

Anticipatory postural adjustments associated with lateral and rotational perturbations during standing

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Abstract

We studied the role of different leg and trunk muscle groups in the generation of anticipatory postural adjustments (APAs) prior to lateral and rotational perturbations associated with predictable and self-triggered postural perturbations during standing. Postural perturbations were induced by a variety of manipulations including catching and releasing a load with the right hand extended either in front of the body or to the right side, performing bilateral fast shoulder movements in different directions, and applying brief force pulses with a hand against the wall. Perturbations in a frontal plane (“lateral perturbations”) were associated with significant asymmetries in APAs seen in the right and left distal (soleus and tibialis anterior) muscles; these asymmetries dependent on the direction of the perturbation. Rotational perturbations about the vertical axis of the body generated by fast movements of the two shoulders in the opposite directions were also associated with direction-dependent asymmetries in the APAs in soleus muscles. However, rotational perturbations generated by an off-body-midline force pulse application were accompanied by direction-dependent asymmetries in proximal muscle groups, but not in the distal muscles. We conclude that muscles controlling the ankle joint play an important role in the compensation of lateral and rotational perturbations. The abundance of muscles participating in maintaining vertical posture allows the control system to use different task-dependent strategies during the generation of APAs in anticipation of rotational perturbation. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Perturbations of vertical posture of a standing individual are frequently associated with self-initiated actions. In particular, fast arm movements, load manipulations such as catching and releasing a load, and interactions with external objects may all be the sources of inertial and reactive forces perturbing the vertical posture. A number of mechanisms serve to maintain the equilibrium. Among them are changes in the background activity of postural muscles seen prior to the perturbation that are commonly addressed as anticipatory postural adjustments (APAs) [1–4]. APAs are believed to be gen-

erated in a feed-forward fashion based on predictions of an upcoming perturbation associated with a planned action; their purpose is to counteract the effects of the perturbation on vertical posture. A number of factors are likely to play major roles in the process of APA generation. Among them are the magnitude and direction of an expected perturbation, properties of a voluntary action associated with the perturbation, body configuration prior to the action, and features of the postural task, in particular, postural stability [5–10].

In studies of APAs during fast arm movements, reproducible patterns have been reported for proximal postural muscle pairs such as rectus abdominis–erector spinae (RA–ES) and rectus femoris–biceps femoris (RF–BF) [11–14]. Changes in the background activity of the tibialis anterior–soleus (TA–SOL) pair were considerably more variable across subjects. These observations allowed Aruin and Latash [14] to suggest that the role of the distal muscles, controlling the ankle joint, was

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relatively minor and might involve fine tuning of the general APA pattern provided mostly by the proximal muscles during fast shoulder movements. The TA–SOL muscle pair controls the ankle joint which is assumed to be primarily involved in postural corrections of unexpected postural perturbations in young, healthy subjects (the “ankle strategy” [22, 23]). In a recent paper, Winter and colleagues [15] have assumed that the anterior–posterior balance during quiet side-by-side standing is totally under ankle joint control. It has been puzzling that the muscle pair providing much of quiet stance balance and later postural adjustments shows relatively irregular behavior during APAs.

However, Zattara and Bouisset [12] have shown significant changes in the contribution of TA–SOL to APAs during unilateral shoulder movements performed by standing subjects. In a later study, substantial involvement of the TA–SOL pair in APAs has been demonstrated during asymmetrical perturbations and under unusual postural conditions involving standing on roller-skates [16]. Based on these data, it has been suggested that the APA pattern is determined by the plane of action: proximal muscle pairs provide the APA during shoulder flexion/extension action, while the TA–SOL pair mainly compensates for lateral and/or rotational perturbations emerging, in particular, during unilateral arm movements.

All these studies, however, have used movements that were associated with both lateral and rotational perturbations of the trunk and, therefore, failed to distinguish between possible effects of these two types of postural perturbations on APAs. The main purpose of the present study has been to separate the effects of rotational and lateral perturbations on APAs seen in different trunk and leg muscle pairs. We tested a hypothesis that muscle pairs whose action is specific to such perturbations should show asymmetries between the left and right homologous muscle groups and these asymmetries should depend on the direction of the perturbation. Muscle pairs whose action is specific to anterior–posterior perturbations only are not expected to show any such effects. Since the magnitude of the APAs and even their presence or absence have been shown to depend on the type of action triggering the perturbation [6, 8], we have decided to use a range of actions associated with rotational and lateral perturbations. Therefore, a variety of actions by the standing subjects was used to induce the perturbations including arm movements, load catching and releasing, and generating brief force pulses with a hand against a stationary external object.

2. Methods

2.1. Subjects

Seven subjects, three males and four females, 27.9 (\pm 2.2) years old, mean weight 66.9 (\pm 5.6) kg, and

mean height 1.68 (\pm 0.04) m, participated in Experiment-1. Experiment-1 was performed in the Motor Control Laboratory of the Pennsylvania State University. Twelve subjects, seven males and five females, 31.0 (\pm 3.06) years old, mean weight 69.9 (\pm 4.48) kg and mean height 1.69 (\pm 0.02) m took part in Experiment-2. Experiment-2 was performed in the Motion Analysis Laboratory of the Rehabilitation Foundation, Inc. All the subjects were right handed and free of any known neurological or peripheral motor disorders. The subjects gave informed consent according to the procedures approved by the Office for Regulatory Compliance of the Pennsylvania State University and by the Institutional Review Board of the Rehabilitation Foundation, Inc.

2.2. Experiment-1

2.2.1. Apparatus

The subjects stood comfortably and quietly on a biomechanical platform (AMTI, OR-6). The signals from the platform were amplified and used to measure reaction forces in three orthogonal directions (along the direction of gravity F_z , parallel to the ground in the sagittal plane F_x , and parallel to the ground in the frontal plane F_y) and moments of forces in three directions (in the sagittal plane, M_y , in the frontal plane, M_x , and around the vertical axis of the body, M_z). Horizontal displacements of the center of pressure in the anterior–posterior (CP_y) and medio–lateral (CP_x) directions were calculated using the following approximation: $CP_{x,y} = M_{x,y} / F_z$. Displacements of the center of pressure were quantified at t_0 with respect to time -500 ms when no APAs were expected. Anticipatory changes in the muscle activity were associated with shifts of the center of pressure (CP). However, these shifts were small and variable across subjects. Therefore, within this study no quantitative analysis of CP is presented.

Disposable pediatric electrocardiographic electrodes (10 mm in diameter) were used to record the surface EMG activity of the following postural muscles in both sides of the body: rectus abdominis (RA), erector spinae (ES), rectus femoris (RF), biceps femoris (BF), soleus (SOL), tibialis anterior (TA), and flexor carpi radialis (FCR). The electrodes were taped over the muscle bellies. The distance between two electrodes of a pair was about 4 cm. The EMG signals were amplified ($\times 3000$), band-pass filtered (60–500 Hz) prior to sampling, and digitized with a 12-bit resolution at 1000 Hz.

A unidirectional force sensor (208A03, PCB Piezotronics, Inc.) was securely attached to the wall. Its signals were amplified (M482M66, PCB Piezotronics, Inc.) and used to record the force applied by the subject’s hand during pushing against the sensor. The sensitivity of the transducer was 2 mV/N; its linearity was better than 0.4%. The entire system was operating in a d.c.-coupled mode, utilizing the sensor’s discharge time con-

stant as established by the built-in microelectronic circuit within the sensor. The system gave approximately a 1% error over 20 s.

A Mac-IIci computer with customized software based on the LabView-3 package was used to control the experiment, collect the data, and perform most of the analyses.

2.2.2. Procedure

Within Experiment-1, the subjects were instructed to generate brief pulses of force by one of the hands against the force transducer fixed to the wall at the shoulder level. A rigid rectangular piece of plastic (7×4 cm) was taped to the palmar surface of the distal phalanges of the fully extended index, middle, and ring fingers of the right or of the left hand. The subject stood on the platform at a certain distance from the wall so that when he/she extended the arm in a horizontal plane, the piece of plastic just touched the transducer. In different series, the subject was standing so that: (1) he/she was facing the wall and the transducer was at the midline of the body; (2) he/she was facing the wall and the transducer was 0.3 m to the right or 0.3 m to the left from the midline of the body; or (3) the wall was in a sagittal plane to the right or to the left from the subject, and the transducer was at the shoulder level, 0.5 m from the shoulder nearest to the wall.

In each condition, the subject was asked to touch the force sensor with the plastic piece but not to exert force on the sensor. After a computer-generated beep, the subject produced a force pulse against the sensor (“pushed against the wall”) within a time interval of 3 s, in a self-paced manner. The recommended magnitude and timing of the force pulse were selected so as to induce a substantial postural perturbation that could lead to loss of balance and making a step, but not to lead to fatigue or discomfort. The subjects were allowed to select their own force pulse characteristics as long as they reproduced them across the trials and series. Force pulses were displayed on-line on an oscilloscope screen, and the experimenter made sure that they were of similar characteristics (peak amplitude and width). In different series, pushes were performed by the right or by the left hand in each of the three mentioned conditions. Each series included six trials. The order of series was pseudo-randomized (balanced). The interval between trials within a series was 8 s; the interval between series was 1 min. The subjects performed two practice trials prior to each series. Fatigue was never an issue.

2.3. Experiment-2

2.3.1. Apparatus

Similar techniques were used in both experiments to record ground reaction forces and moments. A miniature unidirectional accelerometer (Sensotec) was taped to the

wrist of the subject with the axis of its maximal sensitivity oriented in the plane of expected perturbation. The sensitivity of the accelerometer was 50 mV/g at 50 Hz; its mass was 0.005 kg; its range was ±100 g.

Disposable pediatric electrocardiographic electrodes (10 mm in diameter) were used to record the surface EMG activity of the following postural muscles from both sides of the body: rectus abdominis (RA), erector spinae (ES), soleus (SOL), and tibialis anterior (TA). The distance between the two electrodes of a pair was about 4 cm. The EMG signals were amplified by means of differential amplifiers (×3000), and digitized with a 16-bit resolution at 1000 Hz.

A PC computer with customized software based on the LabView-4 package was used to control the experiment, collect the data, and perform most of the analyses.

2.3.2. Procedure

Experiment-2 consisted of two parts. Within the first part, the subjects were required to catch or release a standard load into/from the right hand. Within the second part, the subjects performed fast voluntary arm movements. Before each trial, the subjects were asked to stand quietly, their feet 0.3 m apart. Upon hearing a tone signal (a beep), the subjects were instructed to perform a required action “as fast as possible” within 1–3 s after the signal, in a self-paced manner. Individual trials were performed in series of six. Prior to each series, the subjects were instructed which movements to perform and given two or three practice trials. The interval between the trials within a series was 8 s; the interval between the series was about 1 min. The subjects were asked to make actions within a series as similar to each other as they could. The wrist never showed visible displacement prior to the load impact or prior to the focal voluntary movement. Fatigue was never an issue.

The first part of Experiment-2 included four series (Fig. 1A). In the first two series, the subjects were instructed to hold a load with an attached handle gripped by their right hand. The load was a 2.3 kg solid, brick-shaped object (0.3×0.1×0.05 m) with a comfortable handle attached to the center of its top. The elbow was always fully extended, while the wrist was in the neutral position. In series 1, the shoulder was flexed 90° so that the hand with the load was in front of the body at the right shoulder level. In series 2, the shoulder was adducted 90° so that the hand with the load was in the frontal plane of the body. In both series, the subjects were required to release the load in a self-paced manner by opening the right palm 1–3 s after hearing a computer beep. After the release, the load was caught by the cord attached to the ceiling.

In the next two series (series 3 and 4), the subjects were required to catch a 1.16 kg load into the right palm; the load was held by the experimenter 0.5 m above the subject’s palm and released after a computer generated

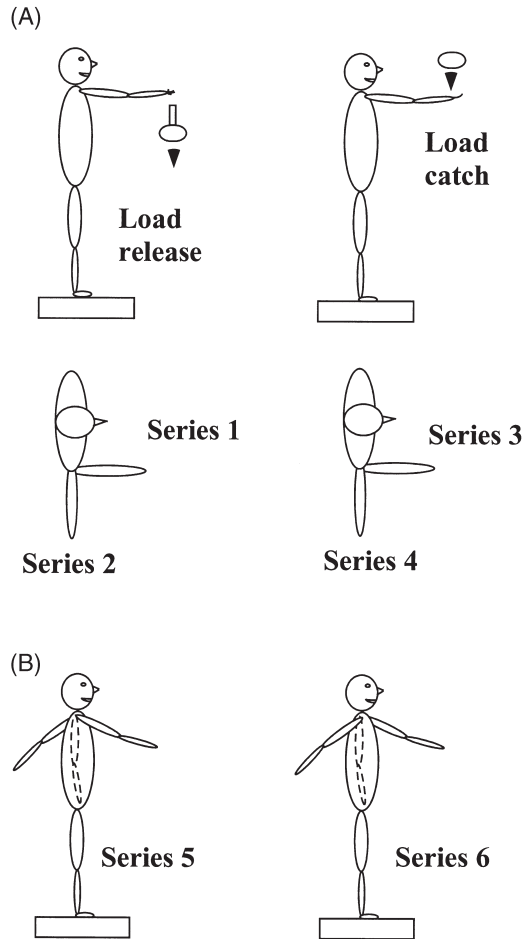


Fig. 1. A schematic illustration of the experimental procedures. A — Load manipulations (side view and view from above): series 1 and 2, load release, series 3 and 4, load catch. B — Fast bilateral arm movements (side view): series 5, simultaneous right shoulder flexion and left shoulder extension movements, and series 6, simultaneous left shoulder flexion and right shoulder extension movements.

beep. The experimenter managed the consistency of the load release height using a marker, attached to a vertical ruler, as a reference point. The load was a solid, round-shaped object with the diameter of 0.1 m. The weight of this load was selected based on pilot trials to match approximately the magnitudes of the APAs seen in postural muscles during the load catch and release series. The subjects were required to look straight at the load. The same arm positions as in the first two series were used.

Within the second part of Experiment-2 (Fig. 1B), the subjects performed two series of fast arm movements: simultaneous right shoulder flexion and left shoulder extension (series 5), and simultaneous left shoulder flexion and right shoulder extension (series 6) over the same nominal amplitudes. A nominal movement amplitude of 45° was recommended to the subjects, but they were free to select a comfortable actual movement amplitude as long as all the movements were similar to

each other. We did not observe asynchronous arm movements in any of the series. The order of series was pseudo-randomized (balanced).

2.3.3. Data processing

Similar data processing procedures were used in both experiments. The trials were viewed off-line on a monitor screen and aligned according to the first visible deflection of a signal from the accelerometer (Experiment-2) or of the EMG signal in the wrist flexor (Experiment-1). This time was considered “time zero” (t_0) in all further analyses.

EMG signals were rectified and low pass filtered at 100 Hz. The area under the rectified EMG curve (EMG integral) was calculated from -100 to $+50$ ms with respect to t_0 ($\int \text{EMG}_{\text{APA}}$) and used for the leg and trunk muscles to characterize the anticipatory EMG changes in the activity of the postural muscles. These intervals of integration were chosen based on previous studies that described APAs typically starting about 100–150 ms prior to the focal movement [8, 14]. These values were corrected for the background EMG integrated over a time period from -500 to -450 ms prior to t_0

$$\left(\int \text{EMG}_{\text{bg}} \right):$$

$$\int \text{EMG} = \int \text{EMG}_{\text{APA}} - 3 \int \text{EMG}_{\text{bg}}$$

The integral values for each muscle and each subject were normalized by the maximal magnitude of the integral seen in all the series within each experiment.

Statistical methods included repeated measures ANOVA's with the main factors being BODY SIDE (right or left) and TASK (levels depended on particular experiments). Student's two-tailed, paired t -tests were also used.

3. Results

3.1. Experiment-1

In Experiment-1, postural perturbations were created by brief force pulses applied by the subject's hand against a force sensor mounted on the wall at the shoulder level. When the subject stood facing the wall and applied force pulses with the right or with the left hand against the sensor mounted at the midline of the body, postural muscles of the left and right sides of the body demonstrated similar early changes in their background activity. These APAs could be seen 100–200 ms

prior to the force increase and typically included a decrease in the background activity of SOL, BF, and ES, and an increase in the background activity of TA, RF, and RA. The patterns were variable across the subjects so that not all the subjects showed EMG changes in all the recorded muscles.

When the sensor was moved to a side (0.3 m from the midline of the body), pronounced asymmetries were seen between the APAs in the left and right proximal muscle pairs. A typical pattern is illustrated in Fig. 2 (averages of six trials by a representative subject). When the push was generated by the right hand, an increase in the background activity of the right BF was seen without

major changes in the activity of the left BF. However, there were considerably larger APA bursts in the left RF and RA. When the push was generated by the left hand, the patterns changed with the larger BF burst seen in the left side of the body and larger RF and RA bursts seen in the right part of the body. The right and left TA–SOL muscle pairs typically did not show APA asymmetries during pushes with the left and with the right hand. In this particular subject, there was a difference between the activation patterns seen in the TA muscles, but this difference was seen after the perturbation and was not seen in other subjects.

Quantitative analysis of \int EMG indices across subjects

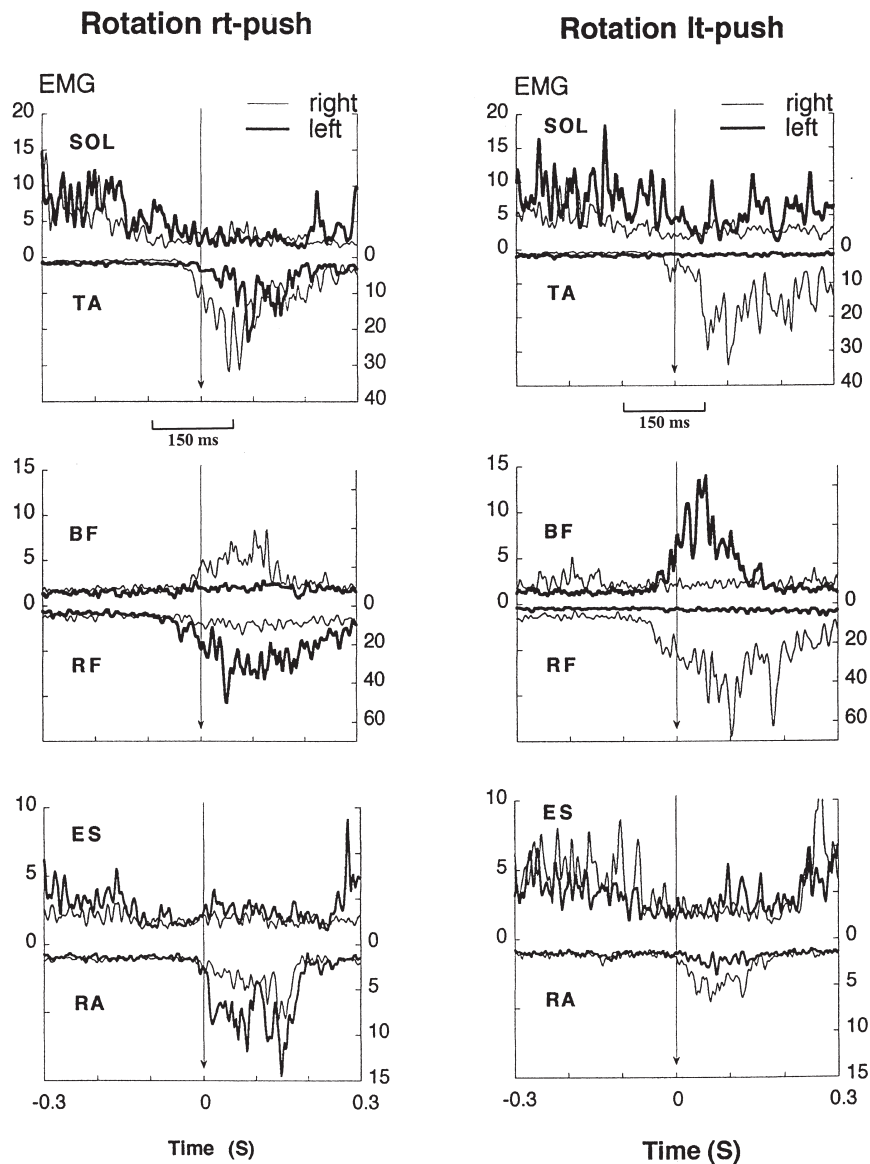


Fig. 2. A typical EMG pattern (averages of six trials for a representative subject) for series of trials with postural perturbations created by brief force pulses applied by the subject's hand against a force sensor mounted at the wall at the shoulder level. Left panels — push was generated by the right hand; right panels — the left hand generated push. Time scale is in seconds, EMG scales are in arbitrary units. EMGs of the muscles of the frontal part of the body are inverted for better visualization. The arrows show the time of alignment (see Section 2). The interval of EMG integration during APAs is shown with bold brackets under the time axis.

was performed using two-way ANOVAs (body side×push side). There were no main effects for any of the muscles. However, there were significant interactions for RF and RA ($F_{6,1}=15.2, p<0.01$ for RF and $F_{6,1}=6.9, p<0.05$ for RA), and a close to significant interaction for ES ($F_{6,1}=4.8, p=0.07$) illustrated in Fig. 3A. No significant interactions were seen for TA–SOL. The interactions observed for the proximal muscles reflected the general pattern illustrated in Fig. 2: a rotational perturbation applied by the right hand induced larger APA bursts in the left RF and RA and larger APA suppressions in the left BF and ES. Opposite results were seen during force pulses applied by the left hand.

In two more series, the subject applied similar force pulses against the sensor mounted on the wall while the subject stood so that the wall was in a sagittal plane (see Section 2). These force pulses created lateral perturbations. The generation of these force pulses was

accompanied by APAs seen in most postural muscles. However, these patterns were rather variable across subjects so that reproducible findings were obtained only for the TA–SOL muscle pairs.

Figure 4 illustrates EMG patterns in these muscles during force pulse generation by the right hand and by the left hand. Averages across six trials by a representative subject are shown. Note that the push by the right hand was preceded by an increase in the background activity of the left SOL and a drop in the background activity of the right SOL. When a similar push was applied by the left hand, the patterns of changes in the SOL background activity reversed, i.e. there was an increase in the right SOL and a decrease in the left SOL. TA showed relatively small changes without an obvious asymmetry between the right and left muscles. The two bottom panels of Fig. 3 illustrate results of the quantitative analysis. There was a significant two-way interaction (body side×push side) for \int EMG-indices in SOL

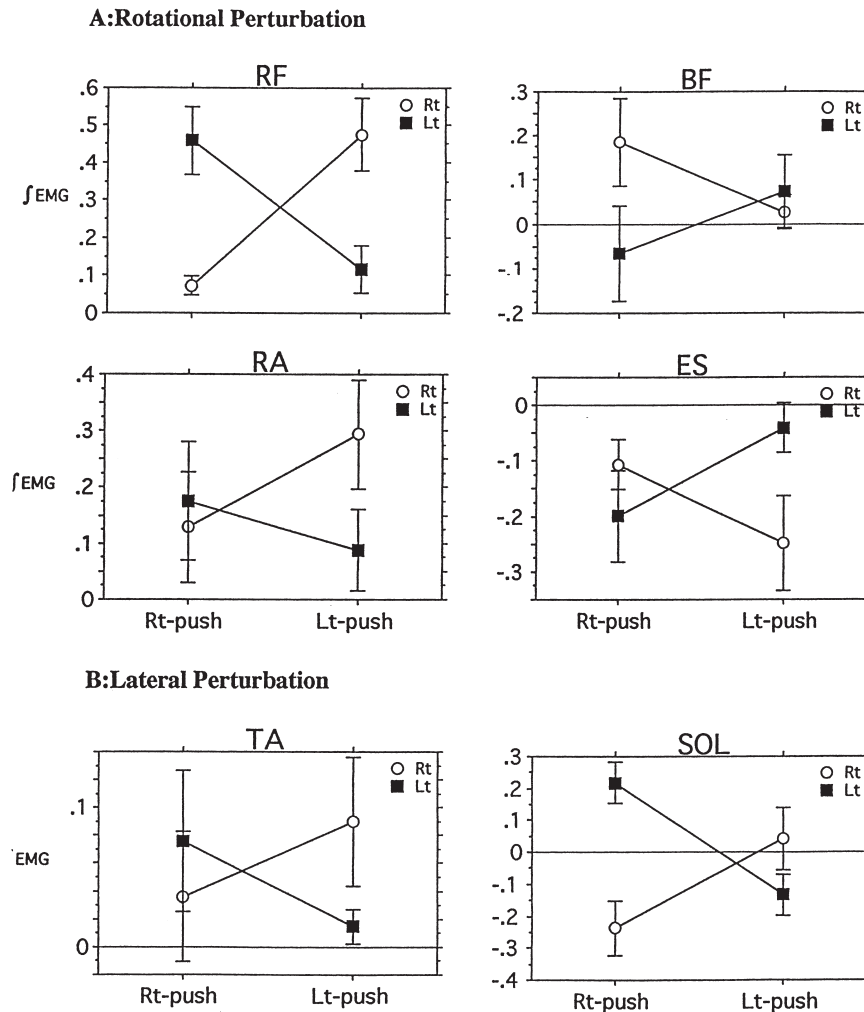


Fig. 3. Quantitative analysis of anticipatory EMG of postural muscles (\int EMG) for rotational and lateral perturbations. Averaged data for seven subjects are presented with standard error bars.

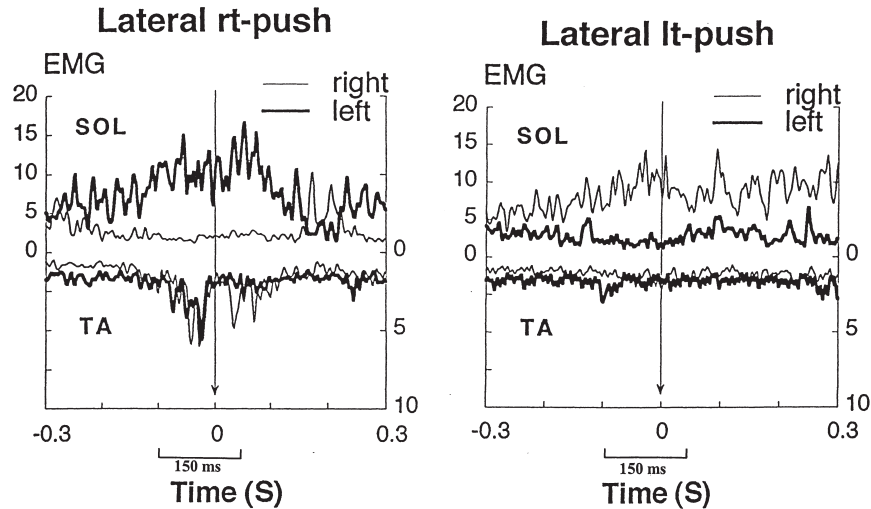


Fig. 4. A typical EMG pattern (averages of six trials for a representative subject) for series of trials with postural perturbations created by brief force pulses applied by the subject's hand against a force sensor mounted at the wall at the shoulder level while the subject stood facing perpendicular to the wall. Left panels — push was generated by the right hand; right panels — the left hand generated push. Time scale is in seconds, the arrows show the time of alignment (see Section 2), EMG scales are in arbitrary units. EMGs of the muscles of the front part of the body are inverted for better visualization. The interval of EMG integration during APAs is shown with bold brackets under the time axis.

($F_{6,1}=8.3$, $p<0.05$) while the interaction for TA was under the level of significance.

3.2. Experiment-2

3.2.1. Part 1: load manipulations

During load catching and releasing trials, APAs could be seen as changes in the background activity (EMG) of postural muscles starting from about 100–150 ms prior to the load release or impact. When the right hand, that was used to catch and release the loads, was in front of the subjects, the trunk muscle pair (RA–ES) showed the most reproducible patterns of anticipatory activation. In particular, both ES muscles demonstrated an anticipatory inhibition of the background activity in load release trials and an anticipatory increase in the activity in load catch trials. RA muscles also showed symmetrical changes in the background activity in the left and right muscles with prevalence of anticipatory activation during both load catch and release trials. Changes in the background activity of the TA–SOL pair were small and poorly reproducible across subjects.

When the subject's right arm was extended in the frontal plane, load catch and release were associated with asymmetrical APA patterns in the left and right postural muscles. Figure 5 illustrates EMG patterns averaged across six trials performed by one of the subjects. Prior to the load release (left panels), there was a drop in the background activity of the left ES and RA, while the activity of the right ES showed an anticipatory increase and the activity of the right RA did not show visible changes. Prior to load catch (right panels), the left ES and RA muscles showed an increase in the background activity while there were no visible changes in

the activity of the right ES and RA muscles. In this particular subject, there were also clear asymmetries seen in the APAs in the TA–SOL muscle pair (upper panels in Fig. 5). However, other subjects showed different patterns of APAs in these muscles.

EMG integrals during APAs were measured in averaged trials for each series and each subject separately, and normalized (see Section 2). Figure 6 presents \int EMG indices averaged across subjects during load release and catch with the right arm fully adducted. Two-factor ANOVAs were run for each muscle. There were main effects of task (catch versus release) for RA ($F_{11,1}=11.67$, $p<0.05$) and ES ($F_{11,1}=52.7$, $p<0.05$), a main effect of body side for ES ($F_{11,1}=11.5$, $p<0.05$) and a body side by task interaction for SOL ($F_{11,1}=25.5$, $p<0.05$). The main effect of body side for RA was close to the level of significance ($F_{11,1}=4.02$, $p<0.07$).

3.2.2. Part 2: arm movements

Bilateral arm movements and load manipulations were associated with relatively small rotational perturbations about the vertical axis of the body (M_z). Averaged across subjects peak-to-peak values of M_z were under 1 N m for all these series. Unilateral arm movements were associated with significantly larger rotational perturbations as reflected in much higher average peak-to-peak M_z values (absolute values ranging between 5 and 7.5 N m). The largest rotational perturbations occurred during arm movements in the opposite directions (peak-to-peak absolute M_z values over 9 N m). The differences among the bilateral unidirectional movements, unilateral movements, and bilateral movements in opposite directions were all statistically significant ($F_{11,1}>35$; $p<0.01$).

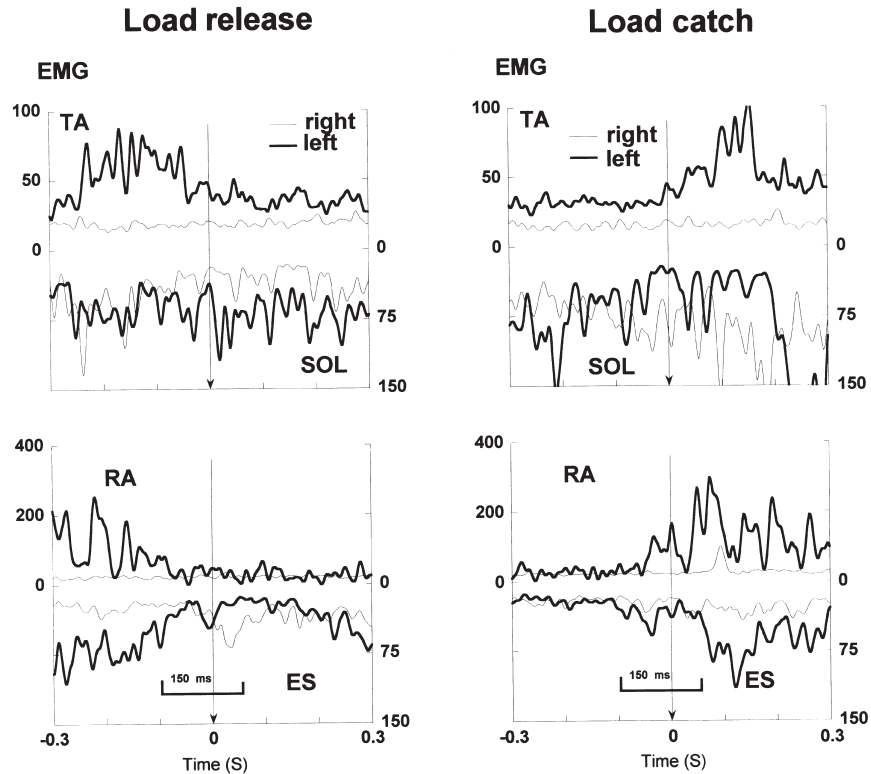


Fig. 5. EMG patterns (averages of six trials) for series of trials with load catch and load release and performed by a representative subject. The right arm receiving or releasing the load was fully extended to the right. Time scale is in seconds, the arrows show the time of alignment (see Section 2), EMG scales are in arbitrary units. EMGs of the muscles of the dorsal part of the body are inverted for better visualization. The interval of EMG integration during APAs is shown with bold brackets above the time axis.

Figure 7 illustrates EMG patterns for two series, right shoulder flexion plus left shoulder extension (left panels) and left shoulder flexion plus right shoulder extension (right panels) averaged across six trials by a representative subject. Note similar APA EMG bursts in the left and right ES in both series. Most significant differences between the series were seen in the APAs in SOL. In particular, during the first series, there was an anticipatory activation of the left SOL and depression in the right SOL; during the other series, this pattern inverted. This particular subject showed pronounced APA asymmetries in the right and left TA muscles. However, other subjects showed more variable patterns for TA, and ultimately, these effects were not significant.

Integrals of anticipatory changes in the background activity of postural muscles are presented in Fig. 8. Note the very small differences in the \int EMG indices in ES and RA between the two series and between the two sides of the body. There were no main effects of two-way ANOVAs (body side by task). There was a significant body side by task interaction effect for SOL ($F_{11,1}=7.5$, $p<0.05$).

4. Discussion

A variety of motor actions by a standing person were used in the present study to generate postural perturbations. These actions included load manipulations, fast arm movements, and force generation against an external object. As such, they represented examples of many groups of actions commonly performed during everyday activities. Arm movements and load manipulations have been commonly used in studies of APAs [1–3, 5, 8, 14, 17]. There have been relatively few studies of APAs during force pulse generation against an external object [18–21]. It is not always easy to separate a postural component of a task from a “focal” component. In particular, arm force generation by standing subjects need to be accompanied by the generation of joint torques by the muscles of the legs if the subject wants to maintain equilibrium. However, a person can generate a force pulse by an arm in the absence of an adequate torque pattern in the leg joints and, consequently, lose equilibrium. Hence, we view changes in the leg muscle activity as determined by the postural component of the task, not by the task of force pulse generation itself. As such, they

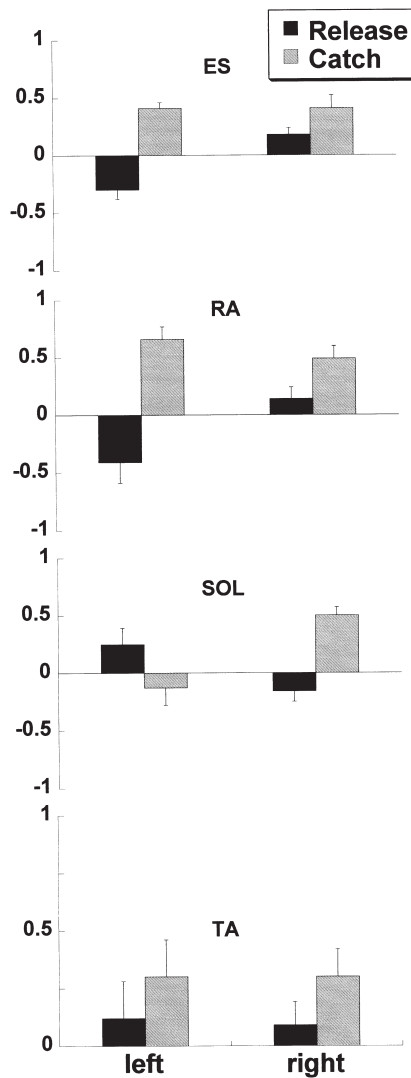


Fig. 6. Normalized integrals of anticipatory changes in the activity of postural muscles averaged across 12 subjects, with standard error bars for load catch and release with the right arm fully adducted.

may be viewed as APAs according to the accepted definition [5].

In all these tasks, modifications of some of the task parameters allow relatively easy changes in the direction of the perturbing forces and moments acting on the body. As a result, one can produce perturbations confined mostly to the anterior–posterior direction, or lateral perturbations (in a frontal plane), or rotational perturbations, or their combinations using similar motor actions. This is important for making comparisons among APA characteristics in different conditions since APAs have been shown to depend on properties of motor actions associated with a postural perturbation [6, 8].

For example, in Experiment-1, a force pulse generated by the subject's hand could produce a perturbation in the anterior–posterior direction when the subject was

facing the point of force application and it was aligned with the midline on the body. A similar force pulse produced a rotational perturbation when the point of force application was moved 0.3 m laterally from the midline of the body. A lateral perturbation in a frontal plane was also generated by a similar action when the wall with the point of force application was in a sagittal plane. Similarly, in Experiment-2, catching and releasing loads by a hand in front of the body produced anterior–posterior perturbations while similar actions with the arm extended to the side (the shoulder adducted 90°) produced lateral perturbations; asymmetrical bilateral shoulder flexion/extension combinations were used to induce rotational perturbations.

Only a few earlier studies of APAs [4, 16] used asymmetrical motor actions to generate postural perturbations that were likely to lead to strong lateral and/or rotational perturbations. However, in these studies, unilateral fast arm movements were used that were associated with a combination of all three perturbations: anterior–posterior, lateral, and rotational. Our manipulations were designed to study APAs specific for these perturbations separately.

5. APAs in preparation to lateral perturbations

In Experiment-1, lateral perturbations were associated with asymmetrical APA patterns in the right and left SOL that showed a significant dependence on the direction of the perturbation. Similar asymmetries in SOL APAs were also seen in Experiment-2. However, the findings in the proximal muscle groups in the two experiments were different. In Experiment-1, no significant effects were found for the RF–BF and RA–ES muscle pairs. In Experiment-2, significantly different effects of the direction of perturbation were found for the proximal muscles, but these effects were similar for the right and for the left muscles showing no interaction effects. The lack of significant effects in proximal muscles could be partly due to the variability among the subjects and different precision in reproducing movement parameters. However, the contrast between significant effects in TA–SOL muscles and the lack of effects in proximal muscle pairs allows us to conclude that the TA–SOL pair plays a major role in counteracting lateral perturbations, while the role of proximal muscles is less obvious and may be task-specific.

Note that most earlier studies reported reproducible APA patterns in proximal muscle groups but not in the TA–SOL pair [11–14]. The apparent contrast of these findings with the “ankle strategy” which is assumed to be primarily involved in postural corrections of unexpected postural perturbations in young, healthy subjects [22, 23] was one of the driving forces behind the present study. Our findings suggest that the role of the TA–SOL

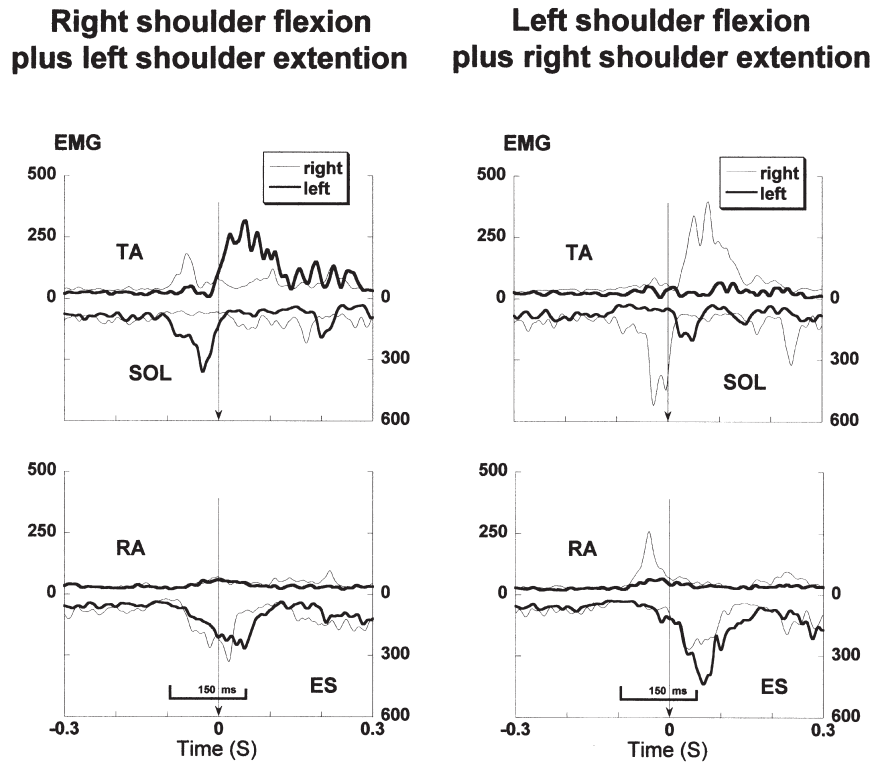


Fig. 7. EMG patterns (averages of six trials) for series of trials with simultaneous right shoulder flexion plus left shoulder extension (left panels) and left shoulder flexion plus right shoulder extension (right panels) performed by a representative subject. Time scale is in seconds, the arrows show the time of alignment (see Section 2), EMG scales are in arbitrary units. EMGs of the muscles of the dorsal part of the body are inverted for better visualization. The interval of EMG integration during APAs is shown with bold brackets above the time axis.

pair during APAs may, in fact, differ from its role during later reaction to postural perturbations. It is also likely to differ from the role of these muscles during quiet standing as assumed by Winter et al. [15], who suggested that the anterior–posterior balance during quiet side-by-side standing was totally under ankle joint control.

A number of studies of compensatory responses in postural muscles to perturbations in different directions in both humans and animals showed a systematic variation of muscle responses with the direction of the perturbation [24–26]. In particular, it was shown that the angular ranges for the activation of distal muscles were relatively narrow while the angular ranges for the activation of proximo-axial muscle pairs were broader. It was also shown that the onset latencies in the proximo-axial muscles varied dramatically as perturbation direction was altered, while the onset latencies in the distal muscles were relatively constant. Based on these findings, it has been suggested that the operational rules for the action of proximo-axial muscles and of the distal muscles are different. It is quite possible that differences in response characteristics between the proximo-axial and distal muscles observed in our experiments are

related to different roles of these muscles in the control of limb dynamics, posture, and interaction torques [27].

6. APAs in preparation to rotational perturbations

Patterns of APAs in preparation to rotational perturbations were significantly different in the two experiments. In Experiment-1, rotational perturbations were associated with asymmetrical APA in the proximal muscle groups (RF–BF and RA–ES) which were dependent on the direction of the perturbation. No such effects were seen in the TA–SOL muscle group. In Experiment-2, however, significant asymmetries were seen between the APAs in the right and left SOL muscles, and these asymmetries were dependent on the direction of the perturbation. No similar effects were seen in proximal muscles.

These differences may be attributed to the differences in the actions that the subjects performed to generate postural perturbations. In Experiment-1, the action was always the same (force pulse generation by a hand), while the positions of the body with respect to the point of force application and the hand that applied the force

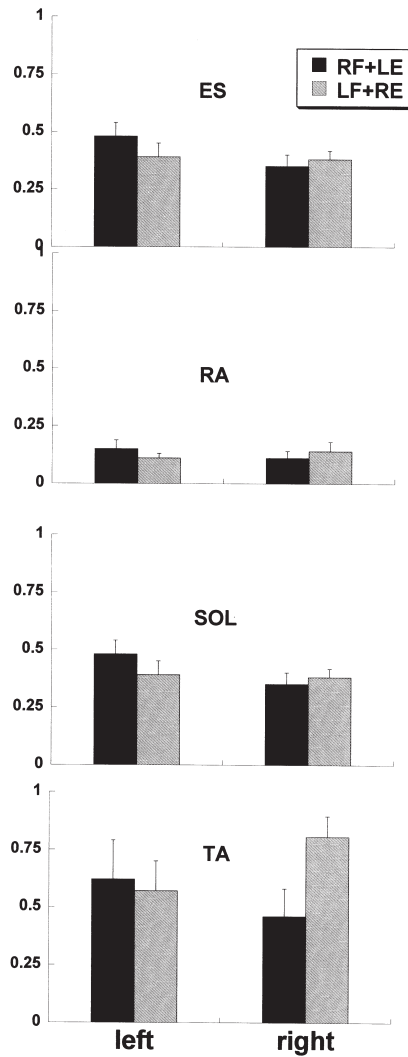


Fig. 8. Normalized integrals of anticipatory changes in the activity of postural muscles, averaged across 11 subjects, with standard error bars, for experiments involving shoulder arm movements. Abbreviations: RF+LE — series experiments with simultaneous right shoulder flexion plus left shoulder extension; LF+RE — series of experiments with right shoulder flexion plus left shoulder extension.

were modified. In Experiment-2, actions performed by the subject were rather different and included fast arm movements into flexion or extension.

In an earlier study, Shiratori and Latash [16] observed only quantitative differences between characteristics of APAs in proximal muscles in two tasks, when the subjects performed bilateral unidirectional shoulder movements and when the subjects performed similar movements with the right arm only. Asymmetrical APAs were seen in SOL similar to the effects observed in Experiment-2. Note that unilateral arm movements are associated with a combination of postural perturbations in different directions. Movements of two arms in opposite directions, however, are expected to lead to mostly

rotational perturbations. With this in mind, Experiment-2 involved a better-controlled rotational perturbation as compared to the experiments by Shiratori and Latash [16]. The similarity of the findings in these two studies, however, suggests that APAs in SOL can indeed participate in compensation of rotational trunk perturbations in standing persons.

Our findings can be interpreted within the referent configuration hypothesis suggested by Feldman and his colleagues [28]. This hypothesis implies, in particular, that the EMG patterns are defined by shifts in the referent body configuration. These shifts can be direction- and subject-specific leading to different EMG patterns observed in response to rotational and lateral perturbations.

7. Concluding comments

There are both similarities and differences between the findings in our two experiments. The similarities involve, in particular, the significant participation of the ankle muscles in the generation of APAs associated with lateral postural perturbations. The fact that this participation was demonstrated in two different experiments involving different actions to generate lateral perturbations suggests that this is a robust finding. The differences, particularly those related to the involvement of different muscle groups during rotational trunk perturbations, emphasize another message. The system for maintaining vertical posture in humans allows different solutions for postural tasks as illustrated, for example, by the presence of at least two kinematic strategies, the ankle and the hip strategy, in response to postural perturbations [22]. As such, it may be viewed as abundant at the muscle level of analysis (cf. Gelfand, Latash [29]). We purposefully do not use the more common term “redundant” [30, 31] because we are convinced that the excessive number of muscles does not represent a problem for the system of postural control but rather a luxury. It allows the control system to use different muscle strategies in dealing with apparently similar mechanical perturbations.

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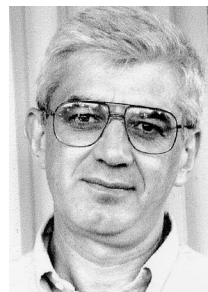
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