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Research report

Anticipatory postural adjustments under simple and choice reaction time conditions

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Abstract

Two different schemes of the central organization of anticipatory postural adjustments (APAs) have been proposed: one of them assumes that postural and focal components of an action are results of a single control process (single-process hypothesis) while the other one suggests that these two components result from two relatively independent control processes (dual-process hypothesis). To distinguish between the two hypotheses, we investigated changes in the relative timing of the postural and focal components under self-paced, simple reaction time (SRT) and choice reaction conditions (CRT). Standing subjects performed one of four small arm movements resulting in a standard postural perturbation (dropping a load). APAs were quantified as changes in the background muscle activity as well as shifts of the center of pressure. APAs occurred at a larger delay prior to the focal movement under the self-paced condition than under the SRT condition. Under the CRT condition, actual RTs were longer than under SRT, but APAs were more similar to those under self-paced conditions. A negative correlation between the reaction time and APA onset was found. The findings demonstrate that the focal and APA components of an action can be decoupled, thus supporting the dual-process hypothesis. Changes in APAs with action suggest a possibility of modifications of a function that transforms two parallel control signals into a single command to the focal and postural muscles, based on postural requirements and behavioral constraints. © 2002 Elsevier Science B.V. All rights reserved.

1. Introduction

During voluntary movements performed by a standing person, external forces, interaction torques, and changes in the body geometry may destroy the postural equilibrium. The notion of anticipatory postural adjustments (APAs) has been introduced to address changes in the background activity of postural muscles and associated shifts of the center of pressure (COP) that are seen prior to the initiation of a voluntary motor action [5,8,12] (for a review see Ref. [21]). The purpose of APAs has been assumed to counteract the mechanical effects of predicted perturba-

tions on balance. For instance it has been shown that APAs, associated with fast arm movements, are generated to minimize the displacement of the center of pressure (COP) [8].

Two different schemes of central organization of APAs have been considered. According to the single-process control scheme, APAs and focal movement are different peripheral consequence of a single control process. Within this scheme, the hypothetical controller makes no distinction between the apparently focal (explicitly required) and postural (implicit, related to the current postural task) components of a motor task. Within the single-process control scheme, one could expect the onset of a focal movement to be time-locked with that of a postural response. Evidence for this type of control has been found in several studies [2,25,26]. In particular, Aruin and Latash [2] showed a modulation of APAs dependent on the magnitude of the motor action triggering the perturbation

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even when the magnitude of the perturbation was constant and predictable.

The other, dual-process (also referred to as parallel-process) control scheme assumes two independent control processes organizing the focal and postural components of an action. Under this type of control, the onset of a focal movement can be dissociated from the onset of an associated postural response. This scheme has been supported, in particular, by observations of selective impairments of APAs in patients with Parkinson's disease and lesions to the cortex [4,14,22,27]. These studies, which have primarily used a load-lifting task, have suggested that different hemispheres modulate the generation of APAs and focal movement relatively independently. While the supplementary motor area and basal ganglia of the hemisphere contralateral to the postural forearm are involved in the modulation of APAs the primary motor cortex of the other hemisphere generates the focal action [22,27].

Additional evidence in favor of the dual-process control scheme was provided by studies of APAs during movements performed under a typical simple reaction time (SRT) procedure [6,13,28]. In these studies, the relative timing of the focal and postural components was different in self-paced (SP) movements as compared to those performed under the SRT instruction. Both quantitative as well as qualitative changes in APA patterns were observed [13]. In particular, under the SRT conditions, APAs occurred later in time, typically simultaneously with the initiation of the focal movement.

The single-process scheme remains a viable alternative to the dual-control hypothesis, however, if one assumes that the postural requirements, behavioral constraints, and amount of foreknowledge can modify the single-control signals that command the focal and postural muscles. Changes in these transformation functions may be seen when there is a major discrepancy between the magnitude of the focal movement and the magnitude of the perturbation [2], or when movements are performed under unusual conditions for postural stabilization (e.g., under water or in weightlessness [10,15,21], or when movements are performed under severe time pressure [7,13]).

In the studies of movements under the SRT instruction, the reaction times (RTs) were rather short, between 130 and 210 ms when measured to the first visible electromyographic reaction in a prime mover muscle. Such short times might not allow APAs to occur at the typical time interval with respect to the focal movement (about 100 ms prior to the prime mover activation [21]).

Under choice reaction time (CRT) instruction one can, however, increase the time available for the generation of APAs. In this case, the single-process hypothesis predicts that APAs will be shifted towards the initiation of the focal movement, just like in SRT experiments [7,13], because the triggering action is a consequence of a hypothetical common control signal. In other words, the CNS is not expected to be able to take advantage of the fact that APAs

can be generated earlier than the focal movement, since the command that generates the focal action is tightly coupled to the command that generates the APA.

The dual-process hypothesis predicts a different result. If a subject knows in advance the magnitude and direction of an upcoming perturbation, he or she can initiate a process leading to an APA as early as allowed by the shortest possible delay (as in SRT experiments), i.e., prior to the initiation of a command signal for the focal action. In other words, the CNS can take advantage of the extra time afforded by the prolonged reaction time in CRT conditions and use APAs more similar to those seen in experiments with SP movements.

A few studies have investigated APAs during CRT instruction [9,18,19]. In these studies subjects were required to generate different responses in reaction to specific stimuli that had different probabilities [9,18,19]. They have shown that the longer the planning time allowed prior to a focal movement, the earlier the onset of the APA. In these studies, however, different postural responses were required under the CRT instruction (a push or a pull on a handle or fast movements with the left or the right arm). Hence, the characteristics of the perturbation were changed, which could alter the observed APA patterns that are known to be tightly linked to the magnitude and direction of the perturbation [1,8,20].

In the current experimental series, we tried to eliminate this confounding factor and studied APA patterns associated with a standard mechanical perturbation under SP, SRT, and CRT conditions. That is, a standard load was released from extended arms by four small arm movements in different directions. The arm movements themselves had no apparent mechanical effect on the direction and magnitude of the perturbation. Note that in this case the focal actions are of approximately equal magnitude and involve similar muscle groups. In this case, the foreknowledge for the generation of APAs in SRT and CRT conditions may be expected to be the same, while the conditions differ in the foreknowledge for the generation of an appropriate focal action.

In this study we were further interested whether actual reaction time or instruction (or both) defines the relative timing of the focal and postural response components. To address this question, we first looked for a relationship between RT and APA onset. In a second analysis, we removed the variance in the APA onsets that was associated with differences in RT and then examined whether instructions could explain any of the remaining differences in the APA timing.

2. Materials and methods

2.1. Subjects

Nine right handed subjects, six men and three women

participated in the experiment. Their average age was 27.1 years (±S.D. 8.2). All the subjects were free of neuro-muscular disorders and their visual acuity was normal or corrected to normal. The subjects gave written informed consent according to the procedure approved by the Office for Regulatory Compliance of the Pennsylvania State University.

2.2. Apparatus

A force platform (AMTI, OR-6) was used to record moment around a frontal axis (M_y), and the vertical component of the reaction force (F_z). Accelerometers (Sensotec) were taped to the dorsal surface of both hands just under the metacarpophalangeal joint of the middle finger. The axis of sensitivity of each accelerometer was at approximately 45° to the required hand motions. Dispos-able self-adhesive electrodes (3M) were used to record the surface EMG activity on both sides of the body in the following muscles: rectus abdominis (RA), erector spinae (ES), rectus femoris (RF), biceps femoris (BF), tibialis anterior (TA), and soleus (SOL, only on the right side due to the limitation in the number of channels). The electrodes were placed on the muscle bellies, with their centers approximately three centimeters apart.

The subject stood in front of a rectangular board on which four similar lights were mounted. The board was placed in such a manner that the center of the board was at the midline of the body, at the eye height, and just beyond the arm reach (see Fig. 1). The subject held a 2.3-kg brick-shaped load (8×16×6 cm) between the hands by pressing on the sides of the load. All four lights were clearly visible to the subject. The visual angle of the lights in the field of vision was 11.2° in the vertical and 22.5° in the horizontal direction. The lights could be individually activated with a switch box, which gave a simultaneous signal to the data acquisition set-up. All signals were sampled at 500 Hz with a 12-bit resolution. A Mac-IIci computer with customized software based on the LabView-2 package was used to control the experiment and collect the data. The data were analyzed off-line with customized software based on the LabView-3 package.

2.3. Procedure

The experiment was organized to test effects of two factors: INSTRUCTION and DIRECTION of movement. There were three levels of the INSTRUCTION factor: SP, SRT, and CRT. Four levels of the direction factor corres-ponded to the four directions of the focal movement: up left, up right, down left, and down right. In total, there were 12 experimental conditions. The order of instructions was counter balanced across the subjects. Subsequently, under each instruction, the four directions were presented in a balanced order.
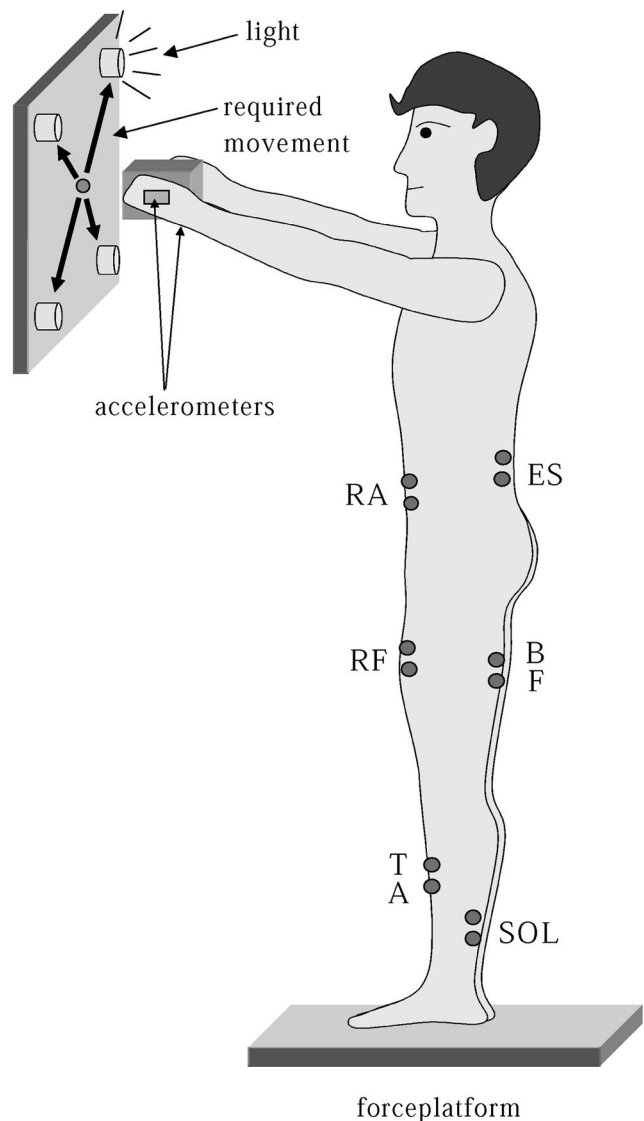
In the initial position, the subject stood on the force

Fig. 1. Subjects were required to release a load by making a small movement (±8 cm) toward one of the four lights placed on a board in front of the subject, i.e., along the thick black arrow. The height of the board was adjusted so the center was always at eye-height. We made sure the arms did not block vision of the four lights. Subjects performed the movements under self-paced (SP) conditions, and under a simple reaction time and a four choice reaction time procedure. Accelerometers taped to the hand were used to determine RTs and perturbation onsets. Surface EMG signals from both sides of the body of rectus abdominus (RA), erector spinea (ES), rectus femoris (RF), biceps femoris (BF), tibialis anterior (TA) and the right soleus (SOL) were recorded. Displacements of the center of pressure were measured using a force platform.

platform holding the load with arms extended, the hands supinated 90°, so that the palms were oriented towards each other. Throughout the experiment, subjects were asked to look at the mark at the center of the load, to specify gaze direction. The feet were placed at hip-width, side-by-side. During all trials, foot position remained the same. After a computer-generated tone, the subjects were required to make a very small but fast arm movement over

about 8 cm to the light that turned on (Fig. 1). The movement always led to a standard postural perturbation associated with the load drop. The subjects were instructed to make all the movements in all the conditions as similar to each other as they could. After the movement termination, the subjects were asked to wait for about 1 s, pick up the load, return to the initial position, and wait for the next signal.

Under the SP condition, the subjects were told to make the movements to a particular light in a SP manner, i.e., not to react to the tone signal immediately. During practice trials, they were reminded to wait 1–2 s after the tone before movement initiation. During off-line analysis, we made sure that no movements occurred during the first 500 ms after the tone.

Under the SRT condition, the subjects were told in advance which light would turn on. After the tone signal, that particular light was turned on within a 1–3-s interval at an unpredictable time. The subjects were required to initiate a movement to the light as quickly as possible.

Under the CRT condition, a similar procedure was followed except that any of the four lights could turn on unpredictably. All four lights were used in a pseudo-random order. Data were recorded for 5 s following the computer-generated tone. Six trials were recorded for the SP condition. Twelve trials were recorded for the SRT and CRT conditions for each of the four lights. Within a series, the time interval between the trials was 10 s. The intervals between two consecutive series were 1 min. Fatigue was never an issue. Before the experiment started, five practice trials were performed to each of the lights under the SP condition. During the actual experiment, prior to each series, the subject was asked to make three practice movements under the corresponding instruction.

2.4. Data processing

All signals were processed off-line, filtered with a 59–61-Hz, eighth order, zero-lag notch filter and a 100-Hz low-pass, fourth order, zero-lag Butterworth filter. The notch filter was applied to assure no 60-Hz contaminations of the EMG signals. All EMG signals were then rectified. Individual trials were viewed on a monitor screen (1 ms resolution) and aligned according to the first visible rise in the acceleration trace of the required arm movement (movement initiation). This moment will be referred to as 'time zero' (t_0). For the trials performed under the SRT and CRT conditions, the time difference between the onset of the light signal and the onset of the required acceleration was measured (reaction time, RT). To avoid trials with possible anticipation of the imperative stimulus and also those with very long RTs, the six *middle* trials (according to the actual values of RT) within each SRT and CRT series were averaged for each subject separately and used for further analysis.

To quantify the APA activity, EMG integrals ($\int$EMG)

were calculated in a window from -200 ms to t_0. These integrals were corrected by subtracting integrated activity from -500 to -450 ms prior to t_0 multiplied by four (the baseline EMG activity, $\int$EMG$_{bl}$). For comparisons across subjects, $\int$EMG values were normalized by the absolute highest value seen over all conditions for a particular muscle and a particular subject. Note that after this normalization all the $\int$EMG values were within the range from $+1$ to -1. Negative values corresponded to a decrease in the background activity during the APA window.

The 100-Hz low pass filtering allowed us to reliably determine the onset of the change in EMG activity (for example, Refs. [13,20]) using both a magnitude and a timing constraint. Onsets of the changes in the muscle activity were determined using a computer algorithm. The algorithm marked the point where the activity was more than one standard deviation away from the mean baseline activity and this change lasted for at least 30 ms. All individual trials were checked visually to assure no errors in this process. In less than 5% of the trials, 'false starts' were detected and onsets were determined manually.

APA onsets of individual trials were calculated with respect to the focal response, with negative numbers corresponding to an onset prior to focal onset. This allowed us to compare SP (which did not have a stimulus), SRT and CRT conditions. To see whether changes in APAs were different with respect to stimulus onset in SRT and CRT conditions we also measured APA onsets with respect to the stimulus.

Horizontal displacements of the center of pressure in the anterior–posterior (ΔCOP$_x$) were calculated using the following approximation: ΔCOP$_x = \Delta M_y / F_z$ where ΔM_y is a change in the moment with respect to its baseline value (defined as the average value within the time interval from -500 to -400 ms). The following characteristics of ΔCOP$_x$ were calculated:

1. displacement of the center of pressure at t_0 (ΔCOP$_0$);
2. displacement of the center of pressure at 50 ms after t_0 (ΔCOP$_{50}$);
3. the average rate of anticipatory COP displacements was calculated within the time window from -100 to $+50$ ms and corrected for its average rate of change within the window from -500 to -300 ms (ΔCOP$_{rate}$). Maximal peak-to-peak displacement of the COP was calculated within a time window from t_0 to $+250$ ms after t_0 (ΔCOP$_{max}$).

Peak to peak acceleration of the moving hand for each condition was calculated. At the end of the experiment, we performed a control series in three subjects who performed similar movements under the SP condition. The control series consisted of six SP movements to each of the four lights without holding the load.

Statistical procedures included repeated measures ANOVA with factors INSTRUCTION and DIRECTION (the factor DIRECTION was included to check whether no effects of focal movement were apparent). Tukey's HSD tests were used as post-hocs. Multiple regression analysis and nonparametric statistics were also used. Appropriateness of the regression models was evaluated using residual plots and the Anderson–Darling test for normality of the data.

A series of regression analyses on APA onset and focal onset were conducted. In the first analysis, RTs from the SRT and CRT series were pooled and regressed against APA onsets of individual trials. Onsets prior to t_0 were assigned negative values. A sign test was used to evaluate the slopes of individual regressions across subjects. In the second analysis, the onset of EMGs was again regressed against the pooled RTs, but then the residuals from this analysis were regressed against the factor INSTRUCTION (SRT versus CRT conditions). This was done for individual muscles, and also for the average of all muscles. Subsequently, we tested whether the un-standardized slopes from these regressions were significantly different from zero, using a single sample t-test.

3. Results

3.1. Reaction times and mechanical characteristics of the movements

All the trials within each SRT and CRT series were ranked according to the actual reaction time and the six middle trials under both reaction time conditions were used for all further analyses (see Section 2). The average RTs were 254 ms for SRT and 301 ms for CRT, an average increase of 18% ($F_{(1,8)}=46.4$; $P<0.001$). RTs were also affected by the direction of movement ($F_{(3,24)}=3.8$; $P<0.05$). In particular, RTs for downward movements tended to be longer than those for upward movements; however, all pair-wise comparisons between different directions were non-significant. No significant interaction between the two factors was found ($F_{(3,24)}=0.267$; $P>0.8$).

To assure that the small arm movements towards any of the four lights were of similar magnitude we calculated the peak-to-peak acceleration. Averaged across all subjects no significant differences for both experimental factors (INSTRUCTION: $F_{(2,14)}=0.61$; $P>0.5$; DIRECTION: $F_{(3,21)}=0.43$; $P>0.7$) were found. The focal movement was accompanied by a reactive motion of the non-focal arm with the peak acceleration, on average, only one-quarter as large as that of the focal movement.

3.2. Anticipatory EMG patterns

The load release was accompanied by early changes in the activity of leg and trunk muscles. The EMG patterns were characterized by two or three alternating phasic bursts in the dorsal-frontal muscle pairs. These changes in the activity of postural muscles could be initiated prior to t_0 or shortly thereafter.

Fig. 2 shows typical EMG patterns averaged across six trials by a representative subject during down-right movements under SP conditions (three left panels). There is an anticipatory increase in the activity of TA, RF, and RA, while SOL, BF and ES show a decrease in the activity. In general, APAs in dorsal muscles occurred earlier than those in ventral muscles. APA patterns were subject-specific: in some subjects, there were no visible bursts or episodes of suppressed activity in some of the muscles.

3.3. Effects of RT and instructions on anticipatory EMG

No significant changes in the APA magnitude under the influence of INSTRUCTION were seen, as quantified within the interval from -200 ms to t_0.

Changes in the baseline activity ($\int$EMG between -500 and -450 ms) of postural muscles were found. Visual inspection of baseline values showed higher levels of EMG activity during SRT conditions. For all muscles except RF, RF L, TA L and RA L significant main effects for INSTRUCTION were found ($F_{(2,6)}>4.5$; $P<0.03$). They confirmed a general increase in postural baseline activity during SRT conditions, while no differences between SP and CRT conditions for any of the muscles were found ($P>0.6$).

Changes in the onset of EMG activity, as determined by the computer algorithm (see Section 2), were seen under the different instructions. As illustrated in Fig. 2, APA onset is delayed in almost all muscles under the SRT condition (middle panels) as compared to SP movements. Under the CRT condition, the EMG onsets are similar to those under the SP condition (compare the left and the right panels).

Repeated measures ANOVA showed significant main effects of INSTRUCTION on EMG onset (with respect to the focal response) in the following muscles: RF-R ($F_{(2,14)}=7.151$; $P<0.02$), BF-R ($F_{(2,14)}=6.61$; $P<0.03$), BF-L ($F_{(2,14)}=5.1$; $P<0.03$), ES-R ($F_{(2,14)}=6.47$; $P<0.02$) and ES-L ($F_{(2,14)}=10.48$; $P<0.002$). Fig. 3A,B shows changes in the EMG onsets with standard error bars, across all subjects; significant differences are marked with an asterisk. While Fig. 3A shows changes in APA onset with respect to the onset of the focal movement, Fig. 3B shows changes with respect to the stimulus onset (for SRT and CRT conditions only). For RF-R and BF-R, the differences in the EMG onsets (with respect to the focal response) between the SP and SRT conditions were significant. For BF-L, ES-R, and ES-L, there were no significant differences between the SRT and CRT conditions. None of the muscles showed a significant difference between the SP and CRT conditions. Fig. 3B shows a

Self paced
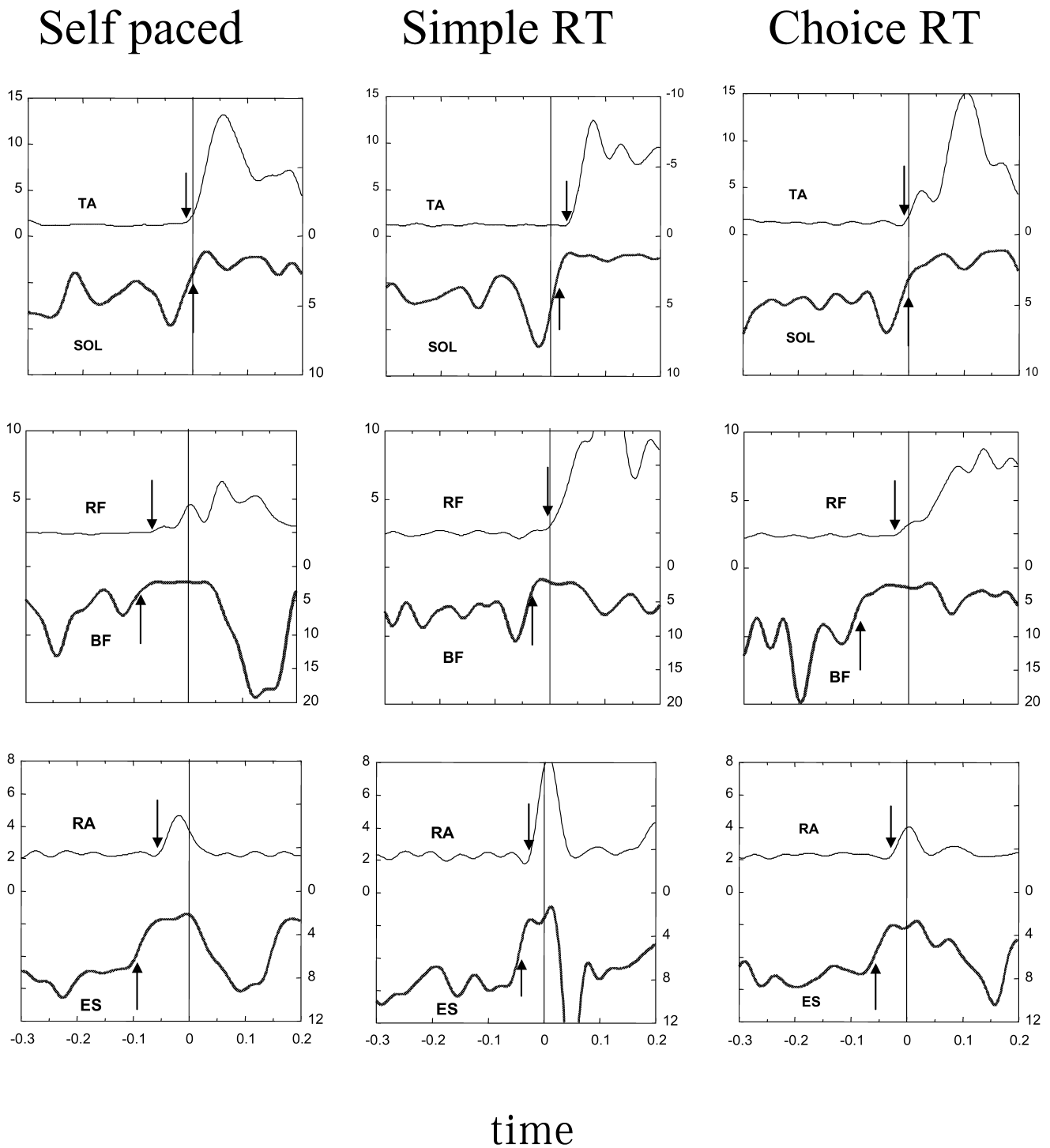
Simple RT

Choice RT

time

Fig. 2. Averaged across six trials EMGs recorded from leg and trunk muscles in a representative subject for load releases performed under self-paced, simple and choice reaction time conditions. Vertical lines show the onset of the perturbation. RA, rectus abdominis; ES, erector spinae; BF, biceps femoris; RF, rectus femoris; SOL, soleus; TA, tibialis anterior. Note the marked decrease in the APAs in TA, RF, BF, RA and ES during simple reaction time conditions. During choice reaction time APAs are more similar to self-paced conditions. EMG activity is in arbitrary units. EMG signals for SOL, BF, and ES are inverted for better visualization.

significant increase in APA onset (with respect to the stimulus) in CRT conditions for RF on both sides of the body. All other muscles showed an increase in onset, these differences did not reach the level of significance, however.

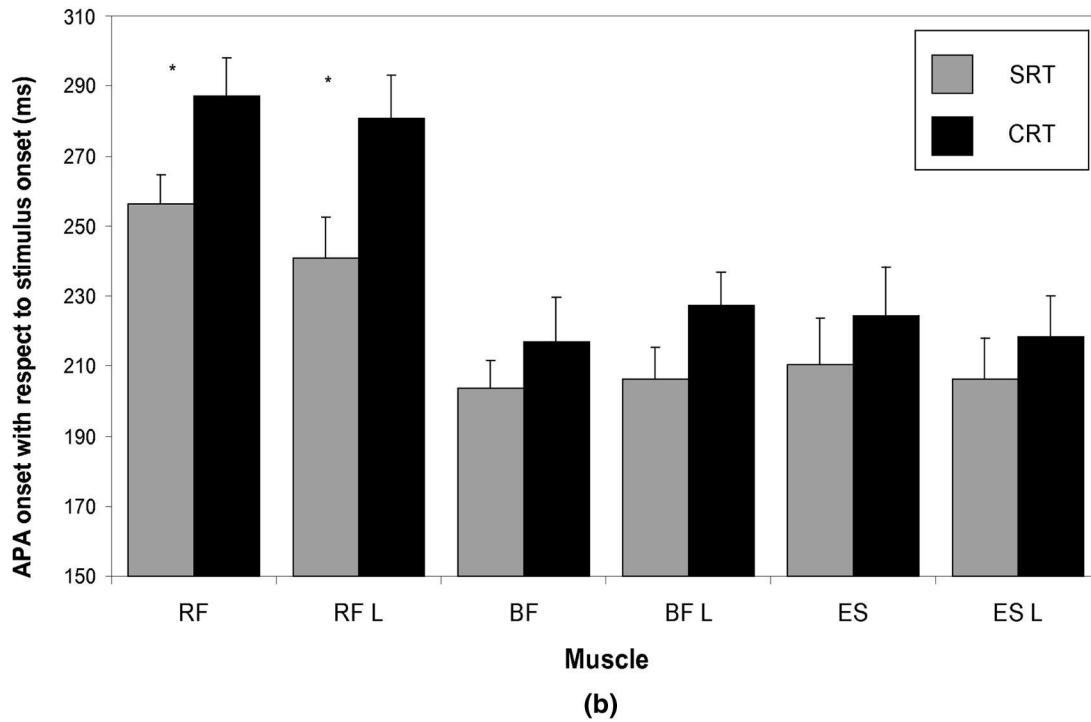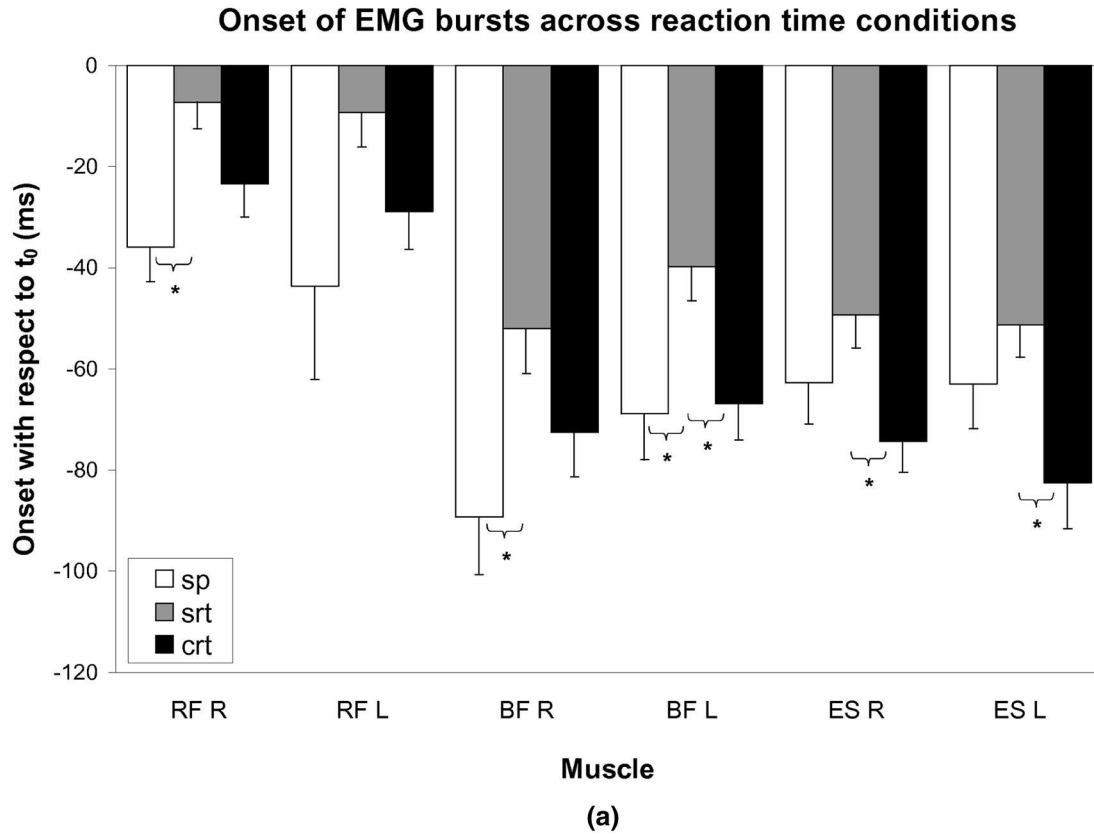On average, the activity of dorsal muscles preceded the

Onset of EMG bursts across reaction time conditions

(a)

(b)

Fig. 3. (A) Changes in the EMG onsets with respect to t_0 for the different reaction time conditions across all subjects. Note the marked delayed onset of muscles under SRT conditions. In none of the muscles the difference between SP and CRT conditions was significant. Other muscles than the ones displayed did not show significant modulation. (B) Changes in the EMG onsets with respect to stimulus onset for the SRT and CRT conditions across all subjects. Note the increased delay during CRT conditions. Error bars are standard error. Significant differences are marked with an asterisk.

onset of the ventral muscles by 50.4 ms (S.D.±12 ms). Significant differences in the variability of APA onset and RTs were found; across all muscles and conditions APAs onsets were 40% more variable than RTs ($P < 0.001$).

Regression analysis was used to determine whether actual reaction time could predict APA onset. RTs from SRT and CRT series were pooled and regressed against APA onsets in individual trials. (The pooling was justified by an ancillary analysis which showed that the correlation between APA onset and RT did not differ between the SRT and CRT series; $F(1,8)=0.14$; $P > 0.7$). In 86% of the cases, the correlation between RT and EMG onset was negative; that is, the longer the reaction time, the earlier the APA onset. A one-sample sign test found a significant negative slope for seven out of the nine muscles. Average slopes (across all subjects) varied between -0.1 and -0.6, indicating that with every 1-ms increase in RT, EMG onset was 0.1–0.6 ms earlier.

In summary, changes in the APA pattern were associated with changes in reaction time. Because SRT and CRT conditions evoke different mean RTs, this (partly) explains why the pattern of APAs is different between these two types of task. To discern whether any of the change in the APA pattern was *directly* brought about by changes in the instructions (i.e., changes above and beyond the RT changes), we conducted the two-step regression analysis that corresponds to a repeated-measures analysis of covariance. In the first step, the pooled RTs from both SRT and CRT conditions were regressed against EMG onsets and the unstandardized residuals were obtained. (These values contain the variance in EMG onset that cannot be explained by changes in RT.) In the second step, the residuals were regressed against the dichotomous factor INSTRUCTIONS (SRT versus CRT) and the un-standardized slopes (which represents the difference between the two tasks) were compared using a paired-samples t-test (see Section 2). In those cases where the slope is significantly different from zero, we can say that, above and beyond the effects of reaction time, the instructions given to the subjects changed the APA onset. Results of this analysis, for both the individual muscles and their average are shown in Table 1.

Table 1 shows that EMG onset was dependent on the task (SRT versus CRT), in addition to the actual reaction time. That is, across all muscles, APAs were delayed by an additional 5 ms under the SRT condition. In all individual muscles but one, this delay for SRT conditions was seen (column two, second row). In three muscles (TA L, TA R and ES R) the effect was significant.

3.4. COP displacement

A clear anticipatory posterior displacement of the COP was observed in all the subjects under all three instructions. Time series of COP displacement, averaged across six trials each, for one of the subjects are shown in Fig. 4.

Table 1
The results from the regression analysis in which the effect of instruction (simple reaction time versus choice reaction time) on EMG onset were tested

Muscle	Mean slope	t	P
All muscles	-5.15	-2.38	0.045
BF L	-15.93	-1.89	0.096
TA L	-14.84	-2.63	0.030
ES R	-12.59	-2.66	0.029
BF R	-11.10	-2.21	0.058
TA R	-9.68	-2.58	0.033
ES L	-8.18	-1.27	0.24
RF L	-3.86	-0.59	0.57
RA R	-0.57	-0.18	0.86
SOL R	-0.49	-0.12	0.91
RF R	-0.02	-0.00	1.00
RA L	5.91	1.62	0.14

Column two shows the mean slope of this regression. A single sample t-test tested whether the un-standardized slopes from the different subjects were significantly different from zero (columns 3 and 4). Across all muscles a significant increase in relative timing between postural and focal components was seen in choice reaction time conditions (second row). Abbreviations for muscles are similar to those in Fig. 2. L, muscle on the left side; R, muscle on the right side.

Different traces represent displacements under different instructions. Note that under the SRT condition, COP displacement starts much later as compared to the SP and CRT conditions. Although the onset of the COP shift was delayed under the CRT condition, as compared to SP movements, the displacement was faster, leading to an equal magnitude of the displacement shortly after the onset of the focal movement.

COP displacement at t_0 differed significantly between the SP and both reaction time conditions ($F(2,14)=9.10$,
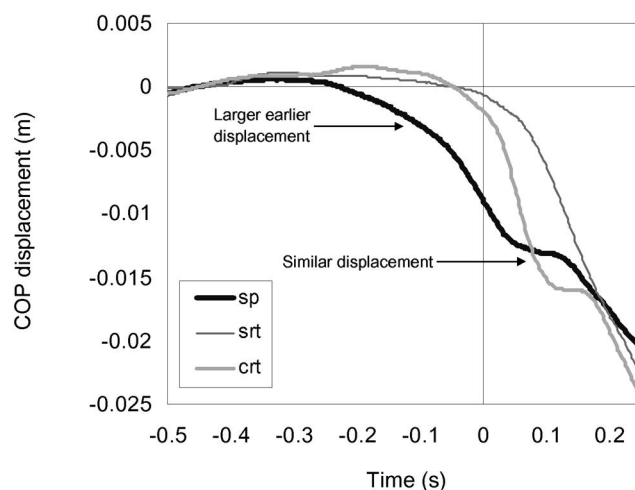

Fig. 4. Time traces of COP displacements in anterior posterior direction under the three reaction time conditions. Note that the backward displacement of the COP initiates prior to the onset of load release (vertical line, t_0). At t_0 the displacement of the COP is larger for self-paced conditions than the reaction time conditions. Shortly after the onset of the perturbation displacement of the COP is similar for SP and CRT conditions.

$P < 0.005$; Fig. 5A). That is, displacement under the SP conditions was significantly larger than under either SRT or CRT conditions ($P < 0.05$).

The difference between the CRT and SP conditions disappeared 50 ms after the onset of the movement while

A COP displacement at t₀

B COP displacement at 50 ms after t₀
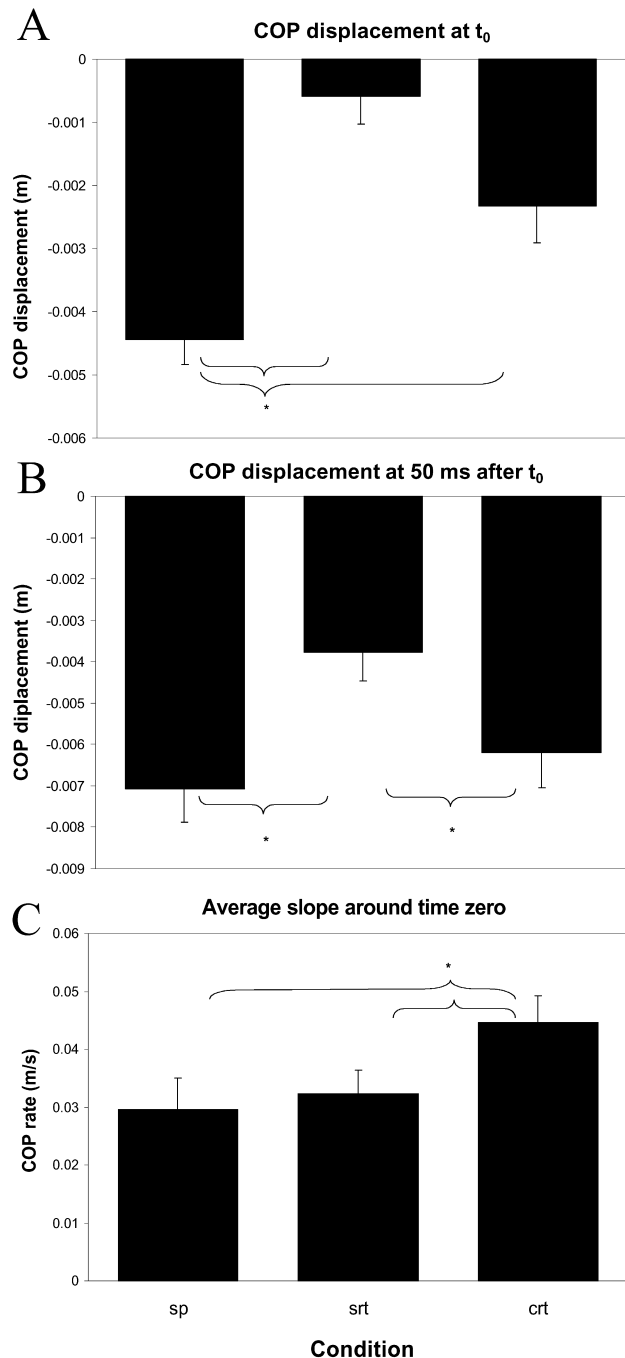
C Average slope around time zero

Fig. 5. Displacements of COP in anterior posterior direction compared to the baseline position across all subjects. At the time of load release (A) displacements are larger than both the reaction time conditions. Shortly thereafter (B) displacements for self-paced and choice reaction time conditions become similar. An increased speed in COP displacement in the interval around time zero was found under choice reaction time conditions (C). Error bars are standard error.

the differences with the SRT conditions remained (Main effect: $F(2,14) = 5.53$; $P > 0.02$). Under the SRT conditions, COP displacement 50 ms after the movement onset was smaller compared to the SP and CRT conditions ($P < 0.05$; Fig. 5B).

This change was brought about by a more rapid COP displacement under the CRT condition (COP$_{rate}$: $F(2,14) = 5.56$; $P < 0.05$). Fig. 5C shows the rates of COP displacement for the three reaction time conditions. The rate of COP displacement, within the interval from -100 to $+50$ ms was larger under the CRT conditions than under the SP and SRT conditions ($P < 0.05$).

Maximal displacement of COP (peak to peak difference from t_0 to $+250$ ms) was different for the reaction time conditions (main effect: $F(2,14) = 7.94$; $P < 0.01$). Under the SRT and CRT conditions, the displacements were larger than under the SP condition (for both comparisons, $P < 0.05$). COP displacement under the CRT condition was somewhat smaller than under the SRT condition (non-significant).

3.5. Effects of direction of the focal movement

In three subjects, additional trials were recorded in which the focal movements were performed without holding the load (see Section 2). No anticipatory bursts in any of the muscles were observed in any of these trials.

However, during the main part of the experiment we observed effects of the direction of the focal movement in integrated EMG activity, onsets of EMG changes, as well as in COP displacements. Fig. 6 shows APA patterns averaged across six trials for an upward-right and a downward-left movement under the SP condition. Note that the activity of both RA and ES muscles is delayed with respect to t_0 during the upward-right movements as compared to the downward-left movements. An opposite pattern is seen in BF, the activity is earlier for the upward-right movements. Table 2 summarizes the effects of movement direction for both ∫EMG and EMG onset indices. Muscles not displayed in Table 2 did not show significant effects. The analysis of EMG onsets and EMG integrals has revealed that leg muscles are more sensitive to left-right differences of the focal movement, while trunk muscles show modulation mostly with movement direction up- or downward. No significant interactions between reaction time conditions and the direction of the focal movement were found.

COP displacements also depended on the direction of the focal movement. Fig. 7 shows COP displacements averaged across six trials for movements in the four directions. These time series show that the COP displacement is increased for upward movements as compared to the downward movements 50 ms after the onset of the movement. No apparent differences between movement to the left or right were observed. Repeated measures ANOVA confirmed a main effect for DIRECTION (COP$_{50}$:
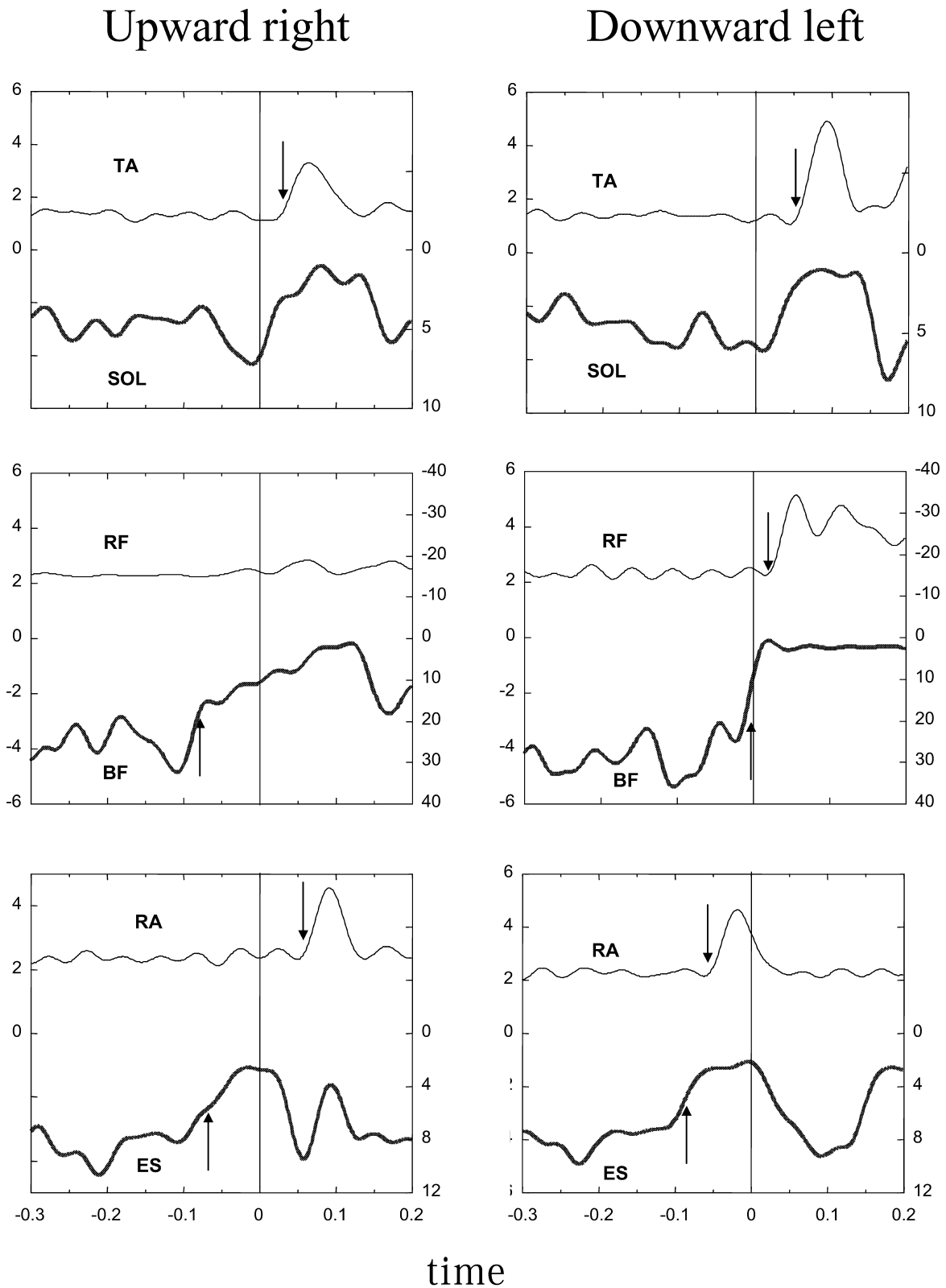
Upward right

Downward left

time

Fig. 6. Averaged across six trials EMGs recorded from leg and trunk muscles in a representative subject during an upward right and downward left movement. Vertical lines show the onset of the perturbation. Note that the bursts of activity in RA and the inhibition in ES start relatively later with an upward movement to the right. In BF an opposite pattern was observed, APAs start later with downward movement to the left. Abbreviations are similar to those in Fig. 2. EMG activity is in arbitrary units. EMG signals for SOL, BF, and ES are inverted for better visualization.

Table 2
Effect of differences in the direction of the focal movement across all subjects for EMG onsets and ∫EMG

Muscle	∫EMG		EMG onset	
	Sign. effect	Post-hoc*	Sign. effect	Post-hoc**
BF-R			X	DownLeft>DownRight
BF-L	X	Left>Right (Up and Down)		
RA-R	X	UpLeft>DownLeft	X	UP>Down (Left and Right)
RA-L	X	Up>Down (Left and Right)	X	Up>Down (Left and Right)
ES-R			X	UpLeft>DownRight, DownLeft
ES-L			X	UpRight>DownRight

Significant main effects from the repeated measures ANOVA are denoted with an X. Post-hoc analysis on individual differences are displayed in the following manner: *∫EMG with increased inhibition or increased excitation compared to condition after > sign; **EMG onset is later than in condition after > sign.
Note that for both ∫EMG and EMG onset BF (R,L) was significantly modulated with the left right differences in the focal movement (see rows 3 and 4). In ES and RA differences between upward and downward were observed (see rows 5–8).

$F(3,21) = 12.21$; $P < 0.001$). Differences in COP displacement between upward and downward movements ($P < 0.01$) were significant, for both the right arm and left arm.

Peak to peak displacement of the COP showed changes with the direction of the movement (COP_{max}: $F(3,21) = 5.19$; $P < 0.01$). Larger displacements were observed with downward movements, compared to the upward movements ($P < 0.05$).

4. Discussion

Our analysis of APAs under different instructions has revealed differences in a number of APA characteristics that allow us to answer the main question formulated in the Introduction and also raise a number of additional issues related to the organization of APAs. In general, the results support the dual-process hypothesis of the APA generation.
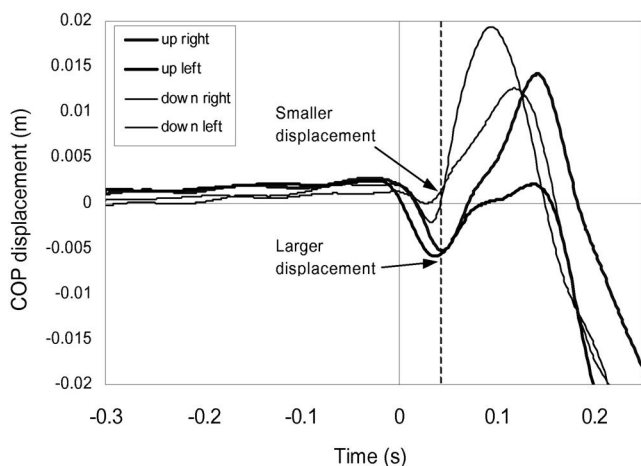

Fig. 7. COP time traces from a representative subject for focal movements to the four lights. Shortly after the onset of the movements (dotted line) COP migrated differently for downward and upward movements. With upward movements a larger displacement was seen than for downward movements.

However, they also confirm the existence of close links between characteristics of APAs and parameters of the action that is used to trigger a postural perturbation. At the end of the discussion, we try to put these findings together and suggests a scheme that is compatible with all the findings of the study.

4.1. Changes in APA timing under reaction time conditions

As described in Section 1, the single-process and dual-process hypotheses [2,21] make qualitatively different predictions with regard to possible changes in the relative timing of APAs with respect to the focal action. The former hypothesis predicts that APAs in CRT conditions will be delayed just like in SRT conditions (cf. Refs. [6,7,13,28]. The latter hypothesis predicts that, if actual reaction time is long enough, APAs in CRT conditions could be similar to those in SP conditions.

In the experiments, we found that APA onsets under SRT conditions were delayed as compared to SP conditions, which is similar to the results reported in earlier studies [7,9,13,19,20,28]. In CRT conditions, APAs occurred earlier than in SRT conditions, and there were no differences between the relative timing of APAs and focal action under the CRT and SP conditions. This result contradicts the main prediction of the single-process hypothesis and is in line with the dual-process hypothesis (e.g., Refs. [9,19]).

We also performed a more detailed study of the relation between the APA relative timing and actual reaction time. The relative APA timing showed a significant relation to the actual value of reaction time such that a 1-ms increase in reaction time corresponded to an increase in the delay between APA and focal-action onsets of between 0.1 and 0.6 ms. In an earlier study [13], we observed certain features of APAs that were related to the instruction, rather than to actual reaction time; i.e., qualitative differences in APAs were seen between the SRT and SP conditions. In

the present study, we have shown that, above and beyond the effects of actual reaction time (which can change for such reasons as attention, fixation, preparation, etc.), EMG onset was also dependent on the instructions. APAs were on average delayed by an additional 5 ms under SRT conditions as compared to CRT conditions. We conclude that the time to program the postural commands, and therefore its anticipatory nature, is also affected by the current task and not only by reaction time, per se.

4.2. Early shifts of the center of pressure

Shifts of the center of pressure (COP) reflect the overall mechanical effects of APAs in all the postural muscles. In our experiments, COP shifts were delayed under both SRT and CRT instructions as compared to those observed during SP movements. During SP movements, COP shifts started very early and proceeded rather slowly. They apparently represented effects of small changes in the muscle activity that we did not identify in the EMG analysis. In CRT conditions, the COP shift apparently started later, was more rapid, and caught up with the SP COP shift at the time of about 50 ms after the focal movement initiation (t_0). If one takes into account typical values of the electromechanical delay (cf. [11]), COP measured at 50 ms after t_0 represented an overall measure of APAs that occurred prior to t_0, i.e., within the time interval where we analyzed EMGs. So, the relatively small differences between the relative timing and magnitude of APAs under the CRT and SP instructions resulted in similar COP shifts by this time.

Under the SRT instruction, COP shifts started late and proceeded slowly so that by the time of $+50$ ms, they were lagging behind the shifts under the other two instructions. A possible reason for the smaller COP displacement during SRT conditions might be found in the increased baseline activity seen in many muscles. It suggests that subjects co-contracted muscles well prior to the movement initiation. Since the available time for preparing a postural response was the shortest under SRT conditions, co-contraction of muscles might be viewed as an adaptive strategy to ensure postural stability.

4.3. APA changes with movement direction

In the experiments, we purposefully tried to make the focal movement as small as possible to minimize its direct effects on posture. The control series, when the subjects performed such movements without holding the load, has shown that focal movements by themselves were not accompanied by visible APAs. Rather unexpectedly, movement direction had significant effects on the characteristics of APAs. This observation is somewhat similar to the one by Aruin and Latash [2] who showed differences in APAs associated with a standard perturbation depending on the action used to trigger the perturbation. However, the study

by Aruin and Latash used very different actions (finger movement versus arm movement) and the APA scaling could be attributed to changes in the magnitude of the focal action (cf. Refs. [16,23]). In the present study different actions involved similar muscle groups on both sides of the body and the movements were of approximate equal magnitude.

The modulation of APAs with movement direction suggests that the CNS interprets the focal movement as being mechanically relevant. The CNS was apparently incapable of decoupling parameters of APAs from those of a focal action. This aspect of our findings seems to be more in line with the single-process hypothesis.

In Section 1 we have stated that the foreknowledge necessary for the generation of APAs was similar in both SRT and CRT conditions. However, since the direction of the focal movement had an effect on APAs, this seems not to be the case. It is reasonable to conclude that only partial foreknowledge for APAs was available in CRT conditions: the subjects knew the direction and magnitude of the perturbation, but apparently a role was played by other factors related to the focal action. This partial foreknowledge under CRT conditions allows one to assume that there was minimal time for the generation of the focal action (as in SRT conditions), but more than minimal time for the generation of APAs. Hence, there is still a distinction between the predictions of the single-process and dual-process hypotheses with the latter predicting earlier APAs in CRT as compared to SRT conditions, as observed in our experiments.

This conclusion is also corroborated by the fact (Section 3.5) that changes in the APA timing due to instruction were relatively independent of changes due to movement direction (no significant interactions between RT and direction factors). APA patterns in ventral/dorsal muscles were always characterized by reproducible excitation/inhibition features. Hence, the effects of the focal action might be viewed as a modulation of a general APA pattern.

This may be viewed as reflecting a feature of the system for the generation of APAs evolved based on the everyday experience. Since in everyday life, features of a perturbation induced by a person's focal action are always tightly linked to properties of the focal action, modulation of APAs with focal action may be a feature that cannot be by-passed, even if a particular experimental procedure decouples the two components of an action. In particular, up and down bilateral arm movements in standing subjects are expected to lead to large perturbations in the anterior–posterior direction and relatively small lateral and rotational perturbations, while unilateral left and right arm movements are expected to lead to relatively large lateral and rotational perturbations [24]. Correspondingly, APAs associated with up and down movements typically show large, reproducible EMG bursts in trunk muscles modulated with the direction of the focal movement [6,7,17,28]. Actions associated with lateral and rotational perturbations show

modulation of EMG patterns in more distal leg muscles [3,24]. Thus, if one accepts the possibility of APA modulation with changes in the action characteristics, the present observations corroborate the earlier hypothesis on the different involvement of different muscle pairs in the generation of APAs to anterior–posterior, lateral, and rotational perturbations.

Another factor affecting APA timing might be the different RTs for the different directions of focal movement, although these differences were not significant. On average, RTs for movements upwards were smaller than those for movements downwards by about 18 ms, while RTs for movements to the right were shorter than those for movements to the left by about 10 ms. These differences could be expected to lead to changes in the timing of the APAs. Based on our assessments of the relation between RT and APA timing, one could expect differences in the APA timing of the order of 1–10 ms. The actual differences were at least three to four times larger. Therefore, changed RTs, by themselves, cannot account for the changed APA timing with the different directions of the focal action.

4.4. Relations between APAs and focal action

Although the main results of the study (changes in the relative timing of APAs with instruction) support the dual-process hypothesis and contradict the single-process hypothesis, other findings, such as the APA modulation with movement direction, prevent such a straightforward view on the organization of APAs. The following two conclusions can be drawn:

1. if a standard perturbation is initiated under different time pressure conditions, the CNS is able to initiate the process of the generation of APAs independently of the process of focal movement generation; and
2. if a standard perturbation is generated by different actions, the CNS modulates the APAs with characteristics of the action even when the actions themselves lead to very small postural perturbations not associated with detectable APAs.

So, we would like to conclude that APAs and focal actions can be initiated independently of each other while their quantitative features are modulated by some common inputs, including the characteristics of planned focal action and the type of task being used. The described changes in APAs with action also suggest the possibility of modifications of a function that transforms two parallel control signals into a single command to focal and postural muscles, based on postural requirements and behavioral constraints.

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