation is unavailable, the CNS uses a proximal to distal approach of muscle activation so as to initially restore the upper body position and maintain the body’s vertical orientation. When the perturbation is predictable, the CNS uses distal to proximal order of muscle activation which first and foremost allows applying forces to the ground thus counteracting the perturbation effect, and after that helps restore the upper body position.

The specific patterns of muscle activation seen in the current study resulted in the COP differences observed between conditions with predictable and unpredictable perturbations. Significant reduction of the compensatory COP displacement seen in conditions when the subjects knew the timing of the forthcoming perturbation provides additional evidence in support of the importance of the anticipatory postural adjustments in the activity of the trunk and leg muscles in the overall control of vertical posture. This is an important outcome of the study which could be used in clinical applications. Since a significant number of individuals with neurological disorders and the elderly have difficulties in maintaining their balance, rehabilitation approaches focused on better use of anticipatory postural adjustment might benefit such individuals.

The patterns of EMG activity observed in the current study provide evidence that there is a relationship between the anticipatory and compensatory components of postural control. In addition, this study provides evidence that the CNS is able to use the anticipatory activation of muscles to prevent further destabilization of balance and as a result, it does not need to call in place large compensatory muscle activity. Also, once body stability is achieved (or at least it is improved to a certain degree), the CNS employs a strategy that involves (1) decreasing globally the activity of postural muscles, and (2) utilizing a reciprocal and co-activation pattern of activation in combination, which was seen for example in RA-ES, RF-BF, and TA-GAS muscle pairs during the CPA2 phase, respectively.

Since the number of subjects was relatively small, the outcome of the study should be validated in future studies with larger sample size.

## 6. Conclusion

The outcome of this study highlights the importance of a relationship between APAs and CPAs in control of posture, and points out the possibility of optimally utilizing APAs in postural control. While examining the patterns of muscle activation between the anticipatory and compensatory periods of postural control, differences were found in the magnitude and sequence of muscle activation dependent on an availability of APAs. As a result, smaller COP displacements were seen after the perturbations.



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**Marcio J. Santos** graduated in Physical Therapy (PT) from the Universidade Estadual de Londrina (UEL), Brazil. He obtained his Master Degree (M.S.) in Human Physiology from the Universidade Estadual de Campinas (UNICAMP), Brazil, and his Ph.D. in Rehabilitation Science from the University of Kansas Medical Center (KUMC), USA. He worked as a post-doctoral research associate in the Knecht Movement Science Laboratory at the Department of Physical Therapy at the University of Illinois at Chicago (UIC), USA. He is currently working as an assistant professor at the Department of Physical Therapy at the Universidade Estadual de Santa Catarina (UDESC), Brazil. He has co-authored various scientific papers in the

motor control, biomechanics and rehabilitation fields, testing healthy individuals and those with disabilities. His present research projects focused on: (1) feedforward and feedback postural control and (2) grip force control in healthy individuals and orthopedic and neurologic patients.



**Neeta Kanekar** received her Bachelor's degree in Physiotherapy from Maharashtra University of Health Sciences, Seth G.S. Medical College & K.E.M Hospital, India and her Master's degree in Physical Therapy from University of Illinois at Chicago (UIC), USA. After practicing as a PT for a few years, she is now pursuing her PhD degree in the program of Kinesiology, Nutrition, and Rehabilitation with a major in Rehabilitation at UIC. She is currently working in the Knecht Movement Science Laboratory in the Department of Physical Therapy at UIC. Her primary area of research is related to rehabilitation, biomechanics, and motor control. Presently her research projects are focused on: (1) feedforward and

feedback mechanisms of balance control, (2) effect of fatigue on postural control, and (3) effect of balance training in healthy individuals, the elderly, and individuals

with musculoskeletal and neurological disorders. She is a member of the Indian Association of Physiotherapists and the National Honor Society of Phi Kappa Phi, USA.



**Alexander S. Aruin** received his Ph.D. in Medical Cybernetics from the Moscow Institute of Artificial Organs and Transplantation in 1978 and a D.Sc. (Ph.D.) in Biomechanics from the Latvian Institute of Traumatic Injuries and Orthopedics in 1990. He was affiliated with the Moscow Institute of Electronic Engineering as Full Professor and Director of the Laboratory of Ergonomics and Biomechanics. After moving to the United States in 1992, he became a faculty at Rush-Presbyterian St. Luke's Medical Center in Chicago and later a faculty member at Pennsylvania State University. He is currently a Professor of Physical Therapy, Bioengineering, and Kinesiology and the Director of the Knecht Movement Science

Laboratory at the University of Illinois at Chicago, a Professor of Physical Medicine & Rehabilitation at Rush University, Chicago, and a Senior Clinical Researcher at Marianjoy Rehabilitation Hospital in Wheaton, Illinois. He has co-authored more than 100 referred papers and two monographs in the fields of biomechanics, kinesiology, motor control and neuromuscular disorders. His primary research interests have been focused on motor disorders and rehabilitation, biomechanics, and motor control. Dr. Aruin develops new technologies for training healthy people and for providing physical therapy and rehabilitation to injured and disabled individuals. He is a member of the American Society for Biomechanics, Society for Neuroscience, and International Society of Motor Control.