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Postural Preparation for Sequential Perturbations

by

Takako Shiratori[1], *Mark Latash*[2]

The study addresses a question: How are anticipatory postural adjustments (APAs) organized in tasks involving two sequential perturbations that come at a short delay? Two possibilities were compared, a linear superposition of APAs associated with each of the perturbations vs. the generation of an APA related to the overall mechanical effect of both perturbations. Standing subjects performed three tasks involving releasing a load (release-only), catching a load (catch-only), and both in a sequence (release-catch). The load mass and release height co-varied to manipulate different mechanical characteristics of the perturbation. APA magnitude was assessed using integrals of muscle activity over typical time intervals. The APAs associated with load release were smaller for release-catch tasks compared to release-only tasks. The APAs associated with catch were smaller in the trunk and leg muscles and larger in forearm muscles for release-catch tasks compared to the catch-only tasks. APAs were sensitive to the flight time as well as the mass of the load. We conclude that APAs associated with each perturbation were generated taking into account the mechanical effects of the other perturbation and/or the effects of APAs associated with the other perturbation. The findings suggest that studies of relative timing of sequential actions may need to consider associated postural adjustments as factors that may shape the performance. They also offer a possibility that difficulties in sequential actions in certain neurological patients may be causally related to their postural impairment.

Keywords*: Anticipatory postural adjustment, posture, electromyography, human*

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[1] *- Currently at: Department of Physical Therapy, Northwestern University, Chicago, IL, USA*

[2] *- Department of Kinesiology, Pennsylvania State University, University Park, PA , USA*

Introduction

Voluntary movements performed by a standing person perturb the balance because of the mechanical coupling leading to transient torques in apparently postural joints and shifts of the body center of mass (cf. Massion 1992). Anticipatory postural adjustments (APAs) prior to the voluntary initiation of a discrete action while standing have been extensively studied (i.e., Friedli et al. 1984; Zattara and Bouisset 1988; Aruin and Latash 1995; Rogers and Pai 1990; Mouchnino et al. 1992; Oddsson and Thorstensson 1986). Yet, only a few researchers examined the organization of APAs associated with sequential actions. Lipshits et al. (1981) observed that when the initial and final postures were identical, as in a stance—tip-toe rising — stance sequence performed without interruption, no APAs were seen prior to the tip-toe rising phase, while APAs were present when rising on the tip-toes was performed separately. Within a squat stance — jump — squat stance sequence, APAs prior to the first jump were different depending on whether the sequence was performed once or repeatedly (Le Pellec and Maton 1999).

In those studies, features of the voluntary actions by the subjects defined mechanical characteristics of the postural perturbations. These features of action components were likely different in sequential actions as compared to the same action components performed individually. For example, rising on tip-toes performed separately requires stabilization of the body in the final posture. This may be expected to affect the whole time course of the action. APAs are known to depend on characteristics of both expected perturbation and action that produces the perturbation (Dufosse et al. 1985, Aruin and Latash 1995). Hence, different APAs observed in those studies could be due to differences in characteristics of the action components. To avoid this problem in the current study, we used load release and catch as postural perturbations whose characteristics could be varied independently of the actions that triggered them. This manipulation allows to address a question: Do APAs associated with a perturbation depend on whether the perturbation occurs alone or as part of a sequence, if both the mechanical features of the perturbation and the action triggering the perturbation remain the same?

When a standing person releases the load held in front of the body, suppression of the baseline activity of dorsal trunk and leg muscles is typically observed about 100 to 150 ms prior to the load release (Aruin and Latash 1995; Aruin et al. 1998). When a standing subject catches a load into the hands extended in front of the body, activation of dorsal leg and trunk muscles is observed as early as 150 ms prior to the load impact (Lavender and Marras

1995; Shiratori and Latash 2001). Hypothetically, at least two strategies can be used to generate APAs in cases of sequential perturbations: 1) A linear superposition of APAs to individual perturbations; or 2) Taking into account the ultimate mechanical effect of the whole sequence of perturbations. In the latter case, APAs associated with each perturbation separately are expected to decrease when the unloading and loading are performed in a sequence, since unloading and loading generate postural perturbations acting in opposite directions.

The use of unloading-loading paradigm has two main advantages: 1) The motor action triggering the perturbation has minimal effect on the perturbation magnitude, and 2) The magnitude and the timing of the perturbations can be systematically changed by manipulating the mass and release height of the load. This paradigm also allowed us to study the importance of different mechanical characteristics of the load release and impact for APAs seen prior to the load release and catching.

Methods

Subjects

Ten healthy male subjects between the ages of 23 and 35 without known neurological or muscle disorders took part in the study. The weight of the subjects was 72.6 ± 4.4 kg; their height was 1.76 ± 0.08 m. All subjects were right handed as defined by their preferential hand use during eating and writing. The subjects gave informed consent approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus

Subjects stood on a force platform (AMTI OR-6) which measured reaction force along the direction of gravity (F_Z) and moment of force in the sagittal plane (M_X). Three loads of the same size (0.17 width x 0.17 width x 0.10 m height) with different masses (1.1, 1.37, and 2.2 kg) were used in this experiment. The loads were made of tin cans filled with different proportions of sand and soft packaging material. On the bottom of each load, soft packaging material was attached to increase comfort when catching the load.

An aluminum rod was attached to the top center of each load. The rod was either held by the subject’s right hand or hung on a latch attached to an external frame (Figure 1A and 1B, respectively). The external frame had a handle that was adjustable in height and a latch attached to the bottom of the handle. The handle on the external frame was held by the subject's right hand, and when the subject extended the fingers, the latch opened and released the load. Varying the rod length allowed the subjects to release the load from different vertical locations while preserving a constant right hand position.

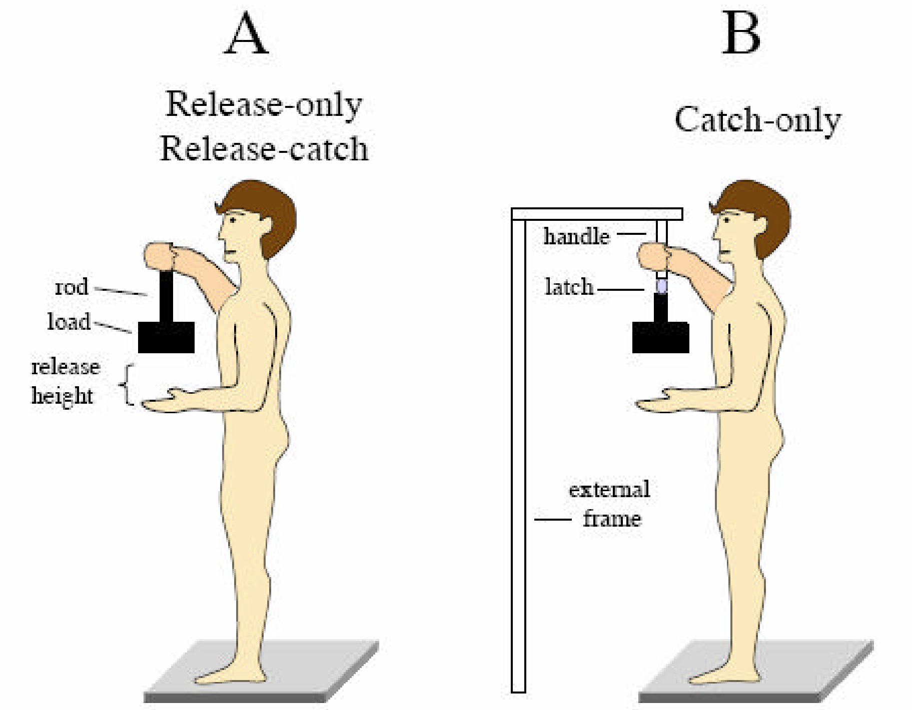

Figure 1

Experimental setup for A) release-only, release-catch, *and B)* catch-only. *The load mass varied from 1.1 to 2.2 kg, and the drop height varied from 0.1 to 0.4 m. The subjects were required to always start from the same arm position. The length of the rod that was either held by the subject or attached to the external frame, determined the drop height.*

Surface electromyograms (EMGs) were recorded in the following leg, trunk, and arm muscles on the left body side using disposable self-adhesive electrodes: tibialis anterior (TA), soleus (SOL), rectus femoris (RF), biceps femoris (BF), rectus abdominis (RA), erector spinae at the L2-L3 level (ES), flexor carpi ulnaris (WF), extensor carpi radialis (WE), biceps brachii (BIC), and long head of triceps (TRI). The electrodes were placed over the muscle bellies, the distance between the two electrodes of a pair was 3 cm. Signals from the electrodes were amplified with the gain of 3000.

A unidirectional accelerometer (Sensotec) was attached to the tip of the right middle finger above the nail to detect the initiation of finger motion leading to load release. Another accelerometer was attached to the dorsal surface of the left hand to detect the instant of load impact. The accelerometer signals were used for data alignment. A Macintosh computer with customized software based on the LabView package was used to collect the data. All the signals were sampled at 500 Hz with a 12 bit resolution. The data were analyzed off-line with the customized software based on the LabView and MatLab packages.

Procedure

Three main tasks were performed: unloading and loading in sequence (*release-catch*), unloading (*release-only*), and loading (*catch-only*). In all tasks, the subjects adopted the same body posture. They were instructed to stand on the force platform with their feet shoulder width apart; the foot position was marked and reproduced across trials. The left hand was designated as the catching hand, and was placed in front of the body at the midline with the elbow flexed at 90 degrees, and the fingers extended to form a flat surface. The arm did not touch the trunk. The ulnar border of the right hand was placed 0.55 m directly above the left palm. The right hand was oriented such that when the subject extended the fingers, the hand aligned with the frontal plane with the palm facing the body.

The *release-catch* task consisted of releasing the load from the right hand and catching it with the left hand. The subject stood on the force platform and adopted the previously described body posture. The subject was instructed to release the load in a self-paced manner by a brisk opening of the right hand fingers after a computer-generated tone and to catch the load with the left hand. During analysis, we will address the *release-catch* task with two names depending on which of the two perturbations (unloading or loading) is being analyzed. When APAs to the release phase are analyzed, the task will be addressed as *RELEASE-catch*, and when the APAs to catch are discussed, the task will be called *release-CATCH*.

During the *release-only* task, the subject adopted the same posture and held a load in the right hand. The subject was asked to release the load with a brisk finger extension after a computer-generated tone. The subject knew in advance that the load would be caught in mid-air by the experimenter and would not hit the subject’s left hand.

For the *catch-only* task, the subject caught the load released from the external frame. The subjects adopted the same posture, but the right hand held the handle attached to the external frame (Figure 1B). The load was clipped into the latch below the handle, at an appropriate height directly above the left hand. The subjects were instructed to release the load by briskly extending the right hand fingers after a computer-generated tone. This finger extension released the load, and the subjects were required to catch the load. The purpose of using the external frame was to eliminate the effects of unloading perturbation while using the same finger extension action to trigger the load release as in the two other tasks.

Each task involved six series of trials with different load masses (1.1, 1.37, and 2.2 kg) and release heights (0.1, 0.25, and 0.4 m); the mass and the height were adjusted to obtain three sets of three series each that would keep constant one of the following load characteristics: mass, momentum at impact, or release height (see Table 1). For the constant mass series, the 2.2 kg load was released from three different release heights (series 1, 2, and 3). For the constant momentum series, the load mass and release height co-varied to obtain similar values of momentum at impact (series 1, 4, and 6). For the constant height series, three different loads were released from the same height of 0.4 m (series 3, 4, and 5). Each series consisted of six consecutive trials. Each trial lasted 5 s with 10 s intervals between consecutive trials. A three-minute break was given after each series. During this time, two familiarization trials were performed. The tasks and series were presented in a balanced order across the subjects.

<Table 1 about here>

Data Processing

EMG signals were filtered with a 2nd order 100 Hz low-pass Butterworth filter and rectified. Signals from the accelerometers and the force platform were filtered with a 2nd order 20 Hz low-pass Butterworth filter. Individual trials were aligned with respect to the accelerometer signal indicating the moment of load release (*RELEASE-catch*, and *release- only* tasks) or impact to the hand (*release-CATCH* and *catch-only* tasks). The moment of load release or impact was determined by a time when the accelerometer signal reached one standard deviation (SD) away from the mean value computed over the first 50 ms of data recording. This alignment was checked visually by comparing to other mechanical channels. This alignment time will be referred to as "time zero-release" ($T_{0,R}$) or “time zero-catch” ($T_{0,C}$). In some cases, a whole-body motion or an arm motion prior to load release or load impact made the accelerometer signal unreliable. Such trials were discarded from analysis (never more than 2 trials within a series).

The following EMG indices were quantified: 1) Anticipatory changes in muscle activity prior to load release, and 2) Anticipatory changes in muscle activity prior to load catch. To quantify the anticipatory changes in the muscle activity prior to load release or impact, EMG signals were integrated from -100 to 0 ms (?EMG$_{(100)}$) with respect to $T_{0,R}$ or $T_{0,C}$. This value was further corrected for the baseline activity defined as the integral from –500 to –450 ms (?EMG$_{(50)}$) with respect to $T_{0,R}$:

$$?EMG = ?EMG_{(100)} - 2*?EMG_{(50)}$$

To compare indices of EMG activity among different tasks and across subjects, normalization of ?EMG was necessary. For each subject, the maximal absolute value of a given ?EMG index for a given muscle across all the series was taken to be unity, and all other values of this particular index for this muscle were normalized with respect to the maximal value. Note that this method limits the range of changes of ?EMG indices to from -1 to +1. Negative values correspond to suppression of the baseline activity during APAs. Symbols ?EMG$_R$ or $\int$EMG$_C$ will be used to represent normalized integrated EMG activity prior to load release or catch corrected for the baseline activity, respectively.

The onset times of changes in the arm muscle activity related to catching (‘APA onset’) were defined using EMG profiles averaged over the trials of a series for each subject. The mean and standard deviation of the baseline activity (from – 500 to – 450 ms with respect to $T_{0,R}$) was calculated for each muscle. Then, the onset of an APA was defined as the time when the muscle activity reached one SD away from the mean baseline level for more than 30 ms within the time interval from - 300 ms to + 30 ms with respect to $T_{0,C}$. We also tried to use the same method to detect the time onsets in the muscle activity related to release or catch for the leg and trunk muscles. However, suppression of the baseline activity that occurred in preparation to unloading in the dorsal muscles of the leg and trunk was generally small and commonly did not reach – 1 SD away from the baseline EMG activity. Also, not all subjects met the APA onset criteria in the leg and trunk muscles prior to catching the load. Thus, APA onset data will only be presented for the arm muscles.

Displacement of the center of pressure (?COP) in the anterior-posterior direction was calculated using the following approximation: ?COP= ?M$_X$/F$_Z$. Anticipatory COP displacement for all experimental series was quantified as the change in the COP location from –100 to 0 ms with respect to $T_{0,R}$ or $T_{0,C}$.

For statistical analysis, each dependent measure (?EMG$_R$, ?EMG$_C$, and ?COP) was analyzed separately using repeated-measures ANOVA with factors *Release-*

Task (two levels: *RELEASE-catch* and *release-only* tasks), *Catch-Task* (two levels: *release-CATCH* and *catch-only* tasks), *Series* (six levels: experimental series 1 through 6 in Table 1), *Height* for the constant mass series (three levels: 0.1, 0.25, 0.4 m) and *Mass* (three levels: 1.1, 1.37, 2.2 kg) for the constant momentum and constant height series. For further comparisons, Student's t-tests with Bonferroni corrections were used.

Results

EMG patterns associated with releasing the load

Changes in the baseline activity (APAs) of leg and trunk muscles could be seen prior to the load release when the release was performed alone (*release-only*) and when the release was followed by a catch (*RELEASE-catch*). Figure 2 shows typical EMG patterns in the trunk and leg muscles for the *release-only* (panel A) and *RELEASE-catch* (panel B) tasks averaged across 6 trials for a representative subject who released the 2.2 kg load from 0.4 m (series 3 in Table 1). The dashed vertical lines indicate the moment of load release, time zero ($T_{0,R}$). When the release was performed alone, the subject showed a decrease in the baseline EMG activity of the erector spinae (ES) and an increase in the baseline EMG activity of rectus femoris (RF) approximately 100 ms prior to $T_{0,R}$. When a load release was followed by a catch, ES showed smaller early suppression of the EMG activity than in the *release-only* task. Also, RF did not show any change in the baseline activity prior to load release in the *RELEASE-catch* task, in contrast to what was observed in the *release-only* series.

Table 1

Experimental series for release-catch, release-only, and catch-only tasks.

Series	**Mass** (kg)	**Height** (m)	**Momentum** (kg•m•s^{-1})	**Dorp Time** (s)
1	2.2	0.1	3.083	.143
2	2.2	0.25	4.873	.226
3	2.2	0.4	6.166	.286
4	1.1	0.4	3.083	.286
5	1.37	0.4	3.840	.286
6	1.37	0.25	3.083	.226

Series 1 through 3 represent constant mass series, series 3, 4 and 5 represent constant height series, and series 1, 4, and 6 represent constant momentum at impact series (shaded in gray).

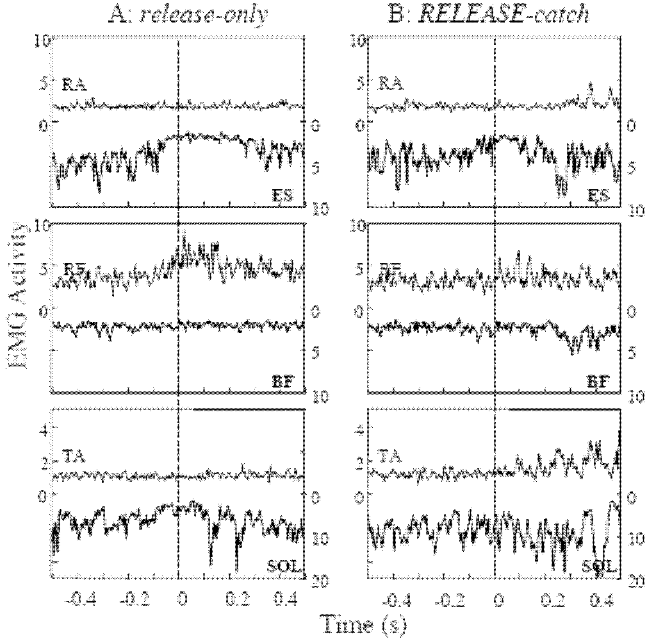

Figure 2

EMG traces averaged across 6 trials performed by a typical subject for the release-only *(A) and* RELEASE-catch *(B) tasks with the 2.2 kg load released from 0.4 m. A decrease in the baseline EMG level can be seen in ES and BF prior to the load release for both tasks. However, the magnitude of suppression is generally smaller for the* RELEASE-catch *task.* RA-*rectus abdominis,* ES-*erector spinae,* RF-*rectus femoris,* BF-*biceps femoris,* TA-*tibialis anterior,* SOL-*soleus. EMG scales are in arbitrary units (bytes). The bottom traces (thicker lines) in each plot are inverted for easier comparison, and their scales are on the right Y-axes.*

APAs associated with load release were quantified using the ∫EMG$_R$ index (see Methods). Across all six experimental series, the magnitude of the EMG suppression in ES was smaller when load release was followed by a catch (*RELEASE-catch*) as compared to the *release-only* task. Repeated-measures ANOVA *Release-Task* x *Series* confirmed the main effect of *Release-Task* ($F_{[1,9]} = 8.25$, $p < 0.01$). Prior to load release, COP shifted backwards; the magnitude of this shift was not different between the *release-only* task (range from 0.0008 to 0.0012 m) and the *RELEASE-catch* task (range from 0.0008 to 0.0018 m).

?EMG$_R$ indices for some of the leg and trunk muscles and ?COP associated with load release tasks were analyzed separately for the constant mass (series 1, 2, 3), constant momentum (series 1, 4, 6), and constant height series (series 3, 4,

5) using repeated-measures ANOVA with factors *Release-Task* and either *Height* or *Mass* (Figure 3). Tibialis anterior (TA) and soleus (SOL) did not show consistent EMG patterns across subjects and their data are not presented in this analysis.

In the constant mass series (Figure 3A), as expected, no differences in ?EMG$_R$ indices were observed between different release heights. However, ?EMG$_R$ indices in some leg and trunk muscles did depend on whether the release was performed alone or was followed by a catch. As compared to *release-only*, *RELEASE-catch* was associated with significantly decreased APAs in RF and RA, and significantly smaller suppression of the background activity in BF and ES (main effect of *Release-Task*, $F_{[1,9]} > 5.30$, $p < 0.05$ for RF, BF, and ES; $F_{[1,9]} = 13.37$, $p < 0.01$ for RA).

In the constant momentum series (Figure 3B), ?EMG$_R$ indices were not different between the *release-only* and *RELEASE-catch* tasks; there were no effects of load mass either (Figure 3B). However, in the constant height series, where loads with different masses were released from the same 0.4 m release height (Figure 3C), ?EMG$_R$ for ES was sensitive to changes in the mass, with larger suppression of the background activity prior to releasing heavier loads (main effect of MASS, $F_{[2,18]} = 7.18$, $p < 0.01$; further comparison showed significant difference in the APA magnitude between 1.1 and 2.2 kg load for the *release-only* task, $p < 0.01$). When the two tasks were compared, APAs in RA and ES were significantly or close to significantly decreased in magnitude in the *RELEASE-catch* task as compared to the *release-only* task (main effect of *Release-Task*, $F_{[1,9]} = 5.1$, $p < 0.05$ for ES; $F_{[1,9]} = 4.36$, $p = 0.06$ for RA).

Anticipatory COP displacement (?COP) showed results consistent with expected mechanical effects of the unloading perturbations. In the constant mass series, no difference in ?COP was observed across different release heights. However, in series with different load masses (the constant momentum and constant height series), a larger posterior shift of COP was observed prior to releasing heavier loads across both tasks. This was confirmed by two-way repeated-measures ANOVA. For both constant momentum and constant height series, there was a main effect of *Mass* ($F_{[2,18]} > 4.7$, $p < 0.05$); further comparisons showed significant differences between the 1.37 and 2.2 kg loads for the constant momentum series and between 1.1 and 2.2 kg loads for the constant height series (both at $p < 0.01$).

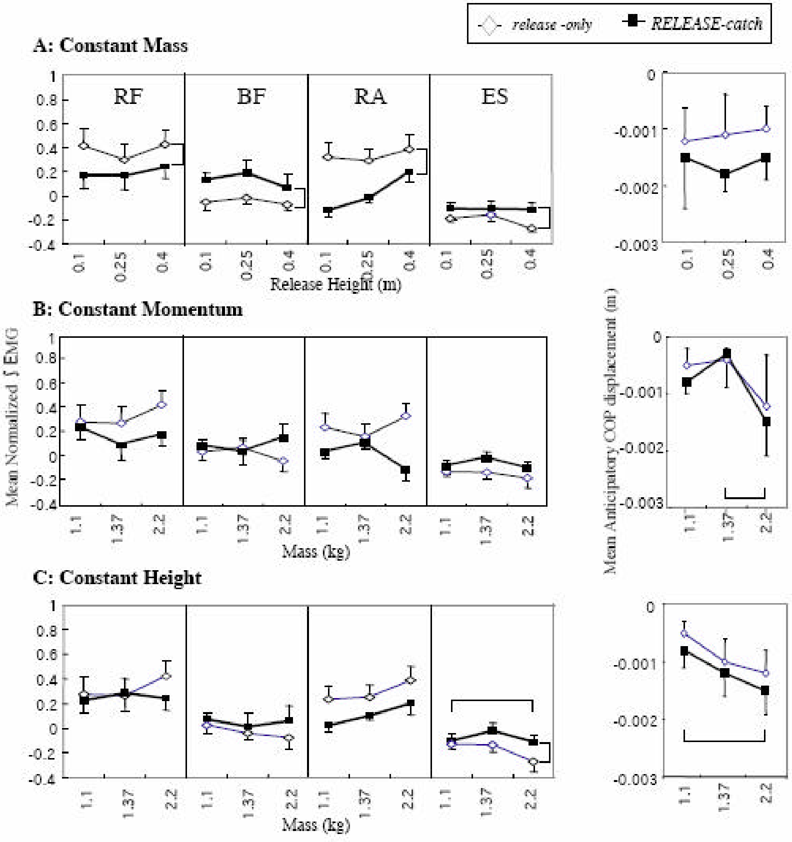

Figure 3

Averaged across subjects, normalized $\int EMG_r$ for A) constant mass series, B) constant momentum series, and C) constant height series for release-only *(thin lines, open symbols) and* RELEASE-catch *(thick lines, filled symbols) for some of the leg and trunk muscles. Vertical brackets indicate significant differences between the tasks. Horizontal brackets indicate significant differences between different masses. The constant mass series (A) showed no effect of height. However, significantly smaller APAs are observed in RF and RA (ventral muscles) and significantly less suppression in BF and ES (dorsal muscles) during* RELEASE-catch *as compared to* release-only. *The constant momentum series (B) showed no effect of task or mass in the leg and trunk muscles. The constant height series (C) showed effect of mass for ES, and effects of task in RA and ES.*

EMG patterns associated with catching the load

Changes in the baseline activity of leg, trunk and arm muscles could be seen prior to load impact when the load was released from the external frame (*catch-only)* and when it was released from the subject's other hand (*release-CATCH*). Figure 4 shows EMG patterns in the arm, trunk, and some of the leg muscles when the 2.2 kg load was released from the height of 0.4 m for the *catch-only* and *release-CATCH* tasks. The data were averaged across six trials performed by a representative subject. The vertical lines indicate the moment of load impact onto the catching hand ($T_{0,C}$). In both tasks, there is a slight increase in the baseline EMG activity in ES and a substantial increase in the activity of all the arm muscles (WF, WE, BIC, TRI) prior to the load impact. When the two catch tasks are compared, the EMG burst in ES prior to the catch in the *release-CATCH* series is smaller than the ES burst observed for the *catch-only* series. In some of the arm muscles (BIC, TRI), the EMG burst prior to catching was larger and its onset was earlier for the *release-CATCH* than for the *catch-only* task.

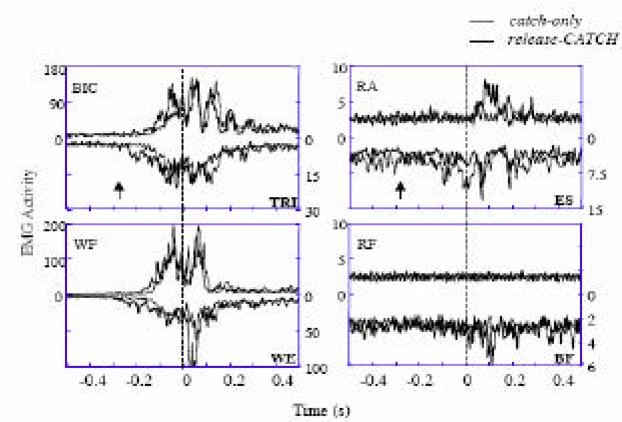

Figure 4

EMG traces averaged across 6 trials performed by a typical subject for the catch-only *(thin traces) and* release-CATCH *(thick traces) tasks with the 2.2 kg load released from 0.4 m. The vertical line indicates the moment of load impact on the catching hand. The arrow indicates the moment of load release. An increase in the baseline EMG in ES and in all arm muscles can be seen prior to the load impact for both tasks. APA in ES prior to catch is smaller in* release-CATCH *than* catch-only *task while some of the arm muscles (BIC, TRI) show a larger baseline level in* release-CATCH *than* catch-only *task for this subject. Abbreviations:* BIC-*biceps brachii,* TRI-*triceps brachii,* WF-*wrist flexor,* WE-*wrist extensor; other abbreviations are as in Fig. 2. The bottom traces in each plot are inverted for easier comparison, and their scales are on the right Y-axes.*

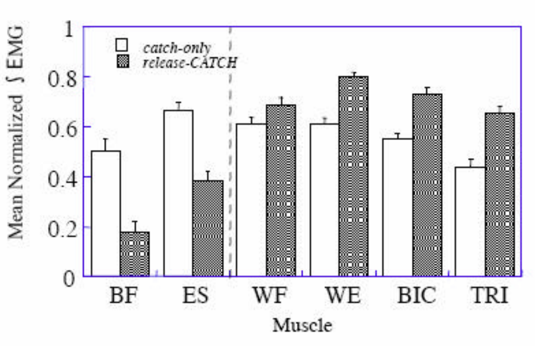

Figure 5

Averaged across subjects, normalized ÆMG$_c$ values across all 6 series for the catch-only *and* release-CATCH *tasks. For BF and ES, significantly larger APA were observed during* catch-only *as compared to* release-CATCH. *All the arm muscles showed significantly larger APA during* release-CATCH *as compared to* catch-only. *Abbreviations are the same as in Figures 2 and 4.*

Note also that all the arm muscles showed an earlier onset in the changes of the baseline EMG activity for the *release-CATCH* task as compared to the *catch-only* task (Figure 4). This effect was significant for all arm muscles across all 6 experimental series confirmed by the repeated-measures ANOVA (*Catch-Task* x *Series*, main effect of *Catch-Task*, $F_{[1,9]} = 6.88$, $p < 0.05$ for ES; $F_{[1,9]} > 10.28$, $p < 0.005$ for all arm muscles).

Prior to load impact, an anticipatory COP shift was observed in the anterior direction. Between the two catch tasks, smaller ?COP was observed prior to load catch for *release-CATCH* compared to *catch-only* (*Catch-Task* x *Series*, main effect of *Catch-Task*, $F_{[1,9]} = 9.01$, $p < 0.05$). COP displacements for *catch-only* ranged from 0.0039 to 0.0052 m, while for *release-CATCH* they ranged from 0.0006 to 0.0027 m.

To further investigate the effects of mechanical characteristics of the perturbation on APAs, ?EMG$_C$ and ?COP indices associated with catching were analyzed separately for the constant mass, constant momentum, and constant height series using repeated-measures ANOVA with factors *Catch-Task* (*catch-only*, and *release-CATCH*) and *Height* or *Mass* (Figure 6).

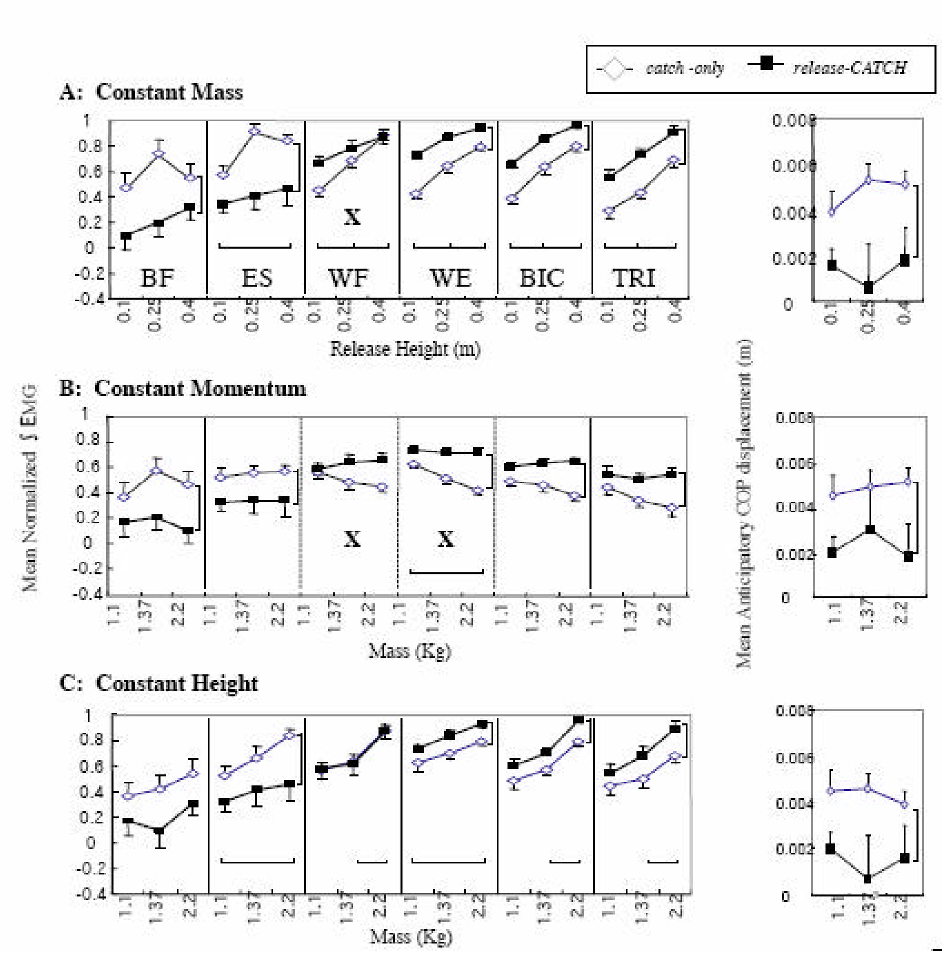

Figure 6

Averaged across subjects, normalized ÆMG$_c$ for A) constant mass series, B) constant momentum series, and C) constant height series for the catch-only *(thin line, open symbols) and* release-CATCH *tasks (thick line, filled symbols). Vertical brackets indicate significant differences between tasks. Horizontal brackets indicate significant difference between masses. X indicates significant* Task x Mass *interaction. Across all series (A,B and C), BF and ES showed smaller APA indices for the* release-CATCH *whereas all arm muscles showed higher APA indices for the* release-CATCH. *Smaller anticipatory COP displacement was observed for* release-CATCH *as compared to* catch-only. *The effect of height was significant during the constant mass series. During the constant momentum series, arm muscles showed increased APA magnitude with height for* catch-only *but not for* release-CATCH. *Effect of mass was significant during the constant height series in BF, ES and all the arm muscles.*

Within the constant momentum series, no changes in the ?EMG$_{C}$ indices for the arm muscles were observed during the *release-CATCH* task, while these indices decreased as load mass increased for the *catch-only* tasks. This has been confirmed by significant or close to significant *Catch-Task* x *Mass* interaction ($F_{[2,18]} > 4.38$, $p < 0.05$ for WF and WE; $F_{[2,18]} = 2.67$, $p = 0.09$ for BIC and TRI).

In the constant mass and constant height series, ?EMG$_{C}$ indices for most muscles were sensitive to changes in the perturbation characteristics indicated by significant main effects of *Height* and *Mass* (Figure 6A, 6C). In addition, there was a significant *Catch-Task* x *Height* interaction for the ?EMG$_{C}$ index for WF ($F_{[1,9]} = 5.62$, $p = 0.01$). It reflected significant differences between the two tasks for the low height values, but not for the larger heights. Within the constant height series, APAs associated with catching were sensitive to load mass. Prior to load impact, ?EMG$_{C}$ indices significantly increased with an increase in the mass across both catch tasks (main effect of *Mass*, $F_{[1,9]} > 13.81$, $p < 0.001$ for all the arm muscles; $F_{[1,9]} = 7.71$, $p < 0.01$ for ES).

Discussion

The main focus of this study has been on differences between APAs seen prior to perturbations associated with load release and catch when these actions were performed separately (*release-only* and *catch-only*) and when the same actions and associated perturbations occurred in a sequence (*release-catch*). In the *release-catch* tasks, the APA indices associated with each perturbation were generally smaller in the leg and trunk muscles than in the *release-only* and *catch-only* tasks. This happened despite the fact that all three components that are commonly believed to affect APAs were the same across the tasks: The magnitude and site of the perturbation, the posture, and the action triggering the perturbation (Aruin and Latash 1995, 1996). In addition, we followed-up on an earlier study of the effects of different mechanical variables characterizing a perturbation on APAs seen prior to load catching (Shiratori and Latash 2001). The findings agree with earlier conclusions on the importance of such variables as momentum, mass, and flight time for the generation of APAs.

Linear superposition of APAs or their scaling with overall mechanical effect of the perturbation?

The linear superposition hypothesis formulated in the Introduction predicted that APAs for each perturbation would remain unchanged when two perturbations occur in a sequence. An expected result of this hypothesis was that APAs associated with release in the leg and trunk muscles would be similar in magnitude between the *release-only* and *release-catch* tasks. Similarly, APAs associated with catch were expected to be similar between the *catch-only* and *release-catch* tasks.

The alternative hypothesis predicted that the CNS would prepare a postural adjustment to the expected overall mechanical effect of a release-catch sequence as a single event. Since the unloading and loading perturbations produce opposite mechanical effects on vertical posture, decreased APAs were expected prior to both unloading and loading when they occurred sequentially, at a short time delay. The results of our experiments are consistent with this hypothesis: The APAs associated with load release were smaller when the release was followed by a catch than when the release was performed alone. In addition, the APAs in the leg and trunk muscles associated with catch were smaller when the catch was preceded by a release than when the catch happened alone.

These results support earlier reports by Lipshits et al. (1981) and LePellec and Maton (1998). Note, however, that in contrast to those studies, our experiment used the same action to trigger perturbations and hence, the observed differences could not be due to effects of changed action on APA characteristics (cf. Aruin and Latash 1995).

The importance of mechanical characteristics and timing of perturbation

In previous studies, APAs associated with both unloading and loading perturbations have been shown to scale with the magnitude of the perturbation (Aruin and Latash 1996; Lacquaniti and Maioli 1989a; Bennis et al. 1996; Shiratori and Latash 2001). In our study, we continued to explore the relations between mechanical characteristics of perturbations and APAs. We also addressed another question: If a change in a mechanical characteristic affects only one of two perturbations that occur in a release-catch sequence, will APAs to the other, unchanged perturbation show effects of that load characteristics?

In particular, the constant mass series examined a condition where the same unloading perturbation was followed by a loading perturbation that depended on the height of the load release. Thus, APAs prior to load release were expected to be similar across different release heights. This was indeed true for the *release-only* task. However, in the *release-catch* task, APAs prior to load release showed a tendency to scale with the height of the load release (see RF, Fig 3A). One explanation for this result is that the time between the two perturbations in the *release-catch* task may be an important factor. When this time is short, the controller treats two perturbations as one and scales the APAs appropriately. When the flight time of the load increases, the mechanical effects of the perturbations on posture become more and more independent of each other, which may be expected to lead to an increase in the APAs associated with load release closer to patterns observed in the *release-only* task. Note that the importance of flight time for the organization of APAs to catching has been emphasized earlier (Shiratori and Latash 2001).

The constant momentum series examined a condition where the loading perturbation (momentum at impact) was constant while the unloading perturbation varied with the mass of the load. In this series, there were no differences in the APAs in the leg and trunk muscles between the task pairs with the perturbations occurring separately and in a sequence (*release-only* vs. *RELEASE-catch* and *catch-only* vs. *release-CATCH*). However, this series has revealed an interesting effect in the arm muscles between the two catch tasks that will be discussed in the next section.

The constant height series was introduced to examine the organization of APAs when the flight time was the same while different loads were released and caught. In the constant mass and constant momentum series, larger APAs associated with catching loads released from greater heights could be due to an increase in the flight time, which allowed the subjects to prepare for the catch perturbation. The constant height series showed that APAs associated with both release and catch perturbations were sensitive to changes in mass at least in some of the leg, trunk, and arm muscles. Taken together, these results suggest that both the timing of the two perturbations and the mechanical load characteristics are important for the generation of APAs.

APAs in arm muscles

All the arm muscles showed an increase in the baseline activity prior to load impact in both *catch-only* and *release-CATCH* tasks. However, there were differences between the two tasks. First, the APAs were larger and started earlier in the arm muscles for the *release-CATCH* task as compared to the *catch-only* task. Second, in the constant momentum series, the *catch-only* task showed APA scaling with release height while no such scaling was observed for the *release-CATCH* task.

An earlier study looked at APAs in arm muscles prior to catching a load that was either released by the subject's other hand or by the experimenter (Shiratori and Latash 2001). It has shown that APAs in the arm muscles are larger for the self-release condition. Thus, larger APAs seem to be associated with actual handling of the load by the subject prior to catching. This could be associated with the subject feeling more confident about the actual mechanical properties of the load and characteristics of the upcoming perturbation. A number of studies have suggested that the controller prefers to err on the under-correction side and facilitate smaller APAs in conditions of uncertainty. For example, APAs diminish prior to shoulder movements when the tasks are performed under unstable conditions, such as while standing with a decreased base of support (Nouillot et al. 1992; Gantchev and Dimitrova 1996; Slijper and Latash 2000) or when the tasks are performed in unusual, unpredictable, and/or fearful context (Aruin et al. 1998; Aruin and Shiratori 2003; Adkins et al. 2002). This may be due to the APAs playing the role of an additional perturbation (Aruin et al. 1998; Krishnamoorthy and Latash 2005). Hence, when insufficient information about a forthcoming perturbation is available, the CNS may decrease APAs as a safe strategy.

When the subject directly handled the load prior to its release, APAs prior to the catch perturbation showed no scaling as long as the momentum at impact was the same. In contrast, when the subject did not hold the load, as in the *catch-only* condition, the APAs scaled with the release height, even if the momentum at impact was constant. Our previous study has shown that the APAs in arm muscles tend to scale better with the momentum at load impact when the load was released by the subject's other hand as compared to the load being released by the experimenter (Shiratori and Latash 2001). In the latter condition, the APA magnitude correlated better with the load kinetic energy (estimated as the product of mass and release height). These findings suggest that the CNS may use different load characteristics to prepare APAs in a flexible manner. When the load mass is directly perceived by the subject (as in *release-catch*), APAs scale with the most relevant mechanical variable, the momentum. When the load is not perceived directly, the scaling may become related to the product of mass and height of the load drop.

Concluding Comments

The coordination of sequential movements has been analyzed in many studies (Benecke et al. 1986; Viviani and Terzuolo 1982; Soechting and Flanders 1992; Carter and Shapiro 1984; Engel et al. 1997). However, the issue of assembling a sequence of actions has typically been considered without taking into account an accompanying problem of dealing with a sequence of postural perturbations. This issue is important, particularly when dealing with patient populations with impaired postural control such as, for example, patients with Parkinson's disease (reviewed in Fahn 1990). These patients are known to show impairments in performing quick sequences of actions (Benecke et al. 1987; Agostino et al. 1992), which may be secondary to the documented APA impairment in Parkinson's disease (Bazalgette et al. 1986; Viallet et al. 1987).

One of our current findings is that time intervals between actions within a sequence are important in defining patterns of postural adjustments (APAs) to associated postural perturbations. This finding suggests that studies of relative timing in sequential actions may need to consider associated postural adjustments as factors that may shape the performance.

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Corresponding Author:

Mark Latash
Department of Kinesiology Rec.Hall-268N
Penn State University University Park, PA 16802, USA
Email: mll11@psu.edu Tel: (814) 863-5374