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RESEARCH ARTICLE

Equilibrium constraints do not affect the timing of muscular synergies during the initiation of a whole body reaching movement

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Abstract The aim of this study was to determine whether the timing of the muscular synergies was influenced by the reduction of the base of support when we initiate a whole body reaching movement. To answer this question, we performed a principal component analysis on electromyographic activities of 24 muscles recorded on the leg, the trunk, and the arm. Our results demonstrated that during the initiation of the whole body pointing movement, only three principal components accounted for at least 95% of the variance for the overall muscular data, both when the equilibrium constraints were normal and when the base of support was reduced. These principal components were strongly correlated despite the fact that the center of mass forward displacement and the center of pressure backward displacements significantly decreased when the base of support was reduced. It suggests that the central nervous system did not change the overall timing of the muscular synergies when new equilibrium constraints were introduced in the task but was rather able to tune their amplitude as evidenced by the modification of the center of mass and center of pressure displacements.

Keywords Muscular synergy · Equilibrium · Principal component analyses · Whole body reaching · Central nervous system

Introduction

According to the motor equivalence problem, a great variety of movements can be performed to reach the same goal, depending on the context (Lashley 1942; Bernstein 1967). The way the central nervous system (CNS) adapts its motor strategy to the context and the way the muscles are coordinated are important issues in the field of motor control. Given the important number of muscles that can be involved in a particular movement, Bernstein suggested that the CNS simplifies the 'problem of redundancy' by grouping some muscles activities together to reduce the number of degrees of freedom to control (Bernstein 1967). More specifically, Torres-Oviedo et al. (2006) and Mussa-Ivaldi and Bizzi (2000) defined muscles synergies as a set of basic motor commands, which linearly combined, may generate a large repertoire of movements. This hypothesis has received a great deal of experimental and theoretical support (Flash and Hochner 2005; Nori and Frezza 2005). By using techniques of dimensionality reductions (such as principal component analyses (PCA), Jolliffe 1986, or non-negative matrix factorisation, Tresch et al. 2002), many studies proved the existence of a synergetic organizations in postural control and reaching tasks (Poppele and Bosco 2003; d'Avella et al. 2003, 2006; Ivanenko et al. 2006; Bizzi et al. 2008). For instance, Ivanenko et al. (2005) observed that for

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various forms of gait, five principal components were systematically maintained.

When synergies are combined to reach a particular goal, their robustness may be challenged by the level of task constraints. For instance, when additional goals are combined to the main task, new muscles synergies can be superimposed to the original ones (Ivanenko et al. 2005 see their discussion). This observation may be particularly salient when additional goals are explicit, namely when the subjects are instructed to perform the task in a particular way. For instance, the strategy employed to reach a target with the whole body is to displace the hands following a curved trajectory (Stapley et al. 1999; Pozzo et al. 2002). At the same time, the angular joints strongly covariated between the upper and the lower limbs (Berret et al. 2009). Interestingly, these authors demonstrated that when the subjects were simply instructed to follow a straight trajectory with their hands, the covariation between angular joints of the upper and the lower limbs decreased despite the hand trajectory was slightly deviated from its natural path. These authors suggested that at a kinematic level, the CNS could combine or separate the movements into autonomous functional submovements according to the task requirements. More simply, a correlated motion between lower and upper limb joints suggested that the CNS has combined two synergies into one, while uncorrelated motion suggested that two separate synergies are used. According to Ivanenko et al.'s hypothesis (2005), this could be achieved at a muscular level by adding a new muscular synergy to the basic ones.

Equilibrium constraints often importantly modify the motor behavior while maintaining the main goal of the task (Hugon et al. 1982; Bouisset and Zattara 1987, 1990; Crenna et al. 1987; Zattara and Bouisset 1988; Mouchnino et al. 1992; Massion 1992). In this case, it is unknown whether the level of similarity between postural and focal synergies is low or poor. More generally, when equilibrium constraints are deeply varied, it is unidentified whether the CNS plans new synergies or whether basic synergies are maintained and tuned in a different manner. This question is all the more appealing because equilibrium and movement constraints both impose reciprocal constraints on each other, challenging the robustness of the selected synergies. In other words, moving one part of the body necessarily imposes a displacement of the center of mass that challenges the equilibrium control. Conversely, equilibrium constraints challenge the efficiency of goal-directed movements (Bourdin et al. 1998; Berrigan et al. 2006).

For instance, when equilibrium constraints are manipulated by reducing the base of support, the center of pressure and the center of mass displacements are reduced (Aruin et al. 1998; Nouillot et al. 1992; Yiou et al. 2007). In addition, it was shown that parkinsonian patients (Bloem et al. 2006; Nunzio et al. 2007; King and Horak 2008; Tagliabue et al. 2009) or elderly people (Horak 2006) used a smaller body inclination to maintain a safe equilibrium when required to reach a target with their arm. These reciprocal constraints are particularly perturbing for the movement initiation, since at the end of the movement, strong reafferences occurred that may allow correcting the on-going movement (Facchinetti et al. 2006).

These drastic changes in the motor behavior could be reached in two different ways. Either the CNS could elaborate a new muscle synergy to adapt the initiation of the movement to the new equilibrium constraints or the CNS could adapt existing motor synergies to preserve the forward displacement of the CoM typically observed in whole body pointing movements (Stapley and Pozzo 1998; Stapley et al. 1999; Pozzo et al. 2001; Pozzo et al. 2002). In this latter case, the amplitude of muscular synergies would be modulated to generate the required behavioral changes leaving, however, the timing of muscles activations reflected in the PCA unchanged.

In order to test both hypotheses and determine whether the timing of muscular synergies was influenced by the reduction of the base of support (BoS) when we initiate a whole body reaching movement, we analyzed the subjects' focal and postural muscle activity using PCA. The equilibrium constraints were significantly increased by reducing the BoS.

Materials and methods

Subjects

The main experiment was conduced with ten healthy participants, all men (aged = 29 ± 5 old, height = 1.78 ± 0.05 m, weight = 80 ± 7 kg and foot size = 0.25 ± 0.06 m) who voluntarily agreed to participate in this study. In addition, a control experiment was performed with six subjects taken among the initial participants, 1 week after the main experiment (aged = 27 ± 3, height = 1.76 ± 0.08 m, weight = 74 ± 4 kg). None of the participants in the principal or the control experiment had any previous history of neuromuscular disease. Written consent was obtained following guidelines of the University of Burgundy. All the experiment was conformed to the Declaration of Helsinki.

Experimental protocol

Main experiment

Participants were barefooted and were asked to point to two targets with the two arms simultaneously, from a natural upright standing position with both index fingertips. The targets were located near the ground, and their distance from the subject was normalized with respect to the subject's height (H). They were placed forwardly at 10 or 30% of H in the sagittal plane from the end of their big toe. The space between the two targets in the vertical plane was equal to the distance between both acromial processes, and they were at 10% of H from the ground. The whole body movement was then symmetrically performed in the sagittal plane (see Fig. 1 for illustrations). The subjects started from a natural upright position. The movement was self-paced, and the subjects were instructed to perform the movement at a natural speed to touch the targets. The targets were mounted on a flexible stalk so that the subjects could not lean on them.

The subjects performed four blocks of six pointing movements in two different conditions of BoS (Normal vs. Reduced BoS) for two different target distances (D1: 10% of H and D2: 30% of H). In the Reduced BoS condition, the subjects stood on a horizontal 50 × 50 cm board made of wood under which a 5 cm large × 5 cm high piece of wood was also fixated (see Fig. 1). The whole system (small piece of wood fixated to the board) was put down the force plate without any fixation. The vertical projection of the malleolus of each foot was located at the rear limit of piece of wood. In the Reduced BoS condition, in order to only modify the equilibrium context and to keep the pointing distance constant with respect to the Normal condition, the targets were raised to the board height. The blocks of (Normal BoS, Reduced BoS) × (D1, D2) conditions were randomised. The trials were disregarded when the board knocked on the floor ($<10\%$ of trials). Importantly, the displacement of the CoP was not exactly the same under the plantar sole and under the small piece of wood. However, the variation was physically very small. The extreme excursion of the Center of Pressure under the plantar sole (x value in Fig. 1) was determined by half of the length of the section ($d = 0.05/2$), the weight of the board ($Wb = 1$ kg), and the weight of the subject ($Ws = 80$ kg) according to the following equation: $x = d \times Wb/Ws$ (i.e. <0.35 mm), which was negligible according to us. We made sure that the subjects kept about the same initial posture in the Normal BoS and Reduced BoS conditions (see the "Results"). Therefore, each subject performed 6 trials × 4 blocks (Normal BoS D1, Normal BoS D2, Reduced BoS D1, and Reduced BoS D2) = 24 trials overall in order to limit fatigue effects occurring around 80 trials (Schmid et al. 2006).

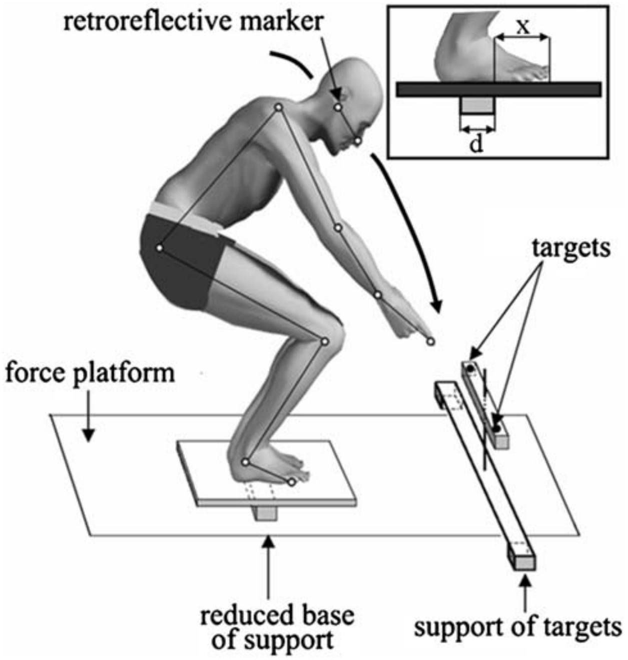

Fig. 1 Motor task and experimental apparatus in the Reduced BoS condition and for the second target distance (D2). *Black sticks* show the eight-segments mathematical model of the body used for the CoM computation. The inset box illustrates the two distances "d" and "x" used to compute the maximal excursion of the CoP displacement under the plantar sole

Control experiment

The control experiment was conduced in order to confirm whether the Reduced BoS condition had an influence on the ankle muscular activities during the static standing posture (i.e., whether the Reduced BoS condition had a significant impact on the initial equilibrium control). In this latter experiment, the subjects were required to maintain a natural standing posture in the Normal BoS and the Reduced BoS conditions previously described. The ankle muscular activities were recorded for both conditions during 10 s and for six trials in each condition.

Body and finger kinematics

The positions of 10 retroreflective markers (diameter = 15 mm) were recorded using an optoelectronic measuring device, VICON (Vicon Motion System, AURION S.r.l., Milano, Italia) at a sampling frequency of 100 Hz. The markers were used to define an eight-links-body model (see Fig. 1) and were fixated on the right side of the body, on the head (the external canthus of the eye, and the auditory meatus), the upper limb (the acromial process, the lateral condyle, the styloid process, and the fingernail of the index), the trunk (regarded as an unbending segment between the acromial process and the greater trochanter), and the lower limb (the greater trochanter, the knee interstitial joint space, the external malleolus, and the fifth metatarsophalangeal of the foot). The recorded position signals were low-pass filtered using a digital fifth-order Butterworth filter at a cut-off frequency of 10 Hz (Matlab filtfilt function). Kinematic recordings permitted the comparison of the initial standing posture and the comparison of the finger trajectory parameters between the Normal BoS and the Reduced BoS, in each distance condition. Moreover, kinematics data were used to compute the length of the foot for each subject. To test whether the pointing performance remained unchanged across conditions, we also computed the 95% confidence ellipse area of the finger endpoint (F_{epArea}) and the distance between the centers of these 95% confidence ellipses ($\Delta C_{\mathrm{ellipse}}$). In addition, the finger movement onset (t_0) and offset (t_{end}) were measured when the linear tangential velocity of the index fingertip was equal to 5% of the maximal velocity before and after the peak value was reached. The time to peak velocity (TPv) was computed as the duration between the peak velocity and the movement onset of the finger, and the movement duration (mD) was computed as the duration between the beginning and the end of the finger movement ($\mathrm{mD} = t_{\mathrm{end}} - t_0$) (see Fig. 2).

Similarly, to check that initial standing postures were identical between the Normal BoS and the Reduced BoS conditions, seven elevation angles (with regard to the vertical axis *Y* geocentric referential) were computed and compared (see Fig. 3; Table 1).

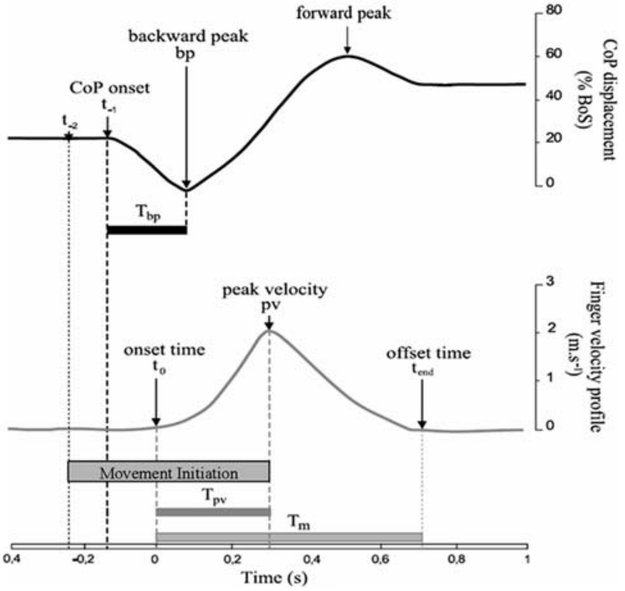

Fig. 2 Definition of temporal and amplitude parameters on typical raw data. *Top*: antero-posterior displacement of the CoP in Normal BoS condition D2, normalized by the BoS length. *Bottom*: finger velocity profile recorded in the Normal BoS condition, D2

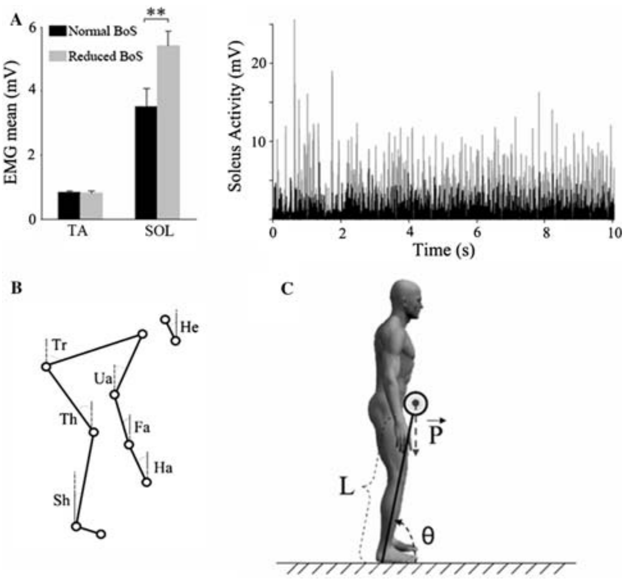

Fig. 3 Control experiment: posture maintenance task. **a** Histograms depict the mean EMG activities of the TA and the SOL during the Normal BoS and the Reduced BoS conditions. *Error bars* indicate the standard deviation. Right graphs show a typical EMG trace of the SOL activity during posture maintenance in the Normal BoS and Reduced BoS conditions. **b** Definitions of the eight elevation angles evaluating the "initial" posture. **c** Illustration of the inverse pendulum model used to evaluate the ankle torque during the posture maintenance task

Table 1 Average values (±SD) of each elevation angle in degrees for all the subjects

	ND1	RD1	ND2	RD2
Sh	−7.2 ± 2.9	−10.6 ± 5.1	−7.8 ± 3.1	−9.3 ± 2.9
Th	−1.6 ± 4.1	−2.1 ± 9.1	−2.5 ± 4.4	−1.6 ± 2.8
Tr	0.3 ± 2.7	−1.7 ± 9.0	0.2 ± 2.5	−0.5 ± 3.4
He	41.3 ± 10.9	42.6 ± 19	45.2 ± 21	41 ± 14
Ua	−1.7 ± 5.4	−6.6 ± 6.3	−3.9 ± 5.1	–5.7 ± 3.6
Fa	22.9 ± 5.4	21.5 ± 8.1	21.8 ± 3.6	20.2 ± 4.1
Ha	20.7 ± 7.9	22.3 ± 6.3	20.8 ± 8.3	22.1 ± 8.1

These values were measured during the initial position in the four experimental conditions

Center of mass and center of pressure recordings and analyses

The center of mass (CoM) was computed using an eight-segments mathematical model consisting of the following rigid segment: head-neck, trunk, thigh, lower leg, feet, upper arm, forearm, and hand. Using this model, the position of the CoM was calculated using documented anthropometric parameters (Winter 1990). The amplitude of the CoM displacement was computed as the absolute difference between the two extreme positions in the antero-posterior (A–P) axis. The positions of the center of pressure (CoP) were recorded using a force platform VICON NEXUS (Vicon Motion System, AURION S.r.l., Milano, Italia) at a sampling frequency of 1,000 Hz. Basically, for this type of movement, the CoP followed an initial backward shift followed by a forward displacement (Stapley and Pozzo 1998; Stapley et al. 2000; Pozzo et al. 2001, 2002; Fig. 2). The amplitude of the backward peak (Δ_{bp}) was calculated with respect to the mean value of the average initial position (baseline). The baseline was computed for each trial as the mean of the CoP position for 0.5 s before the movement initiation. The amplitude of the CoP (Δ_{CoP}) was computed as the absolute difference between the two extreme positions. These two parameters were expressed in percentage of the participants' foot length, which is equal to the position of the fifth metatarsophalangeal of the foot minus the position of the external malleolus. In addition, the following temporal parameters were computed: the CoP movement onset (t_{-1}) was defined as the moment at which A–P CoP velocity exceeded 5% of its backward peak. The time-lag between t_{-1} and the moment at which the CoP reached its backward peak was termed the backward peak duration (T_{bp}).

Electromyographic recordings

Before pasting the surface electrodes (the interval between each electrode for one recorded muscle was 2 cm), the subjects were instructed how to selectively activate each muscle (Kendall et al. 1993). Simultaneously, their skin was shaved and cleaned with alcohol to ensure low resistance. Then, the surface (electromyographic) EMG activities were recorded at a sampling frequency of 1,000 Hz (ZERO WIRE EMG system, AURION S.r.l., Milano, Italia). Each electrode was equipped with a little unit for signal processing and 6 tele-transmissions. The following 24 muscles were recorded for each subject, on his right side : tibialis anterior (TA); soleus (SOL); peroneus longus (PERL); gastrocnemius lateralis (LG); vastus lateralis (Vlat); vastus medialis (Vmed); rectus femoris (RF); semitendinosus (ST); semimembranosus (SM); biceps femoris (long head) (BF); adductor longus (ADD); gluteus maximus (GM); rectus abdominis, superior portion (RAS); internal oblique (OI); erector spinae, recorded at L2 (ESL2); (these fifteen first muscles were considered as "postural" muscles in our task); serratus anterior (SER); pectoralis, superior portion (PECS); latissimus dorsi (LD); rhomboid (ROM); deltoideus anterior and posterior portions (DELTA and DELTP, respectively); biceps brachii (BIC); brachioradialis (BRA); and triceps brachii (TRIC) (these nine last muscles were considered as "focal" muscles). For all these muscles, electrodes were placed to minimize cross talk from adjacent muscles contractions according to Ivanenko et al. (2005) guidelines. The EMG signals were band-pass filtered between 10 and 450 Hz. The roots mean square (RMS) of the EMG signals was calculated over time-intervals of 10 ms.

EMG analysis

A principal component analysis (PCA, Jolliffe 1986) was performed on the overall EMG activities to extract the muscular synergies used during the whole body pointing task initiation. PCA is a standard statistical technique generally used to extract a low-dimensional structure from a high-dimensional data set, using a linear technique. Mathematically, the method involves the eigenvalue decomposition of a data set covariation matrix in order to find the principal directions in the high-dimensional space. In the context of muscle synergies, PCA has been used as a dimensionality reduction tool applied to the muscle space. Physiologically, the underlying assumption is that two correlated EMG signals could belong to the same muscle synergy and that, in general, a specific EMG signal could originate from a linear combination of different muscle synergies. Therefore, PCA is a covariation analysis that allows us (1) to find a simpler organization in EMG activities and (2) to quantify the whole motor strategy in terms of muscles synergies (principal components) and weightings coefficients. Here, it has to be noticed that this kind of analysis concerns the timing of EMG activities and not the amplitude of EMG signals. Importantly, because the PCA needed a substantial amount of data to be performed properly, the PCA was applied from 100 ms before the onset of the CoP displacement to the time to peak velocity of the index. The PCA was performed on the EMG data 100 ms before the onset of the CoP displacement to take into account the electromechanical delay between the beginning of the EMG activity and the beginning of the CoP displacement (Schenau et al. 1995). For the validity of the PCA, it was inappropriate to perform this analysis only on the period of anticipatory postural adjustments (i.e., to stop the analysis at the hand movement onset). In this case, it would have been too restrictive and would have limited the number of data incorporated in the PCA. By prolonging the PCA until the time to peak velocity of the hand, the EMG values that were incorporated in the PCA were more likely to be influenced by feedbacks and would limit the similarities of the PCA between the condition with and without equilibrium constraints and play against our second hypothesis. We called this period the period of initiation of movement. This period is thus constrained by the PCA itself. This analysis was performed on smoothed waveforms that were obtained by using a low-pass filter at 5 Hz (similarly to Ivanenko et al. 2005, 2006). For each of the 240 trials, we considered an input matrix composed of 200 rows (temporal frames) and 24 columns (the number of muscles) and applied Matlab z-score and princomp functions to this 240 × 200 × 24 matrix. The PCA allowed us to write each principal component as a linear combination of the EMG waveforms. The variance accounted for (VAF) by the first principal component (noted PC1%) was defined as the ratio between the first eigenvalue and the sum of all the eigenvalues. Denoting by PC_j the jth principal component and by M_i the ith muscular activity, we obtained, for $1 \leq j \leq 24$:

$$\mathrm{PC}_j(t) = \sum_{i=1}^{24} C_{ij} M_i(t)$$

We selected the number of PCs based on a threshold of VAF fixed at 95%. The PCA analysis performed on the EMG data did not allow the comparison of the EMG level of activation between the conditions, because the gain is different for the subjects and the muscles. Thus, for each subject and each muscle, the EMG values were normalized with respect to the maximum of the EMG activity observed in the twelve trials of the same condition of distance (i.e., maximum of the Normal BoS and Reduced BoS condition for D1 and for D2 separately). Then, each trial was incorporated in a single matrix and was independently considered (240 trials (with 10 subjects and 24 trials) × 200 data × 24 muscles).

The weighting coefficients (c_{ij}) $1 \leq i,j \leq 24$ were the coefficients of the eigenvector matrix. These weighting coefficients illustrate how muscles were encoded in each principal component. Moreover, to test the similarity between a PC recorded in the Normal BoS condition with the corresponding PC recorded in the Reduced BoS condition, determination coefficients (r^2) were calculated. We also tested the similarity of the weighting coefficients between the Normal BoS and the Reduced BoS conditions to check whether the muscles activities were similarly encoded in PCs. As for the analysis performed at the ankle joint, the VAF for each PC was calculated from the eigenvalues. All PCA were extracted for a temporal window between times t_{-2} and T_{pv} for each trial. They were averaged and compared between each condition.

Statistical analyses

All analyses were performed with Statistica (StatSoft Enterprise wide-systems). We first checked that each variable was normally distributed (Shapiro–Wilk W test) and had equivalent variances (Levene's test). Two different one-way ANOVAs with repeated measures were performed to compare the Normal BoS and Reduced BoS conditions for the D1 (1st ANOVA) and the D2 (2nd ANOVA). Post hoc analyses were conducted with the Neuman-Keuls test. The reported results were considered significant for $P < 0.05$. $P =$ refers to a single P-value. Ps$\geq$ refers to several P-values. In this latter case, the minimal value is notified in a mathematical inequality.

Results

Control experiment: effects of the Reduced BoS during a quiet upright standing

In the control experiment, we observed that the EMG activity of the SOL significantly increased (+54%, $P < 0.01$) when the participants were standing on the Reduced BoS (see Fig. 3a) despite the fact that the TA activity remained constant ($P = 0.93$). The initial position of all the limbs was not significantly affected by the Reduced BoS. Each elevation angle (defined on Fig. 3b) remained constant (maximum variation <4°, $P = 0.11$; see Table 1).

We did not find any statistical significant variation of the CoM initial position (<1 cm on the vertical axis, and less than 1 cm in the antero-posterior axis, $P = 0.24$). However, when we modeled the eight-link-body like an inverse pendulum (i.e., all the body mass is placed at the CoM, and the ankle joint is assumed to be fixed, see Fig. 3c), the CoM position was more inclined (by 3°) in the Reduced BoS compared to the Normal BoS condition. This small difference was not statistically significant, but sufficient to explain the increase of the SOL activity in the Reduced BoS condition. Indeed, based on the equation $\mathrm{T} = \mathrm{m}\cdot\mathrm{g}\cdot\mathrm{L}\cdot\cos\theta$ where T, m, g,L, and $\cos\theta$ were the ankle joint torque, the body mass, the acceleration of gravity, the length of the lever arm, and the elevation angle, respectively, this variation corresponded to an increase of 48% of the joint torque in order to maintain an upright standing posture. This result was obtained using measured parameters (m, L, $\cos\theta$) from the six participants. To sum up, the size of the Reduced BoS used was small enough to induce significant muscular adaptations expressed by an increase in the SOL electrical activity while no significant modification appeared at the kinematics level. Indeed, the joint angles and the CoM position of the eight-link-body model did not statistically vary. The CNS seemed to reinforce the equilibrium control during a quiet standing posture in the Reduced BoS condition by increasing the SOL tonic activity.

Main experiment: learning inside each block did not influence the results

In order to check whether learning could have influenced our results, we performed regression analyses for the movement time of the finger, the ΔCoP and the ΔCoM for the six trials of each block and compared the value of the obtained slopes to zero. The results demonstrated that the slopes were not statistically different from zero (in average $T = 0.65$ $P = 0.34$ for the movement time of the finger, $T = 0.81$ $P = 0.45$ for the ΔCoM, and $T = 0.71$ $P = 0.56$ for the ΔCoP parameters) suggesting that learning inside each block did not influence our results.

The Reduced BoS conditions did not affect the finger kinematics parameters

The finger movement duration (0.68 s ± 0.15 s on average), the mean velocity (0.92 m s^{-1} ± 0.16 m s^{-1} on average), and the time to peak velocity of the finger (on average 0.28 s ± 0.02 s) were not statistically different between the Normal and the Reduced BoS conditions for the same condition of target distance (Table 2 Ps ≥ 0.63). Areas of the 95% confidence ellipses of the fingertip final position were not affected by the reduction of the BoS (5.74 ± 2.3 cm^2 and 5.97 ± 1.7 cm^2 for the Normal BoS and Reduced BoS conditions, respectively, $P = 0.57$). The distance between the centers of these ellipses was not significantly different in the Normal BoS and the Reduced BoS conditions (1.07 ± 1.23 cm, $P = 0.24$ and 1.19 ± 2.6 cm, $P = 0.34$ for D1 and D2, respectively). Taken together, the above results demonstrated that the hand kinematics in both the Normal BoS and the Reduced BoS conditions was not significantly different (Table 2).

The Reduced BoS conditions modified the amplitude of the CoP and the CoM displacements

As expected, the CoP and the CoM displacements were reduced in amplitude during the Reduced BoS condition. A typical qualitative pattern of the CoP displacement is depicted in Fig. 4 (upper part) for the two distances. The backward peak and the peak-to-peak amplitude of the CoP both significantly decreased (minus 46%, $P < 0.05$ and 61%, $P < 0.001$, respectively), regardless of the target distance (see Fig. 4 histograms). On average, the projection of the peak-to-peak A–P CoP displacement on the force plate was 3 (±0.8) cm while the BoS was 5 cm long for the reduced condition. It contrasted with the peak-to-peak A–P CoP displacement observed in the Normal condition which was 8 (±1.8) cm on average.

Table 2 Average values (±SD) of the kinematics parameters for all the subjects in the Normal BoS D1, Reduced BoS D1, Normal BoS D2, and Reduced BoS D2, respectively

	ND1	RD1	ND2	RD2
Mv (m s^{-1})	0.80 ± 0.14	0.76 ± 0.16	1.10 ± 0.11	1.03 ± 0.09
Pv (m s^{-1})	1.54 ± 0.33	1.48 ± 0.29	2.04 ± 0.43	1.84 ± 0.30
TPv (s)	0.25 ± 0.02	0.27 ± 0.02	0.29 ± 0.03	0.31 ± 0.03
mD (s)	0.65 ± 0.15	0.62 ± 0.20	0.71 ± 0.16	0.70 ± 0.07
F_{EP}AREA (cm^2)	3.68 ± 1.5	3.94 ± 1.2	7.88 ± 3.5	8.18 ± 2.1
$\Delta C_{\mathrm{ellipse}}$ (cm)	1.07 ± 1.23		1.19 ± 2.6	

From top to bottom: the mean velocity of the finger (m s^{-1}), the peak velocity of the finger (m s^{-1}), the time to peak velocity (s), the movement duration (s), the area of the finger end point (cm^2), and the distance between the center of each ellipse (cm)

The amplitude of the A–P CoM displacement significantly decreased of 47% in the Reduced BoS conditions (Ps < 0.01) compared to the Normal BoS condition (3 and 6 cm in the Reduced BoS and Normal BoS conditions, respectively). Figure 5 shows the CoM trajectory in the sagittal plane for the different equilibrium contexts. Discrepancies between the Normal BoS and the Reduced BoS trajectories were present as soon as the motion started. However, even if the Reduced BoS conditions altered the amplitude of the CoM displacement along the A–P axis, the global shape remained similar in the two equilibrium contexts (Normal BoS and Reduced BoS) regardless of the target distance (D1 and D2).

The timing of the muscle synergies was maintained for the initiation of the whole body movement despite the reduction of the BoS

The EMG activities for the 24 muscles were depicted in Fig. 6 for a typical subject. Interestingly, a visual inspection revealed a strong similarity between most of the muscular patterns in the Normal BoS and the Reduced BoS conditions. During the initiation of the movement, we observed a common deactivation of antigravitary muscles associated with a synchronized activation of their antagonist for the ankle (SOL vs. TA), the thigh (SM + BF vs. RF + Vmed), and the trunk (ESL2 vs. RAS + OI). These observations could be associated with the so-called Hufschmidt phenomenon (Hufschmidt and Hufschmidt 1954), in which a general deactivation of extensor muscles can be noticed for downward movement (also see Cheron et al. 1997 for a similar result). It was interesting to note that such behavior was preserved despite the strong reduction of the BoS.

For a quantitative study of these muscular activities, we performed a PCA (See "Material and methods"). Three principal components (PC) were sufficient to capture the activity of the 24 muscles and the sum of the VAF by the three first PCs was superior to 95% on average (see Fig. 7a). The VAF by PC1 was 71% on average while the VAF by the PC2 and PC3 were 21 and 6%, respectively. To determine whether the obtained PCA values were similar in each Normal BoS and Reduced BoS conditions,

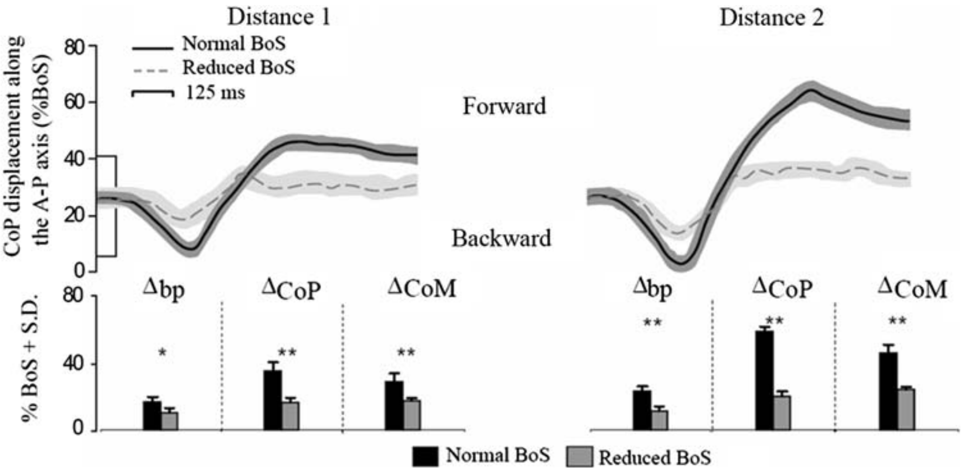

Fig. 4 Effect of the Reduced BoS on the CoP and CoM. *Top*: mean CoP displacements in the antero-posterior axis, in the Normal BoS D1, Reduced BoS D1, Normal BoS D2, and Reduced BoS D2 conditions. The *white rectangle* on the left illustrates the BoS length. *Bottom*: histograms show the mean values of bp, CoP and CoM in the four experimental conditions. For all graphs, *error bars* indicate the standard deviation across participants

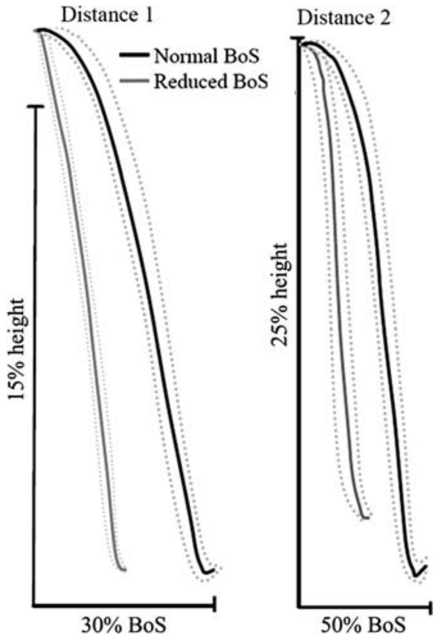

Fig. 5 Center of mass trajectory. *Left*: trajectory of the CoM in the sagittal (vertical) plane at D1. *Right*: same data at D2

we performed a simple correlation between them. This analysis revealed that these waveforms were very similar when comparing the Normal BoS and Reduced BoS conditions (on average $r^2 = 0.98$). This result indicated that the temporal muscular organization during the initiation of the whole body movement was preserved even if the BoS was strongly reduced. More precisely, for each PC, a comparison between the weighting coefficients of each muscle was performed. These weighting coefficients were representative of the role played by one muscle in each PC. For each PC, regression analyses were performed for the weighting coefficients of each muscle in the Normal BoS and the Reduced BoS conditions. The computed r^2 values were 0.69, 0.76, and 0.34 for the PC1, PC2, and PC3, respectively. These values indicated whether the weight of each EMG activity remained more or less the same in the Normal BoS and the Reduced BoS conditions. The correlation coefficient was low for PC3; however, its VAF was only equal to 6% on average, which means that the PC3 only accounted for 6% of the variance of the signal (Fig. 7a). Moreover, r^2 values significantly increased ($t = 3.87$, $P < 0.05$) when considering the leg and trunk muscles (indicated with a star symbol in Fig. 7b). Coefficients became 0.74, 0.90, and 0.57 on average for the PC1, PC2, and PC3, respectively. To conclude, the weight of each muscle in the first two PCs was not statistically different between the two conditions. This observation was reinforced when only the axial muscles were taken into account in the analysis.

For each subject and each muscle, the EMG values were normalized with respect to the maximum of the EMG activity observed in the twelve trials of the same condition of distance (i.e., maximum of the Normal BoS and Reduced BoS condition for D1 and for D2 separately). A visual inspection of all EMG traces (Fig. 6) suggested that the level of co-contraction between each pair of agonistic and antagonistic muscles was roughly the same. The level of muscle co-contraction was not directly evaluated. However, the weighting coefficients were strongly correlated between the Reduced and Normal conditions (Fig. 7). As EMG signals were normalized using the same maximal value in both conditions, it confirmed that the levels of co-contraction were similar.

Discussion

The aim of this study was to determine whether the timing of muscular synergies was different or similar when a whole body reaching movement was initiated with or without high equilibrium constraints. In other words, we

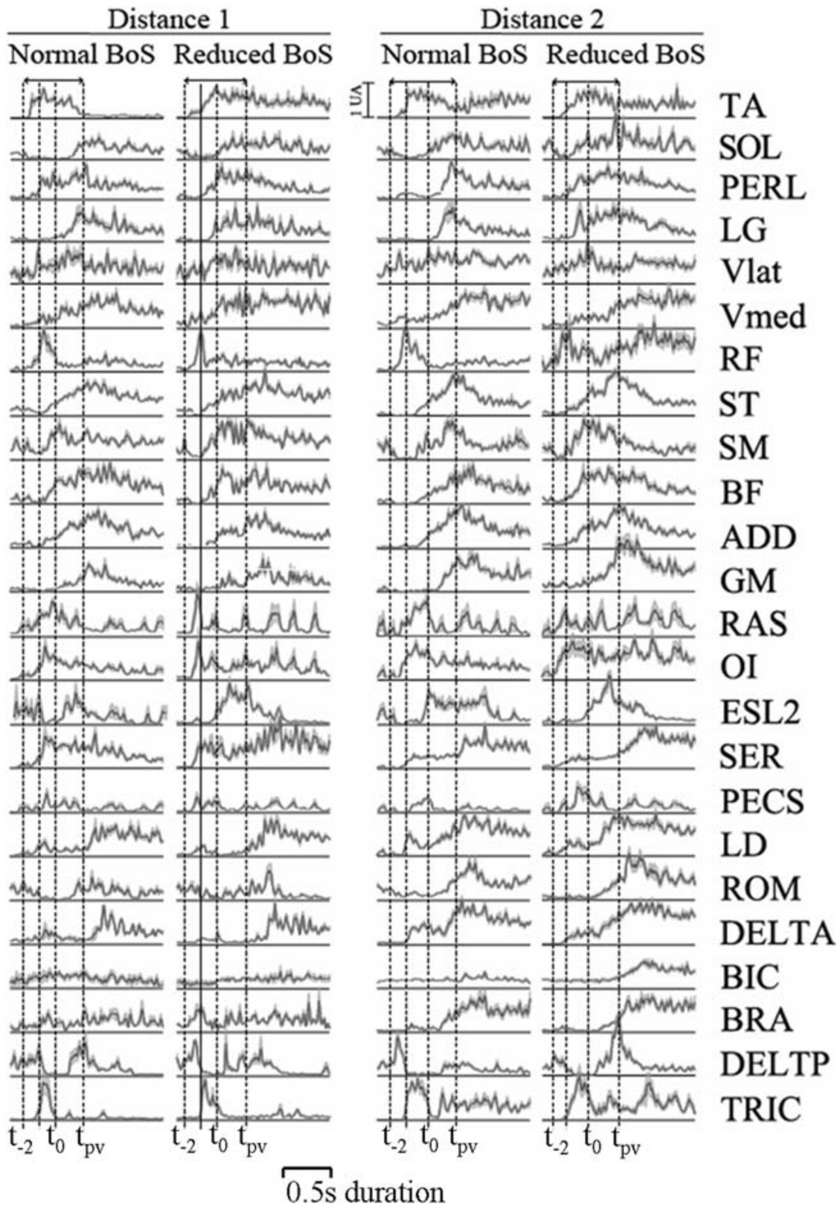

Fig. 6 EMG activities averaged for each experimental condition from a typical subject for the 24 muscles recorded. From left to right, RMS (10 ms integrations) signals in the four experimental conditions, namely Normal BoS in D1, Reduced BoS in D1, Normal BoS in D2, and Reduced BoS in D2, respectively. RMS activities were normalized by the maximum RMS value for each trial

investigated whether the muscular synergies that initiated the movement changed when equilibrium constraints were introduced in the task. To answer this question and to assess the level of similarity between the timing of the muscle synergies, we performed a PCA on the EMG activities of 24 muscles from the whole body. The main results demonstrated that during the initiation of the whole body pointing movement, only three PCs accounted for at least 95% of the variance for the overall EMG data in both the Normal BoS and the Reduced BoS conditions, namely with less and much more equilibrium constraints.

For these two conditions, the two-first PCs were strongly correlated despite the fact that the amplitudes of the CoM forward and the CoP backward displacements were markedly different. The third PC had a marginal impact on the data since it only accounted for 6% of the variance. This meant that the patterns of activations obtained from the 24 muscles could be summed-up to only two main waveforms that were independent from the level of equilibrium constraints. Interestingly, some authors assessed the effect of changing the BoS size on postural control associated with voluntary movement (Aruin et al. 1998; Nouillot et al. 1992; Yiou et al. 2007). Specifically, these authors showed that reducing the BoS size induced a drastic attenuation of anticipatory postural dynamics and anticipatory electrical activities in postural muscles. Similar results were also reported when subjects performed whole body movements in fear of falling (Adkin et al. 2002). According to the authors, this attenuation could reflect a deliberate strategy meant to avoid the potential destabilizing effect induced by

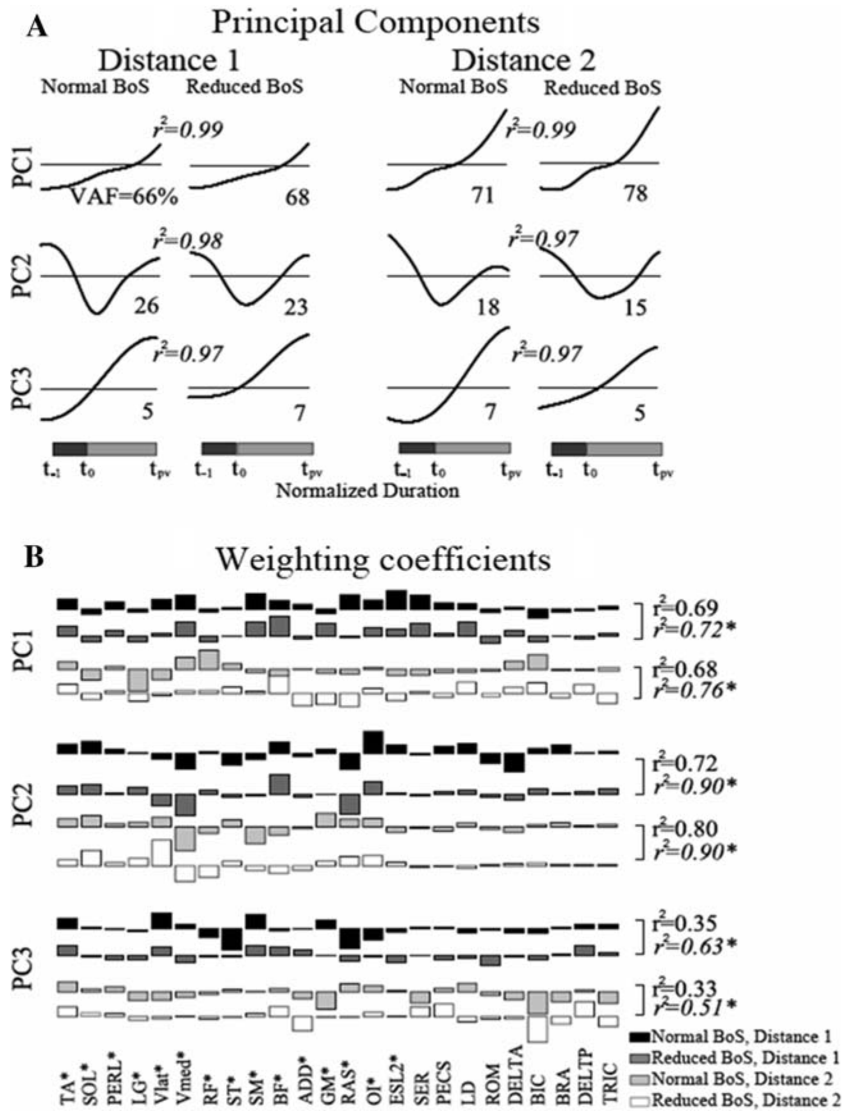

Fig. 7 Results of the PCA for the ten participants and the 24 muscles. **a** Three principal components (PC1, PC2, and PC3) obtained in the four experimental conditions. The VAF by each PC is reported as a percentage near each waveform. The determination coefficient (r^2), measuring the similarity between PCs in Normal and Reduced BoS conditions, is given in italics. **b** Corresponding weighting coefficients (or "loadings") for each muscle in each PC in the four experimental conditions. Again, the r^2 values are reported and the stars indicate the result for a r^2 analyses performed exclusively on the muscles of the trunk and lower limbs (also marked by *stars*)

the anticipatory postural dynamics themselves under unstable or anxious conditions. In our study, we also observed that the CoM and the CoP displacements were attenuated in the Reduced BoS condition. Consequently, our results are in line with the development of such a "protective" strategy. Importantly, according to the PCA, our results suggested that these drastic changes in the CoM and the CoP displacements could be reached without changes in the timing of the EMG activities during the initiation of the movement. By contrast, the gain of the EMG activities might be tuned into a flexible manner to adapt the existing muscular synergies to various contexts of equilibrium constraints. Thus, the CNS did not change the overall muscular strategies but was able to adjust the existing ones despite important constraints and behavioral changes.

Such conclusions were supported by a previous study (Berret et al. 2009) that investigated the effect of the same equilibrium constraints on several kinematics parameters such as the angular coordination or the CoM and the finger trajectories during a similar whole body pointing movement. These authors performed PCA on elevation angles and angular displacements in Normal and Reduced BoS conditions. Their results did not reveal significant modifications of the covariations of elevation angles in the experimental conditions with strong equilibrium constraints despite numerous significant changes in the angular displacements. These observations lead the authors to conclude that reaching and equilibrium subtasks were integrated in one single coordinative structure when subjects reached beyond arm's length in standard equilibrium condition and that such a single coordinative structure was resilient under high equilibrium constraints.

With respect to previous results using PCA analyses (Ivanenko et al. 2005; Berret et al. 2009), our results strongly suggested that constraints imposed to the endpoint trajectory but not equilibrium constraints were probably critical for the emergence of new PCs (suggesting new synergies). Indeed, by comparing all the tasks in which additional PCs were superimposed to basic ones, we noticed in the literature that explicit extrinsic constraints were imposed during the control of the endpoint trajectory (e.g., “stooping in place when walking,” “kicking a ball when walking,” “curving hand path,” and “keeping a straight hand path while pointing with both arm”). In all these examples, one constraint or one subtask was superimposed to another one. This probably induced the addition of another synergy to perform the additional subtask. This consideration is in line with the classical distinction made by Paillard (1971) between “topocineses,” a movement made with pure ecological spatial constraints and “morphocineses” a movement purely made to produce a shape with no specific spatial goal. It is interesting to note that in Berret et al. experiment, new PCs could be observed for movement involving a mixture of “topocineses” and “morphocineses” (imposed finger paths). This observation is also in line with more recent results by Desmurget et al. (1997). For arm-reaching movements, these authors previously demonstrated that unconstrained and compliant movements involved different planning strategies. In their experiment, they compared reaching movements with the same spatial goal made with either the index fingertip (unconstrained) or using an “intermediate tool” (e.g., hand-held cursor, pen, manipulanda, etc.) which involved a motion constrained by external contact (compliant). They observed different kinematics of the endpoint for the two types of movement and concluded that different planning strategies could be involved in spite of the fact that the task and the motor goal were the same. In addition, similarly to Berret et al. (2009) experiment, Desmurget et al. (1997) observed that the instruction to perform straight movements with the endpoint modified the kinematics of unconstrained movements, but not those of compliant movements. However, they could not settle whether the differences observed and due to the various movements, constraints were sustained by similar or distinct muscular synergies. By contrast, PCA analyses seemed interesting to better resolve this question, since it was possible to distinguish and isolate PCs representative of different motor synergies and to focus on the neurophysiological processes that allowed motor flexibility.

Explicit goals, which were planned at a higher level compared to more implicit constraints, could be processed differently and by different pathways to select new muscles synergies programmed in the motor area. The ways new synergies are optimally combined with those that already exist in the task remain to be explored.

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