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RESEARCH ARTICLE

Role of lateral muscles and body orientation in feedforward postural control

Marcio J. Santos · Alexander S. Aruin

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Abstract The study investigates the role of lateral muscles and body orientation in anticipatory postural adjustments (APAs). Subjects stood in front of an aluminum pendulum and were required to stop it with their right or left hand. An experimenter released the pendulum inducing similar body perturbations in all experimental series. The perturbation directions were manipulated by having the subjects standing on the force platform with different body orientations in relation to the pendulum movements. Consequently, perturbations were induced in sagittal, oblique, and frontal planes. Ground reaction forces and bilateral EMG activity of dorsal, ventral, and lateral trunk and leg muscles were recorded and quantified within the time intervals typical of APAs. Anticipatory postural adjustments were seen in all experimental conditions; their magnitudes depended on the body orientation in relation to the direction of perturbation. When the perturbation was produced in the lateral and oblique planes, APAs in the gluteus medius muscles were greater on the side opposite to the side of perturbation. Conversely, simultaneous anticipatory activation of the external obliques, rectus abdominis, and erector spinae muscles was observed on the side of perturbation when it was induced in the lateral plane. The results of the present study provide additional information on the directional specificity of anticipatory activation of ventral and dorsal muscles. The findings provide new data on the role of lateral muscles in feedforward postural control and stress the importance of taking into consideration their role in the control of upright posture.

Introduction

Any voluntary movement, especially a fast one, induces a postural perturbation due to the dynamic and inter-segmental forces that shift the center of mass. In order to preserve body equilibrium, the central nervous system (CNS) uses two types of adjustments in the activity of muscles that are involved in control of posture (Massion 1992). The first one, known since a pioneering work by Belenkiy et al. (1967), is associated with the activation of muscles prior to the actual perturbation of balance, and is called anticipatory postural adjustments (APAs) (Massion 1992). The assumed role of APAs is to minimize the negative consequences of a predicted postural perturbation using anticipatory adjustments (Bouisset and Zattara 1987a; Massion 1992). Another type of adjustment in the activity of postural muscles is the compensatory reaction, which deals with actual perturbations of balance that compensates for the suboptimal efficacy of APAs and is initiated by sensory feedback signals (Park et al. 2004; Alexandrov et al. 2005).

There are a number of factors that affect APAs including: the magnitude and direction of the perturbation, characteristics of voluntary action associated with a perturbation, and a postural task. For example, it was shown that APA magnitudes are scaled with the magnitude of the perturbations (Lee et al. 1987; Aruin and Latash 1996; Aruin et al. 2003) or body stability (Nardone and Schieppati 1988; Aruin et al. 1998; Nouillot et al. 2000). Moreover, it was reported that APAs are directionally

M. J. Santos · A. S. Aruin (✉)
Department of Physical Therapy (MC 898),
University of Illinois at Chicago,
1919 W Taylor St (4th floor),
Chicago, IL 60612, USA
e-mail: aaruin@uic.edu

specific (Aruin and Latash 1995a) and depend on the characteristics of a motor action (Aruin and Latash 1995b; Aruin et al. 2003).

Most of what is known about the role of APAs in postural control is based on the investigation of self-initiated perturbations induced in the anterior/posterior (A/P) direction (Belenkiy et al. 1967; Friedli et al. 1984, 1988; Bouisset and Zattara 1987a; Latash et al. 1995; Gantchev and Dimitrova 1996; Benvenuti et al. 1997; De Wolf et al. 1998; Massion et al. 1999; Shiratori and Latash 2001; Kasai et al. 2002; Slijper et al. 2002). Only a few studies were performed to investigate the APA organization using self-initiated perturbations performed in planes other than anterior–posterior plane (Vernazza et al. 1996; Vernazza-Martin et al. 1999). These studies, however, utilized an arm-raising paradigm that has certain limitations associated with the fact that APAs depended on the velocity of the movement: they are larger when the velocity of the forthcoming movement is high (Horak et al. 1984; Lee et al. 1987; Mochizuki et al. 2004).

It is known that the majority of real life activities require multi-dimensional balance control that could be achieved only by precisely coordinated activation/inhibition of ventral, dorsal, and lateral muscles on both sides of the body. It is also recognized that lateral muscles play an important role in the control of posture. For instance, the function of the gluteus medius muscle is to stabilize the hip joint during gait initiation (Rogers et al. 1993) or lateral postural disturbances (Gilles et al. 1999). The involvement of the lateral muscles in postural control, such as the external oblique, are central in the maintenance of an asymmetrical posture or when dealing with asymmetrical perturbations to the body (Granata et al. 2001). Yet, a majority of APA studies investigated the involvement of only the ventral and dorsal trunk and leg muscles using a self initiated perturbation performed in either the sagittal or frontal planes (Friedli et al. 1984; Aruin and Latash 1995b; Forrest 1997; Slijper and Latash 2000; Shiratori and Latash 2001; Aruin and Shiratori 2004; Shiratori and Aruin 2007). Only few studies were performed to investigate the organization of APAs in muscles that maintain lateral stability of the body (Lavender et al. 1993; Granata et al. 2001), suggesting a need to run a detailed study on the role of lateral muscles in feed forward control of posture.

The aim of this study, therefore, is to investigate the anticipatory changes in the activity of the lateral muscles together with the commonly studied ventral and dorsal leg and trunk muscles. We hypothesized that the level of anticipatory activation of lateral muscles depends on the direction of perturbation. Additionally, we hypothesized that there will be synergistic APA activity in lateral, ventral, and dorsal muscles and the level of involvement of a particular muscle will depend on the perturbation direction. To test these hypotheses we designed an experimental paradigm in which the standing subjects were required to stop a pendulum released by the experimenter: this introduced a constant body perturbation as the mass of the pendulum and the distance that the pendulum moves from remained unchanged. Throughout the experiments the subjects were positioned differently in relation to the pendulum movement, which produced perturbations in frontal, sagittal, or oblique planes. Thus, the experimental paradigm allowed keeping both, the magnitude and predictability of the forthcoming perturbation the same while the plane of the perturbation was manipulated.

Methods

Subjects

Ten healthy young adults (6 women and 4men; mean age 28.2 years, range 22–41 years) participated in the study. None of the subjects had history of orthopedic problems, neurological disorders or any other pathology that would impair their performance during the study. The subjects signed the informed consent approved by the Institutional Review Board of the University of Illinois at Chicago.

Testing protocol

The subjects were required to stand bare foot on the force platform with their feet shoulder width apart and in front of an aluminum pendulum attached to the ceiling. The pendulum was size adjustable ($l = 1.1$–1.4 m) to match the subjects' shoulder height with a foam covered hand bar at its distal end. A load ($m = 1.36$ kg) was attached to the pendulum next to the hand bar. A rope from the hand bar was put through a pulley system; the pulley system was attached to the ceiling. Perturbations consisted of unidirectional forces applied to the subjects' hand using the pendulum that was pulled a fixed distance away from the subjects' hand (0.8 m) and released by the experimenter. The subjects were required to stop the pendulum with their right or left hand while standing in five different positions (Fig. 1). These positions were: (1) sagittal plane, when the perturbation was induced in the sagittal plane of the body (0°) (2) and (3) lateral planes, when the perturbation was induced perpendicular to the sagittal plane of the body, i.e., lateral on the right and left sides of the body (+90° and –90°, respectively), and (4) and (5) an intermediary position between standing perpendicular to the plane of perturbation and when the plane of perturbation coincides with the sagittal plane, i.e., oblique on the right and left sides (+45° and –45°, respectively). Depending on the

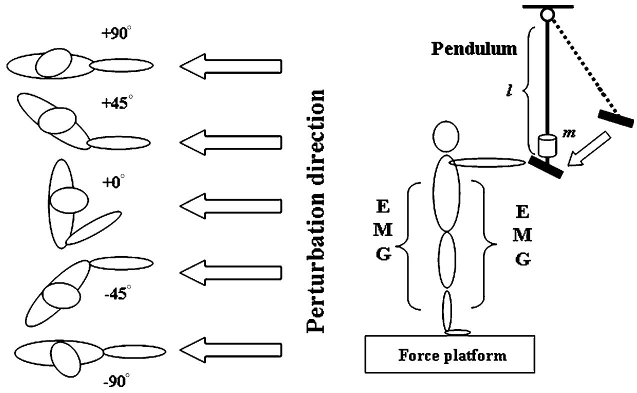

Fig. 1 The experimental setup. *Left* view of the subject from above. *Arrows* show the direction of pendulum movements. The angles between the sagittal plane of the body and direction of perturbation are in degrees. *Right* side view of the subject. *l* is the length of the pendulum and *m* is an additional mass

orientation of the body, one of their shoulders was flexed, elevated or abducted at 90°, their elbow was slightly flexed (20°—30°), and their wrist and fingers were extended. The opposite arm was relaxed and extended on the corresponding side of the body. In each experimental series the subjects were required to look at the pendulum released by the experimenter and to stop it six times. In the sagittal position, the subjects used their right and left arms positioned closely to the middle of their body three times to stop the moving pendulum when it was released by the experimenter.

Instrumentation

Electrical activity of muscles (EMG) was recorded bilaterally from the following left and right lower limb and trunk muscles: rectus femoris (RFL and RFR), biceps femoris (BFL and BFR), rectus abdominis (RAL and RAR), external obliques (EOL and EOR), erector spine (ESL and ESR), and gluteus medius (GML and GMR). After the skin was whipped down with alcohol, disposable pediatric electrodes with 15 mm skin contact area (Red Dot 3 M) were attached to the muscle belly of each of the above muscles (Basmajian 1980). The electrode material utilized was silver chloride (Ag/AgCl), and the inter-electrode distance was approximately 20 mm. After all skin preparations, a ground electrode was attached to the anterior aspect of the leg over the tibial bone. The EMG signals were amplified and filtered (10–1,000 Hz, analog filter, gain 2,000) by means of differential amplifier (RUN Technologies, USA). An accelerometer (PCB, USA) was attached to the handle bar of the pendulum, and the accelerometer signal was used to register the moment of the pendulum impact. The ground reaction forces and moments of forces were recorded using a force platform (AMTI, USA) positioned at the floor. The EMG signals, signals from the force platform, and accelerometer were digitized with a 16-bit resolution at a frequency of 2,000 Hz using customized LabView software.

The EMG activity in the left and right soleus (SOL), gastrocnemious (GAS), tibial anterior (TA), and peroneals (PER) muscles was recorded in a separate pilot experiment involving two subjects from the same subject pool. The identical experimental protocol was used and the data was analyzed in the same way as it was done in the main experiment.

Data analysis

The EMG signals were rectified and filtered with a 100 Hz low pass second-order Butterworth filter. The ground reactions forces were filtered with a 20 Hz low pass, second-order Butterworth filter. Then, each trial was viewed on a computer screen off-line using a LabView program and aligned with the first abrupt deflection of the accelerometer signal, which correlated to the moment of body perturbation. The alignment time was referred to as “time zero” (T0) for all further analysis. Then the six trials for each condition were averaged.

Anticipatory EMG activity ($\int \mathrm{EMG}_{100}$) was quantified as the integral of EMGs during the 100 ms time frame before T0. The $\int \mathrm{EMG}_{100}$ was further corrected by the EMG integral of the baseline activity from 500 to 450 ms before T0 ($\int \mathrm{EMG}_{50}$) as described below:

$$\int \mathrm{EMG} = \int \mathrm{EMG}_{100} - 2 \int \mathrm{EMG}_{50}$$

A customized Matlab program (MathWorks Inc., USA) was used to calculate the $\int$EMGs and the center of pressure displacements (COP). Horizontal displacements of the center of pressure (COP) in antero-posterior (COPy) and lateral (COPx) directions were quantified as the changes at T0 in relation to their respective baseline (500–450 ms before T0). The COPy displacements coincided with the perturbations direction while the CPOx displacements were orthogonal to the path of the perturbations. The subjects changed the orientation of their body in relation to the pendulum movements and axes of the force platform. To avoid a need to move the force platform, the moment (My) signals were multiplied by –1 while calculating the CPOx displacement in the series with the subjects stopped the pendulum with the right upper extremity.

Multiple repeated measures ANOVAs followed by post hoc analysis were used to compare the $\int$EMGs, COPy, and COPx among the five conditions for each side. Statistical significance was set at $P < 0.05$. A paired t test was used to compare each condition between sides.

Results

Profiles of muscle electrical activity

Figure 2 shows EMG traces (averaged over six trials for a representative subject) for ventral and dorsal leg and trunk muscles. EMG traces for lateral muscles are shown in Fig. 3. The vertical lines at T0 represent the moment of contact of the pendulum with the subject's hand. The EMG patterns in most of the ventral and dorsal trunk and leg muscles changed according to the subjects' positions throughout the five experimental conditions. For example, anticipatory inhibition in left BF and an anticipatory burst of activity in right BF is seen in response to the series with the body's right side facing the pendulum (+90° and +45°). However, this is replaced with an anticipatory burst of activity in left BF and anticipatory inhibition in the right BF in the series where the body's left arm receives the perturbation (–90° and –45°). A similar, but less pronounced pattern was observed in the ES muscles. The bursts of anticipatory activation seen in the right RF series with the body's right side facing the pendulum (+90° and +45°) as well as in conditions with perturbations acting in sagittal plane (0°) and intermediate position (–45°) disappear in conditions with –90° orientation of the body in relation to the direction of the upcoming perturbation. The activation of the left RF shows a reversed pattern: the bursts of anticipatory activation seen in the RFL series with the body's left side facing the pendulum (–90° and –45°) as well as in conditions with perturbations acting in sagittal plane (0°) and intermediate position (+45°) disappear in conditions with +90° body orientation. Rectus abdominis muscles did not show clear anticipatory activation in this particular subject. Similarly, the anticipatory activation of the gluteus medius (GM) is greater at the lateral and oblique planes at the contra-lateral side of the perturbations (Fig. 3). Furthermore, a bilateral anticipatory activation of the GM in series with the sagittal plane of the body coinciding with the direction of perturbation was noted (0°). The external oblique muscles (EO) demonstrated increased anticipatory activation in the oblique planes (±45°) at the ipsilateral sides of the perturbations. For this particular subject, such a pattern of activation is clear only at the right side (EOR), when the body's left side is facing the pendulum (Fig. 3).

Integrals of electrical activity of muscles

Figures 4 and 5 show ∫EMG indices averaged across subjects. As depicted in Fig. 4, the anticipatory activation is seen in the ventral (RFR, RFL, RAR, and RAL) muscles in all experimental conditions. At the same time, dorsal muscles (BFR, BFL, ESR, and ESL) demonstrated mostly anticipatory inhibition. Similarly, anticipatory activation is seen in lateral (EOR, EOL, GMR, and GML) muscles in all experimental conditions (Fig. 5). While the body position in respect to the direction of perturbation affected the

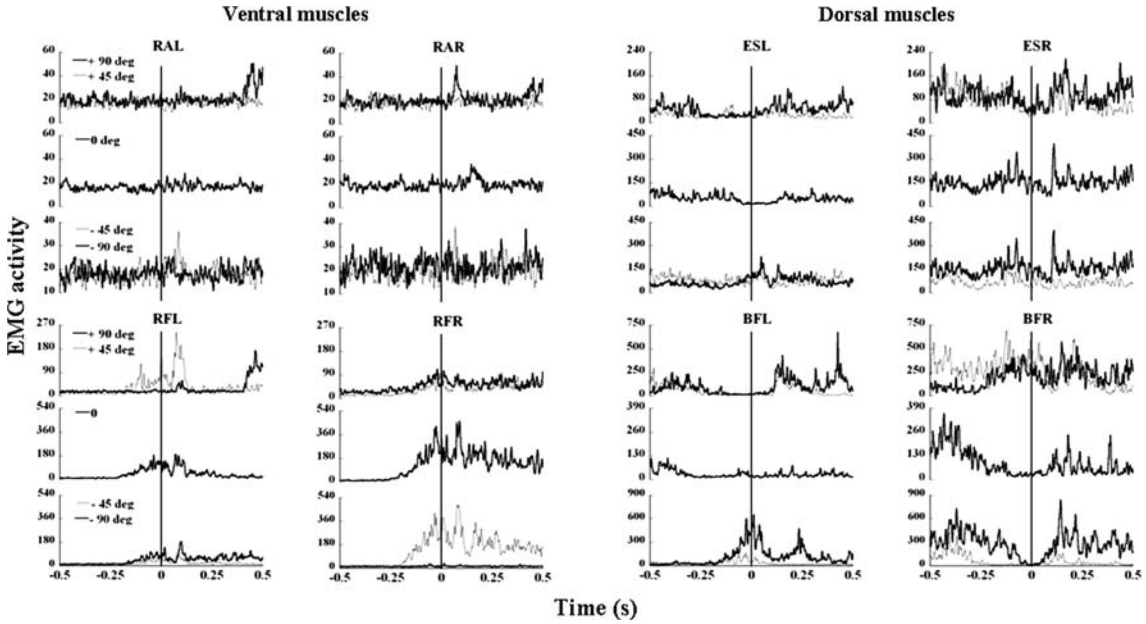

Fig. 2 A typical EMG pattern (averages of six trials for a representative subject) for ventral and dorsal leg and trunk muscles. *RA* rectus abdominis, *ES* erector spinae, *RF* rectus femoris, *BF* biceps femoris. Left (*L*) and right (*R*) muscles are shown. The *vertical lines* at T0 represent the moment of contact of the pendulum with the subject's hand. The angles between the sagittal plane of the body and direction of perturbation are shown in the *left panels*. Time scales are in seconds and EMG scales are in arbitrary units

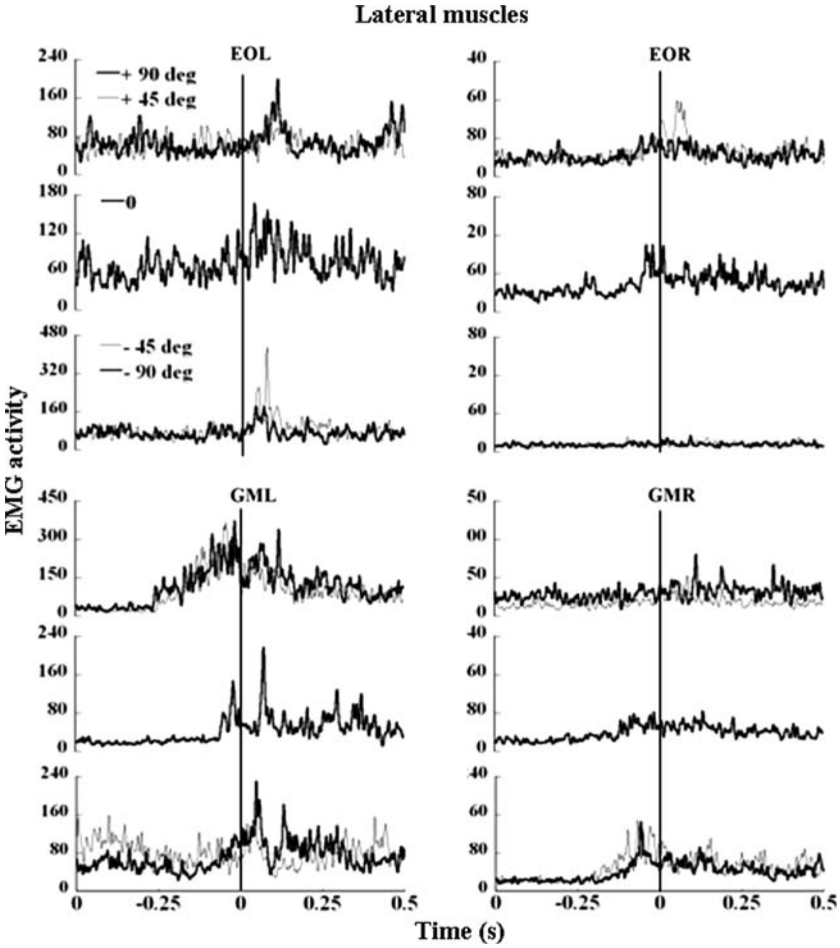

Fig. 3 A typical EMG pattern (averages of six trials for a representative subject) for lateral muscles. *EO* external obliques, *GM* gluteus medius. Left (*L*) and right (*R*) muscles are shown. The vertical lines at T0 represent the moment of contact of the pendulum with the subject's hand. The angles between the sagittal plane of the body and direction of perturbation are shown in the *upper left panel*. Time scales are in seconds and EMG scales are in arbitrary units

anticipatory activation of the ventral, dorsal, and lateral muscles, there were differences in their involvement in feedforward postural control.

Ventral and dorsal muscles

The RFL $\int$EMG indices across the conditions were significantly different ($P < 0.01$). The post hoc analysis revealed that the $\int$EMGs in the +90° position were significantly smaller than in all other positions (i.e., –45°, 0°, –45°, and –90° conditions, $P = 0.01$, $P = 0.01$, $P = 0.02$, and $P = 0.02$, respectively). In addition, the anticipatory $\int$EMG indexes at –90° were significantly smaller than at +45° and 0° ($P = 0.04$ and $P = 0.02$, respectively). Similarly, RFR $\int$EMG indices across the conditions were significantly different ($P < 0.01$). Further post hoc analysis revealed that the RFR $\int$EMG index in the condition of standing frontally to the pendulum movements (0° position) was significantly larger than $\int$EMG indices obtained in conditions with +45 and +90° body orientation in relation to the pendulum movement ($P < 0.01$). Moreover, the $\int$EMG indices for the body positions at +90° and –90° were significantly smaller than indices in the –45° position ($P < 0.01$ and $P = 0.01$, respectively).

Overall, the anticipatory $\int$EMG indices of the BFL and BFR were significantly different among the conditions ($P < 0.01$ and $P < 0.01$). The $\int$EMG indices in BFL changed from inhibition at +90°, +45°, and 0° to activation at –45° at –90° positions; the difference between +90° and –90°, between +45° and –90°, and between +45° and –45° positions was statistically significant (post hoc analysis, $P = 0.04$, $P = 0.03$, and $P = 0.04$, respectively). In addition, the anticipatory activation in BFL in the series with the body position at –90° approached the level of significance and was greater than at 0° and –45° positions ($P = 0.05$ and $P = 0.05$, respectively). Anticipatory $\int$EMGs indexes in the BFR demonstrate an inverse pattern across the conditions compared to $\int$EMGs in BFL. Thus, the $\int$EMG indices in BFR changed from inhibition at –90°, –45°, and 0° to activation at +45° at +90° positions. The difference between +90° and –45°, between +45° and –90°, and between +45° and –45° positions was statistically significant (post hoc analysis, $P = 0.04$. $P = 0.03$ and $P = 0.04$, respectively).

The general patterns of activation of the dorsal muscles (ESL and ESR) were similar to the patterns of activation of

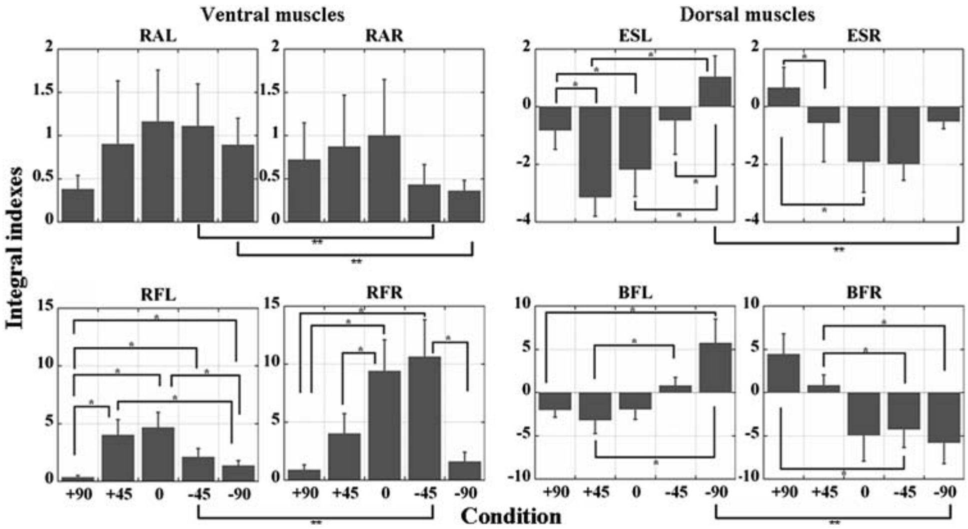

Fig. 4 Anticipatory ∫EMG indexes for ventral and dorsal leg and trunk muscles averaged across 10 subjects. Mean values and standard *error bars* are shown. * denotes significant differences within the conditions while ** indicates significant differences between sides ($P < 0.05$)

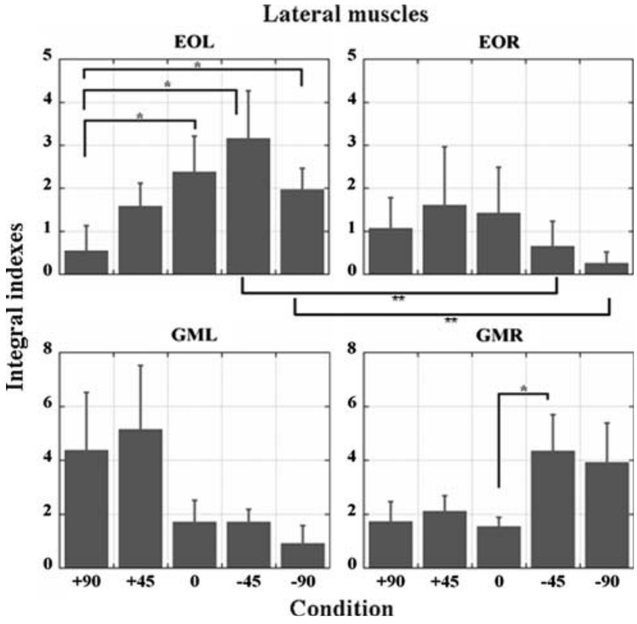

Fig. 5 Anticipatory ∫EMG indexes for lateral muscles averaged across 10 subjects. Mean values and standard *error bars* are shown. * denotes significant differences within the conditions while ** indicates significant differences between sides ($P < 0.05$)

the posterior muscles of the lower limb (BFR and BFL). The ∫EMGs indexes for ESL changed from activation in the series with the body orientation at –90° to anticipatory inhibition in all other experimental series with the –45°, 0°, +45°, and +90° positions of the body; the difference across conditions was statistically significant ($P < 0.01$). The post hoc analysis revealed significant differences between –90° and the three conditions, –45°, 0°, and +45° ($P = 0.03$, $P = 0.01$, and $P = 0.01$, respectively). In addition, the anticipatory inhibition in the position +90° was significantly smaller than the conditions +45° and 0° ($P = 0.03$, $P = 0.03$). Furthermore, the ∫EMGs indexes in the position of +45° changed significantly from inhibition to activation at the –90° position ($P = 0.01$) An inverse pattern of activation was observed in the right ES: the anticipatory activation in the series with the +90° body position (that is reflected on the positive ∫EMGs) was replaced with the anticipatory inhibition in all other experimental series (+45°, 0°, –45°, and –90°). Although, there were no significant differences across the conditions for ESR, post hoc analysis demonstrated significant differences between +90° and both +45° and 0° positions ($P < 0.01$ and $P = 0.03$, respectively). At the same time, the magnitudes of anticipatory ∫EMG indices in the right and left rectus abdominis muscles (RAR and RAL) were always positive and did not show significant differences between the conditions.

Lateral muscles

The ∫EMG indices for the EOL showed significant differences among the experimental conditions ($P < 0.01$) and the ∫EMG for EOR approached the level of significance (Fig. 5). The post hoc analysis detected that the anticipatory ∫EMG indices of the EOL in the series where the perturbation was induced on the right side of the body (+90°) was significantly smaller than those induced in the series with –0°, –45°, and –90° orientation of the body ($P = 0.02$ $P = 0.03$, and $P = 0.02$, respectively). The EOR anticipatory ∫EMG indices approached the significance level between the conditions at 0° and +45° ($P = 0.07$, detected by post hoc analysis).

The magnitudes of the ∫EMG indices of the GM muscles also reflected the dependence on the orientation of the body in relation to the direction of perturbation. Thus, the anticipatory ∫EMGs for GMR in experiments with the perturbation induced in all five-body positions were statistically significant ($P = 0.02$). In addition, ∫EMGs between the series with perturbations induced in the sagittal plane (0°) were significantly smaller compared to $\int$EMGs calculated for the experimental series with the position of the body at the –45° ($P = 0.03$). $\int$EMGs in GML did not show a statistically significant difference across experimental conditions.

Effect of side

When the $\int$EMG indices for RFR and RFL were compared in pairs between sides, the anticipatory activations were significantly different only at the –45° position, with the right greater then the left side ($P < 0.01$). The BFR muscle showed an anticipatory inhibition at the –90° position that was significantly different from the anticipatory activation showed at the left side for the same position ($P = 0.01$). Similarly, for –90°, the ESR changed significantly from inhibition at the right side to activation at the left side ($P = 0.02$). The $\int$EMGs in the rectus abdominis were significantly different between sides for the positions –45° and –90° (Fig. 4). The $\int$EMG indexes in the RAR in these two positions showed smaller anticipatory activation than RAL ($P = 0.03$ and $P = 0.04$, respectively). The differences between sides in EOR and EOL muscles were detected in the positions at –45° and –90° (Fig. 5). The $\int$EMG indexes at the right were smaller than the left side ($P = 0.03$ and $P = 0.01$, respectively). Finally, the GMR and GML muscles did not show any significant differences between sides.

Center of pressure displacements data

The maximum COPx displacement was 0.0029 m and reached 0.013 for COPy. Although the overall displacements of the center of pressure were small, COPy displacements were significantly larger than those of the COPx ($P < 0.01$). Except for 0° position, the COPx displacements were in the posterior direction which is indicated by their positive values. COPy displacements were in the direction opposite to the direction of perturbation in all experimental conditions (Fig. 6). Changes in the direction of perturbation had no statistically significant influence on either CPOx or COPy displacements.

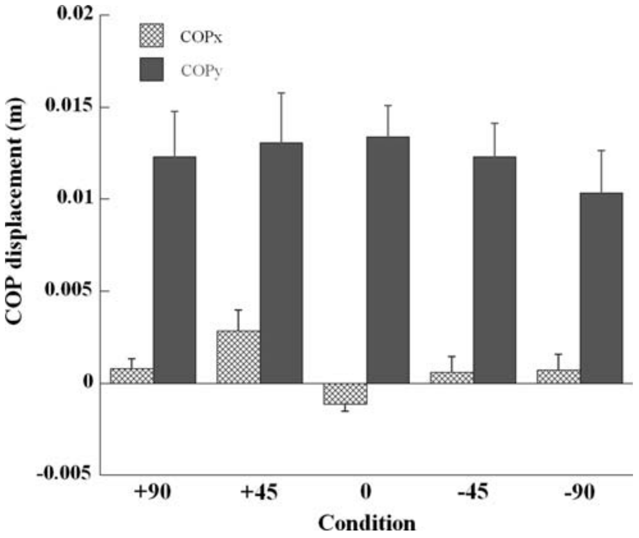

Fig. 6 Mean values and standard error bars of the displacement of center of pressure (COP). *Filled columns* show the displacement of center of pressure that coincides with the direction of perturbation; *hatched columns* show COP displacement in the direction orthogonal to the direction of perturbation. COPy positive values correspond to displacements in the direction opposite to the perturbation. Positive values of COPx correspond to shifts of the center of pressure backwards

Discussion

It is known from previous studies that ventral and dorsal trunk and leg muscles are activated prior to either self generated (Aruin and Latash 1995a, b) or external perturbations (Aruin et al. 2001b; Shiratori and Latash 2001). These studies revealed that changes in the anticipatory activity of these muscles depend on the direction and magnitude of the perturbations (Aruin and Latash 1996; Toussaint et al. 1997; Bouisset et al. 2000), body configuration (Aruin 2003), and postural demands (Nardone and Schieppati 1988; Nouillot et al. 1992; Aruin et al. 2001a; Adkin et al. 2002; Aruin 2003). While it is known that involvement of lateral muscles is crucial in the maintenance of posture in the presence of body asymmetry or in asymmetrical perturbations, available information on the contribution of these muscles in feedforward postural control is scarce.

The current study was focused on investigation of the role of lateral as well as ventral and dorsal muscles in anticipatory control of posture. We utilized external perturbations created by the pendulum released by the experimenter. The pendulum mass was unchanged and it was released the same distance from the subject's extended arms. Therefore, the subjects experienced the same magnitude of perturbations associated with the pendulum impact in all experimental series. The only difference was the direction of the perturbation (the pendulum impact) in relation to the body position. This resulted in a specific anticipatory activation of leg and trunk muscles

Directional specificity of ventral, dorsal, and lateral muscles

Directional specificity of APA in ventral and dorsal muscles was described prior to the initiation of multidirectional bilateral arm raising movements in standing subjects (Aruin and Latash 1995a) and catching or releasing a load (Latash et al. 1995) or in seated individuals performing tasks of force exertion against a stationary frame (Aruin and Shiratori 2003). For example, it was shown that the anticipatory activation patterns in the ES muscles changed gradually from bursts of activity to inhibition when individuals raised their arms in diverse directions as fast as possible ranging from shoulder flexion to shoulder extension, respectively (Aruin and Latash 1995a).

The results of the current experiments revealed a similar direction-specific pattern of anticipatory activation of dorsal muscles. For example, APA bursts in the ESR and BFR muscles, when a lateral perturbation (+90°) was induced, gradually changed to inhibition in the series with the perturbation induced in the opposite direction (–90°). The reversed pattern could be observed in the ESL and BFL muscles (Fig. 4). At the same time, previous experiments with external perturbations induced by catching the load released by the experimenter showed that the same 0° body orientation was associated with increased APAs in the dorsal muscles (ES, BF) while the ventral muscles (RA, RF) showed smaller APAs (Shiratori and Latash 2001). The divergence between the results of these two studies could be explained by the differences in the way the external perturbations were induced. In the present study, the pendulum impact was applied in the horizontal plane while in the former study, loads acted in the vertical plane.

The outcome of the current study confirmed that lateral muscles (GM and EO) demonstrate a direction-specific APA pattern of anticipatory activation as well. Indeed, the GM anticipatory activations were more marked during lateral perturbations (±90°), especially at the contra-lateral side. At the same time, GM activities in conditions with the perturbation acting in frontal plane (0°) were the smallest (Fig. 5). Similar direction-specific APA patterns in the lateral muscles (tensor fascia latae (TFL) were observed in standing subjects during one leg lifting in different directions, i.e., diagonal front, diagonal back and lateral (Hughey and Fung 2005). The TFL showed maximal activations in the loaded leg prior the subjects' lateral lift of their contra-lateral leg.

It is also important to mention that as the principal function of the GM during double stance is to provide lateral stability to the pelvis (Kapandji 1970), the GM activity tends to increase when the body weight is transferred to the ipsilateral leg to avoid the pelvis sagging to the contra-lateral side (Pauwels 1980). Thus, it was demonstrated that the GM muscles are usually more active at the contra-lateral side of the stepping leg during walking (Rogers et al. 1993; Kirker et al. 2000). Past studies also showed that the reactions of GM to the sideways pushing are critical to maintain the postural stability (Gilles et al. 1999; Kirker et al. 2000). For instance, activation of the GM at the left side and inhibition of the GM at the right side was described in healthy subjects after predictable pushing perturbation delivered to the left side at the pelvis level. The subjects in our study activated the GM in both sides prior to the lateral perturbations. However, EMG activity was greater at the contra-lateral side (Fig. 7a). Differences in the GM activations between these two studies might be explained by the time the muscular activities were calculated (anticipatory vs. compensatory reactions) and by the level at which perturbations were applied in these two studies (pelvis level vs. shoulder level). In the current study, the lateral perturbation induced at the shoulder level resulted in the subjects moving away from the upcoming pendulum impact (confirmed by the COP shift toward the side contra-lateral to the perturbation); this was associated with the anticipatory activity of GM at the contra-lateral side. Similarly, APAs in the EO muscles predominantly at the ipsilateral side of the perturbation were increased in comparison with the 0° position to deal with the lateral impact. In addition to the lateral positions, the APAs in the EO muscles were primarily increased in the oblique position (±45°) at the side of the

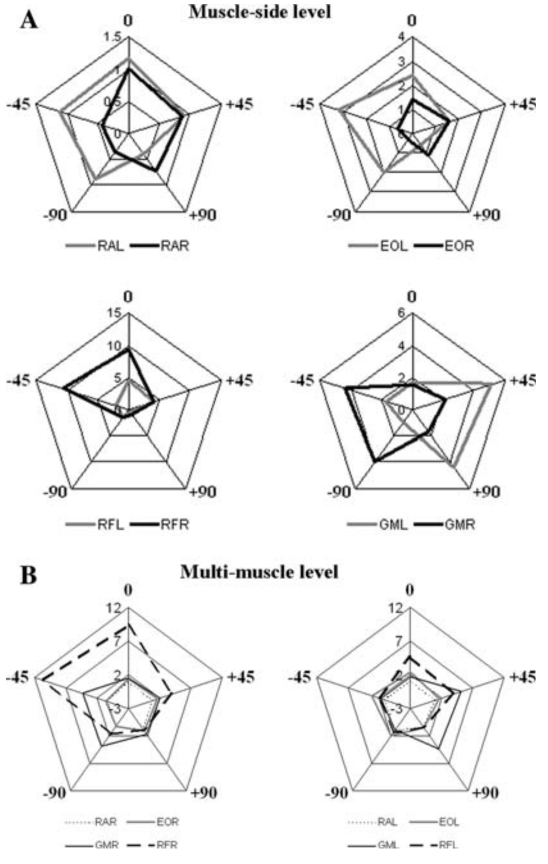

Fig. 7 Anticipatory ∫EMG indexes at the muscle side level (**a**) and multi-muscle level (**b**) as a function of perturbation direction

perturbation. Because these muscles are the prime movers of the trunk rotation (Bogduk and Twomey 1991), their activation prior to the impact in this body position was increased to provide rotational stability to the subjects' trunk. Similar muscle activation patterns were described during experiments with sudden downward loads applied to a plastic box held by the subjects standing in a forward-flexed posture (Granata et al. 2001). Thus, when the subjects stood in asymmetrical position, i.e., 45° twisted to the left side, with the box oriented sagittally and symmetrically to sudden loading, the EOL increased its anticipatory activity significantly compared to the symmetrical positions. APA magnitudes in EOR and EOL muscles in the current study clearly and progressively decreased from the oblique plane at the side of the perturbation to lateral plane at the opposite side of the perturbation.

The side-specific patterns of activation of lateral muscles prior to perturbations induced in both the lateral and oblique directions could be most clearly seen in the EOL and EOR (Fig. 5) and in GML and GMR (Fig. 7a) muscles. For example, a small APA activity in EOL accompanied by a larger activity in EOR could be seen in experiments with the perturbation induced in the lateral direction (+90°). The inverse pattern of anticipatory activation is seen when the perturbation direction is changed (–90°) (Fig. 5). At the same time side-specific APA patterns are observed in ES and BF muscles. For instance, anticipatory inhibition in BFL is accompanied with anticipatory burst of activity in BFR when the perturbation is induced in the lateral plane (+90°); an inverse pattern could be seen when the direction of perturbation is changed to (–90°) (Fig. 4). It seems that the CNS of a healthy individual optimizes the way of dealing with the expected perturbation using a side-specific activation of trunk and leg muscles directed at better body stabilization. It is however, not known at the moment how the side-specific APA patterns are changed in individuals with neurological disorders. At the same time, there is a consensus regarding the importance of trunk stabilization via specific activation of trunk muscles and its improvement with exercise (Vezina and Hubley-Kozey 2000; Arokoski et al. 2001; Souza et al. 2001).

It is also important to mention that there are differences in the body biomechanics between the sagittal and frontal planes: motion in the sagittal plane could be performed at the ankle, knee and hip joints independently while movements in the frontal plane in the hips and ankle joints are restricted and movements in the knee joint are negligible so that a change in one joint angle leads to a change in the others. In addition, a stiffness control was described at the ankle plantar flexor muscles for sagittal plane motion and at hip abductor/adductor muscles for frontal plane motion (Winter et al. 1996). This suggests that side-specific differences in APAs between lateral muscles and ventral and dorsal muscles observed in the current study could also be associated with mentioned above differences in biomechanics of the body.

Dealing with mechanical consequences of the perturbation: which mode of anticipatory muscle activity is utilized?

In the majority of previous studies APAs have been defined as changes in the patterns of muscle activity that produce forces and moments acting against the mechanical effect of an expected perturbation (Bouisset and Zattara 1987b; Friedli et al. 1988; Krishnamoorthy and Latash 2005). Moreover, anticipatory COP shifts have been observed either before self-initiated (Aruin and Shiratori 2004) or external predictable perturbations, for example, in load-catch experiments (Aruin et al. 2001b). During the load-catch condition, individuals shift their body weight posteriorly before the load impact. It looks like that posterior COP shift was associated with accommodating the predicted effect of the perturbation that, if not corrected, would decrease body stability as it might happen if the falling load is caught in conditions of forward lean. Thus, it seems reasonable to shift the body backwards in a feed-forward manner in order to prepare for accepting the load. Thus, one could expect that in anticipation of the perturbation, the subjects would lean towards the pendulum trying to minimize the destabilizing effect of the impact. As a result, the anticipatory activation of the frontal muscles should have been observed in order to resist the pendulum impact. Indeed, the anticipatory activations of these muscles were seen in this study (for example, in RAL and RAR, Fig. 7). However, the overarching strategy was in fact a shift of the COP away from the predicted perturbation. In other words, the subjects seemed to "flee" away from the impact even though they knew, based on performance of the practice trials that it would not be harmful. It is possible that the CNS used anticipatory shifts of the body backwards in order to better absorb the pendulum impact. The existence of such a "protective" strategy to absorb the perturbation could be suggested based on the results of EMG analysis of the arm muscles during a task of catching a ball (Lacquaniti and Maioli 1987). It was also suggested recently that the role of APAs is associated with providing maximal safety of the postural task component (Krishnamoorthy and Latash 2005). Thus, it is possible that the COP shift away from the predicted perturbation is a deliberate strategy that the CNS uses to provide maximal safety and protection while maintaining vertical posture in the presence of a perturbation.

It is known that anticipatory shifts of the center of mass and center of pressure are achieved by coordinated changes in the activity of agonist–antagonist muscles pairs as well as across a variety of postural muscles. In the former, the CNS uses a reciprocal or co-activation patterns while in the latter a group of muscles would act in a "concerted manner", as it was coined in the literature (Macpherson 1991), thus, creating a synergy. A reciprocal activation of agonist and antagonist muscle groups enables the precise stabilization of body segments in space observed for single-joint movements (Hallett et al. 1975; Bonnet 1983; Rothwell et al. 1986; Mustard and Lee 1987; Gottlieb et al. 1989) and for multi-joint movements (Friedli et al. 1984; Hong et al. 1994; Latash et al. 1995). A co-activation of the muscles at the joint increases joint stiffness and viscosity in order to augment joints stability in the case of a planned perturbation (Hogan 1985; Hogan et al. 1987; Kearney and Hunter 1990).

In the current experiments a reciprocal pattern of activation could be seen in the rectus abdominis-erector spinae and rectus femoris–biceps femoris muscle pairs on both right and left sides of the body in most of the experimental conditions (Fig. 4). Thus, bursts of activity seen for example in left RA were accompanied by inhibition in left ES muscles; a similar reciprocal pattern could be observed in RF–BF muscle pair. The only exception was a co-activation of RA–ES and RF–BF muscle pairs seen on the side of the perturbation. This happened only when the lateral perturbation is induced on the right or left sides of the body (+90° and –90°, respectively).

On one hand, a co-activation pattern could be seen in EO–GM muscle pair across all experimental conditions. On the other hand, while both left and right EO–GM muscles show anticipatory bursts of activity, the level of its activation depends on the orientation of the body in relation to the perturbation direction. It seems that the CNS precisely adjusts activity in the ipsilateral and contra-lateral lateral muscles thereby stabilizing the body prior to the planned perturbation. This could be seen most clearly in the EOL and EOR muscles (Fig. 5).

It looks like the CNS controls activation of muscles on two levels, on a muscle side level and on a multi-muscle level. A side-specific activation at the muscle side level could be observed in RA, RF, EO, and GM (Fig. 7a). Most clearly, it is seen in GML and GMR muscles that demonstrate a "butterfly"-like side-specific pattern of anticipatory activation. For example, larger anticipatory activation in GML muscle was observed when perturbations were induced in oblique and lateral plans on the right side of the body (+45° and +90°) and in GMR muscle when perturbations were induced on the left side of the body (–45° and –90°). At the same time, anticipatory activation in GML and GMR muscles were small when perturbation was induced in the sagittal plane (0°).

At the multi-muscle level, several muscles acted in combination creating a synergy. Such a synergistic activation of RA, RF, EO, and GM could be seen in most of experimental conditions (Fig. 7b); it is more pronounced in the +45°, +90° as well as –45° and –90° directions. It looks like the coordinated activation of these muscles resulted in shifting the body weight to the leg opposite to the side of perturbation. At the same time, for the sagittal plane (0°), the posterior COP shift was due to the activation of the frontal muscles TA and RF and small inhibition of the dorsal muscles SOL and BF.

It seems that the CNS precisely estimates the effect of a predicted perturbation and uses synergistic anticipatory activation of selected muscles that could provide the best body stabilization. The results of the current experiment demonstrated that this is a possible scenario: APAs in lateral muscles were seen prior to the perturbations induced in the lateral and oblique planes and anticipatory activity in ventral and dorsal muscles were present when perturbations were induced in the sagittal plane (0°). A particular list of muscles and their level of involvement in the anticipatory adjustment depended on the direction of a perturbation.

How is the anticipatory activation of ventral, dorsal, and lateral muscles arranged in the presence of lateral perturbation? It appears as though the CNS modifies commonly used flexible muscle synergies or creates new ones in order to best meet the functional demands of the task. The utilization of muscle synergies for feedback postural control is described in the literature (Horak and Nashner 1986; Macpherson et al. 1986; Henry et al. 1998). The present study provides new data on the utilization of muscle synergies in feedforward postural control in the presence of lateral perturbations. For instance, we observed a reciprocal activation of ventral and dorsal muscles when the task demands are relatively easy or a co-activation of muscles when the task demands are more challenging. In addition, a coordinated anticipatory activation of a number of muscles including ventral, dorsal, and lateral ones could be seen.

Using reciprocal activation of muscles and successfully adjusting it with the task demands could be a relatively easy job for a young individual. It has been also shown that young adults could easily change their EMG patterns with changes in stability conditions during standing (Krishnamoorthy et al. 2004). However, it might be challenging for an elderly individual or for someone with a neurological impairment. For example, it is known that the elderly (Blaszczyk et al. 1997; Bleuse et al. 2005) and individuals with neurological impairments (Aruin and Almeida 1997; Garland et al. 1997; Massion et al. 1999) commonly use a co-activation of muscles in both feedforward and feedback postural control. It is believed that the CNS of these individuals deliberately utilizes such a less efficient but safer co-activation EMG pattern to overcome certain limitations associated with disease or advanced age. It is also known from the past studies that the GM EMG activity is altered in the elderly (Allum et al. 2002), in individuals who have sustained a stroke (Hedman et al. 1997; Kirker et al. 2000), and in those with hip osteoarthritis (Sims et al. 2002). However, it is not known at the moment whether such individuals would use anticipatory activation of laterals muscles to the same extent as the healthy subjects did in the current experiment. It is quite possible that a deficiency in anticipatory activation of not only ventral, dorsal, but also lateral muscles especially while dealing with perturbations induced in lateral plane, might be a reason why the elderly and some patients have difficulties in balance maintenance and in turn have an increased risk of falls. Thus, if it is the case, learning how to use anticipatory activation of lateral muscles together with the activation of ventral and dorsal muscles could potentially help such individuals in dealing with many activities of daily living involving body perturbations in lateral plane.

Conclusion

The results of the current experiment suggest that the CNS deliberately uses direction-specific pattern of anticipatory muscular activation in the ventral, dorsal, and lateral muscles in order to counteract the perturbation. Moreover, the CNS could modify available muscle synergies or create new synergies to deal with the increased difficulties of the task.

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