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Journal Title: Experimental Brain Research

Volume: Volume 202, Number 2

Publisher: Springer (part of Springer Nature): Springer Open Choice Hybrid Journals | 2010-04-01, Pages 485-491

Type of Work: Article | Post-print: After Peer Review

Publisher DOI: 10.1007/s00221-009-2135-4

Permanent URL: <https://pid.emory.edu/ark:/25593/tv25f>

Final published version: <http://dx.doi.org/10.1007/s00221-009-2135-4>

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Accessed November 22, 2019 10:35 AM EST

Published in final edited form as:

Exp Brain Res. 2010 April ; 202(2): 485–491. doi:10.1007/s00221-009-2135-4.

Postural responses to unexpected perturbations of balance during reaching

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Abstract

To study the interaction between feedforward and feedback modes of postural control, we investigated postural responses during unexpected perturbations of the support surface that occurred during forward reaching in a standing position. We examined postural responses in lower limb muscles of 9 human subjects. Baseline measures were obtained when subjects executed reaching movements to a target placed in front of them (R condition) and during postural responses to forward and backward support-surface perturbations (no reaching, P condition) during quiet stance. Perturbations were also given at different delays after the onset of reaching movements (RP conditions) as well as with the arm extended in the direction of the target, but not reaching (P/AE condition). Results showed that during perturbations to reaching (RP), the initial automatic postural response, occurring around 100 ms after the onset of perturbations, was relatively unchanged in latency or amplitude compared to control conditions (P and P/AE). However, longer latency postural responses were modulated to aid in the reaching movements during forward perturbations but not during backward perturbations. Our results suggest that the nervous system prioritizes the maintenance of a stable postural base during reaching, and that later components of the postural responses can be modulated to ensure the performance of the voluntary task.

Introduction

During standing, feedforward postural activity of trunk and lower limb muscles is necessary when reaching forwards with the arm to touch a target or object (Gahery 1987; Massion 1992). Preparatory postural adjustments initiate movements of the body, while associated postural adjustments decelerate it as the arm reaches the target (Leonard et al. 2009). Both preparatory and associated postural adjustments are feedforward in nature and thought to be initiated by collaterals from descending pathways for voluntary movement (Dufosse et al. 1982) based on prior knowledge of the dynamics of the moving limb (Bouisset and Zattara 1981).

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In contrast, an unexpected perturbation of the support surface during standing requires compensatory feedback postural responses in the limb and trunk in order to correct for the disturbance (Nashner 1977; Horak and Nashner 1986). The muscle activity evoked by postural perturbations are feedback in nature, activating muscles in proportion to the induced disturbance of the body center of mass (Lockhart and Ting 2007; Welch and Ting 2008; Welch and Ting 2009) and is thought to be mediated by the brainstem (Stapley and Drew 2009). In humans, the onset of the initial automatic postural response (APRs) is approximately 70–120 ms after surface displacement with longer latency functional responses occurring between 120 and 180 ms (Horak and Macpherson 1996; Nashner 1976).

Both feedforward and feedback modes of postural control activate the same limb and trunk muscles. However, little is known about their interaction when unexpected perturbations occur during postural adjustments accompanying voluntary movements. Previous studies have examined voluntary motions that were triggered by postural perturbations and suggest that such feedback postural responses can either delay or contribute to a voluntary motion (Nashner and Cordo 1981; Burleigh et al. 1994). When subjects are instructed to voluntarily shift their CoM forward or backward in response to a support-surface perturbation, feedforward EMG activity to initiate sway is delayed until the corrective postural adjustments have counteracted the disturbance (Nashner and Cordo 1981). However, if subjects are instructed to take a step forward and the support-surface is displaced backward, feedback postural responses are modified in a way that contributes to the forward progression of the CoM, rather than restoring the CoM in the backward direction, to retain it within the support base (Burleigh et al. 1994). These results suggest that when voluntary acts are cued on the occurrence of a postural disturbance, the postural response can be modified according to a desired act. However, interactions between feedforward postural adjustments and feedback postural responses have not been studied during the more behaviorally relevant conditions of an unexpected perturbation occurring during voluntary movement (e.g., reaching for a handle as the bus moves).

Therefore, we investigated postural responses to perturbation that occurred during forward reaching in a standing position. To examine whether the feedback postural responses are modified by planned postural adjustments accompanying reaching, we evoked support-surface translations both away (backward) or towards (forward) the reach target at different times during the movements. These perturbations caused body sway towards and away from the reach target, respectively. We hypothesized that the initial postural response to perturbation would be similarly evoked during quiet standing and during an ongoing voluntary movement. We further hypothesized that longer latency postural responses to perturbation are modulated to aid in the performance of the voluntary task.

Materials and Methods

Subjects

Nine male subjects, without any neurological, visual or orthopedic disorders, participated in the study. Their mean age was 20.2 ± 1.1 years, mean height 1.80 ± 0.06 m and were they all right-handed. All gave their informed voluntary consent to participate. Experiments had the

approval of the Georgia Tech/Emory University and McGill University Institutional Review Boards.

Experimental apparatus and set-up

Subjects stood barefoot on 2 force plates (Model OR6, AMTI, Watertown, MA) that measured 3D forces and moments. They stood comfortably at their normal stance width on the force plates. Foot position was marked for each subject and care was taken that the feet remained in the same position. The activity of 4 lower limb muscles was recorded at 1080 Hz. Due to their significant activation patterns during postural perturbations and voluntary reaching, the following lower limb muscles were recorded bilaterally: tibialis anterior (TA), vastus lateralis (VL), soleus (SOL) and medial gastrocnemius (MG). Only right side EMGs will be reported. EMG data was high-pass filtered at 35 Hz (3rd-order zero-lag Butterworth filter), demeaned, rectified, and low-pass filtered at 40 Hz (1st order zero-lag Butterworth filter). Bilateral kinematics were collected using a Vicon motion capture system (ViconPeak Inc., Lake Forest, CA). A full body (Plug-in-Gait) model was used, but in this communication kinematics will be used only to quantify movement times using finger motion.

The force plates were mounted upon a moveable platform capable of delivering ramp-and-hold perturbations in multiple directions in the horizontal plane. Custom programs written in MATLAB (The Mathworks, Natick, MA) and Workbench (Baldor Electric Co., Fort Smith, AR, USA) were used to control platform motion and initiate and synchronize data collection with the Vicon system. Perturbations had a displacement of 10 cm in the anterior or posterior directions with a peak acceleration of 590 cm/s^2 (0.6g), velocity 40 cm/s, and total ramp duration of 400 ms. Subjects wore a battery powered chest trigger that signaled when the finger began to move. The trigger signal was used to initiate platform perturbations at different times following reach onset. The system had a variable processing delay of 20ms \pm 3ms between reach and perturbation onsets. The actual perturbation onset times were verified by measuring the latency between the signal from the switch and platform acceleration onset posthoc.

Experimental procedures

Upon an auditory cue, subjects executed reach to point movements towards a shoulder-height target, a thin wooden dowel 1 cm in diameter mounted on a tripod, at a distance of 130% their outstretched arm length. This target distance could be attained comfortably using a combined arm and trunk movement, but did not place subjects at their limits of stability. The target could not be used as a support. Subjects began with their right finger on the chest trigger with shoulder slightly abducted and arm flexed. When standing quietly they pointed towards the target after the cue at a natural speed and remained in the final position. No other constraints were given.

Four experimental situations were used in the experimental sessions: 1) unperturbed reaches (R), 2) surface perturbations without reaching (P), 3) reaches during which surface perturbations occurred by unexpectedly during reach movements (RP), and 4) perturbations when the arm was held outstretched in the direction of the target (perturbations/arm

extended, P/AE). For the P, P/AE and RP conditions, both backward and forward perturbations were given (causing forward and backward sway, respectively). For the RP conditions, perturbations were given at different delays following the onset of voluntary reaches; both the direction (forward or backward) as well as the latency of the perturbation were randomized. For both forward and backward RP trials, perturbations occurred randomly at 8 different delays (25ms, 65ms, 105ms, 145ms, 185ms, 225ms, 265ms, and 305ms) after the onset of movement thus making 16 conditions (8 delays \times 2 perturbation directions) for the RP trials. Therefore, a total of 21 conditions were randomly presented during experimental sessions. For each of the conditions 10 trials were recorded. This made a total of 210 trials for each of the subjects.

Data analysis

As reaching movements and platform perturbations occurred along the anteroposterior plane (y) plane, hand marker position was only analyzed along the y-axis. Marker signals were low-pass filtered at 20 Hz (second order zero-lag Butterworth filter) to eliminate any high frequency noise. Reach onset, reach end and movement time (MT) were determined when the hand marker was respectively greater or less than a threshold of 10% of peak velocity. To account for any differences in reaching time between subjects, trials collected from the 8 delays in the RP condition were sorted into 4 groups based on the percentage of total reach distance (as defined as the distance between the finger and shoulder markers in the y-axis) when the perturbations occurred (0–25%, 25–50%, 50–75%, 75–100%). Thus, for the RP conditions trials were placed into 4 groups (respectively, RP1, RP2, RP3 and RP4).

Postural response latencies were measured trial-by-trial as the time between platform onset and the onset of the compensatory EMG burst. Soleus and MG were analyzed for backward perturbations, and TA and VL for forward perturbations. The onset of the APR for these muscles was defined as one standard deviation above the mean background activity prior to perturbation. All latencies were verified manually and measurements were taken using the hi-pass filtered, rectified EMG data to eliminate any artificial changes in slope. To examine differences in the level of EMG activity in various muscles between the P, P/AE, and RP conditions, the mean activity was calculated for specific time bins for each trial. Bin 1 corresponded to a 50 ms period after the onset of platform displacement, bin 2 as a 100 ms period starting from the initial APR onset and bin 3, 100 ms after bin 2.

Statistical analysis

For each direction of perturbation (forward or backward), a one-way repeated measures ANOVA compared whether the mean of any of the experimental conditions differed significantly from the aggregate mean across the experimental conditions (Zar, 1999). For each factor the ANOVA tested the null hypothesis that no differences all variables were equal in the different bins between the different experimental conditions. If significant main effects arose, a Tukey post hoc test was used to identify which conditions were significantly different from the P condition. Statistics were reported if a significant interaction effect was recorded and the values for the RP or P/AE conditions were significantly different from the P condition. To evaluate the variability of end-point finger position in the different reach conditions, the finger marker was plotted and an ellipse with a confidence interval of 95%

was drawn around the points in each condition. The confidence ellipse represented the Gaussian bivariate ellipse for the sample in each plot. It was centered on the sample means of the x and y coordinates of finger position at movement end. The unbiased sample standard deviations of x and y determined its major axes and the sample covariance between x and y, its orientation.

Results

Total movement time was similar across all conditions of reaching (R and backward RP conditions; $F(4,756)=5.6, p>.05$; R and forward RP conditions; $F(4,747)=8.7, p>.05$). In the R condition, preparatory and associated postural activity was similar to that previously reported (Leonard et al 2009). Reach only (R) movement times for all subjects ranged from 260 (6) to 464 (20) ms with a mean of 293 (± 14) ms. During perturbed reaching (RP), movement times ranged from 233 (± 4) to 495 (± 23) ms (mean of 291 ± 9 ms) when backward perturbations occurred, and 220 (± 5) to 482 (± 16) ms (mean of 305 ± 11 ms) when forward perturbations did. Consistent with the initiation of forward body displacement during preparatory postural adjustments, SOL and MG muscle were inhibited prior to reach onset, whereas TA and VL were activated (Fig. 1A). Consistent with braking forward motion during associated postural adjustments, extensor muscles VL, MG, SOL became active towards the end of reaching.

Similar to prior studies, postural perturbations elicited clear bursts of muscle activity on average 106 and 132 ms after the onset of the disturbance in the P and PA/E conditions. MG and SOL were activated for backward perturbations while TA and VL were activated for forward perturbations. During backward perturbations, MG showed a discrete burst and shut down quickly afterwards, increasing again around the time of platform deceleration (Fig. 1B). In response to forward perturbations the initial, short latency TA burst was followed by a period of sustained activation lasting beyond the end of platform displacement (Fig. 1C).

Postural responses evoked during reaching had similar onset latencies to postural responses during quiet standing. For backward perturbations (Fig. 2A), no main effect differences in latency across the 6 conditions were found for the SOL muscle. For the MG muscle post hoc analysis (significant main effect; $F(5,683)=38, p<.05$) showed the P/AE condition was slightly delayed. However, latencies were at most 10 ms longer. For forward perturbations (Fig. 2B), the TA onset latencies had a range of 17 ms across all conditions, and no main effect differences were found between conditions. Finally, VL onset was significantly earlier in all RP conditions compared to P or P/AE conditions (main effect: $F(5,647)=29.7, p<.05$). However, all VL onsets were within 14 ms of the P condition.

EMG amplitudes preceding the active postural response to perturbation (bin 1) were higher when reaching occurred (RP) compared to quiet stance in P and P/AE conditions (significant main effects; MG; $F(5,699)=22.4, p<.001$; TA; $F(5,684)=50.1, p<.001$). All RP values significantly different from P are shown for MG and TA in Fig. 2. During the initial postural response to perturbation (bin 2) EMG amplitudes were similar across perturbation and RP conditions. No significant differences were found in MG or TA activity in bin 2, the initial

feedback response to perturbation, except for TA during the P/AE condition (Fig. 2C, main effect $F(5,686)=14, p<.05$).

During the later postural response (bin 3) the amplitude of muscle activity depended upon condition. The activity in bin 3 was largely unaffected by platform deceleration for all RP conditions (see Figs. 1B and C for RP1). For backward perturbations, MG activity was significantly lower in early reach compared to quiet standing and showed a general trend towards increasing mean activity as perturbations were later during reaching and in the arm extended condition (see arrow, Fig 2C). For forward perturbations TA activity was consistently and significantly lower in the RP conditions ($F(5,699)=134, p<.001$) compared to P and P/AE, the latter condition indicating that it was not a biomechanical effect of an outstretched arm. Finally, perturbations during reaching had little effect upon mean position, variability and orientation of end finger position, compared to the R condition (Figs. 2E, F).

Discussion

We investigated the interaction between reaching movements and the maintenance of posture when the support surface was unexpectedly translated. Ongoing reach movements had little effect on the initial onset times and amplitude of automatic postural responses to perturbation. However, for perturbations inducing a sway of the body away from the target, the later postural activity normally used to restore balance after a perturbation was decreased in amplitude to facilitate reaching the target. Postural responses can therefore be elicited independent of an ongoing voluntary task. However, later components of the feedback responses showed significant interaction with the feedforward postural adjustments as they were modulated to aid in the performance of the voluntary task.

The fact that the postural activity associated with the forward voluntary reach movements did not modify the initial postural response suggests that the nervous system prioritizes the maintenance of a stable postural base. Similar conclusions were made by Muller et al. (2007) and Redfern et al. (2002) using a paradigm in which postural perturbations were presented at different times before or after a reaction time (RT) task. However, they gave no specific measurements of the latency and amplitude of the initial postural response to perturbation. Our study showed that the onset latency of the APR was time locked with respect to perturbation onset and amplitude constant, regardless of the ongoing voluntary movement. This may suggest that the feedback control of short latency APRs arising from ascending somatosensory afferent information from the feet and legs is independent from the descending signals for the aPAs accompanying the reach.

In contrast, the characteristics of the longer latency postural responses agree with the proposals of Burleigh et al. (1994), that descending voluntary commands interact with the ascending information arising from the perturbations. Such an interaction would provide the basis for how the subjects managed to maintain similar end point precision during RP trials in comparison to the unperturbed reaches. To understand this, the effects of platform perturbations upon body displacement and sway need to be considered with the activity produced during the longer latency postural adjustments (bin 3). Backward perturbations induce a forward sway of the body, but also a net displacement of the CoM backwards.

During RP conditions, the forward sway would therefore aid the action of reaching forward towards the target but would be, to some extent, neutralized by the platform displacing the body backwards. Moreover, even though the amplitude was different between the long latency postural responses (Fig. 1B) and the voluntary activity needed to brake the reach (Fig. 1A), the functional effect of that muscle activity would have been similar, namely ankle plantar-flexion. It is unsurprising therefore, that the mean activity in bin 3 was either slightly lower in RP1 and RP2 (as in these conditions subjects had sufficient time to correct final position during the reach), or equivalent to the P activity (RP3, RP4, P/AE). A different situation was produced during forward perturbations. These perturbations induced backward sway and a net displacement of the CoM forward and thus traveling towards the target. The initial postural response activity would have corrected for the sway, but the longer latency activity had to be reduced as the body was traveling towards the target to avoid the possibility of overshooting the target. This reduction in muscle activity occurred before the platform decelerated even for the earliest RP condition (see Figs. 1B and C). The end result was that end finger position differed little in all RP and R conditions for both backward and forward perturbations, but in the latter, long latency flexor muscle activity had to be reduced.

Our results lead to the question to what extent are the long latency responses based solely on feedback from the moving surface or are they actually voluntary in nature? Can subjects voluntarily modulate postural responses after 200 ms to correctly achieve the task goal and maintain stance? It has been shown that expectation of a previously encountered perturbation leads to a modulation of postural response amplitude at 100 ms (Horak et al. 1989; Diener et al. 1991). Based on our present results, we would also suggest that long latency postural activity for restoring a perturbation can be voluntarily modulated when the arm and hand must reach out to a target. This would agree with Schillings et al.'s (2000), findings that appropriate behavioral responses for compensating for stumbling occur at a longer latency after obstacle avoidance. Moreover, longer latency postural responses possess a greater cortical involvement (Jacobs and Horak 2007).

Neurophysiological evidence suggests that common neural mechanisms exist for the generation of feedforward and feedback postural responses. Recent work has shown that neurons in the brainstem pontomedullary reticular formation contribute not only to the feedforward postural adjustments preceding and accompanying voluntary reaching (Schepens and Drew 2004; Schepens and Drew 2006; Schepens et al. 2008), but also to compensatory postural responses to unexpected perturbations of balance (Stapley and Drew 2009). The robust appearance of the initial automatic postural response during quiet standing and reaching in this study is consistent with the idea that it is elicited by afferent sensory stimuli via brainstem sensorimotor feedback loops (Jacobs and Horak 2007). Interestingly however, the fact that the Bin1 (activity during the passive period following a perturbation) increased in the RP conditions for TA and MG would suggest that the startle associated with repeated perturbations increased the activation level of the sensorimotor system. As discussed by Carlsen et al (2004), this could have ensured the robustness of the short latency responses, especially when reaching (RP). The later modulations of the response suggest that there is a subsequent contribution of cortical feedback loops incorporating the goal of the voluntary task. The integration of feedback and feedforward postural adjustments during

the longer latency components of the responses involving such cortical signals may take place in the brainstem.

Acknowledgments

Supported by CFI and NSERC grants to PJS. HT held a Georgia Tech President's Research Fellowship and a Michael Birnbaum Scholarship.

References

- Bouisset S, Zattara M. A sequence of postural movements precedes voluntary movement. *Neurosci Lett*. 1981; 22:263–270.
- Burleigh AL, Horak FB, Malouin F. Modification of postural responses and step initiation: evidence for goal directed postural interactions. *J Neurophysiol*. 1994; 72:2892–2902. [PubMed: 7897497]
- Carlsen AN, Chua R, Inglis JT, Sanderson DJ, Franks IM. Can prepared responses be stored subcortically? *Exp Brain Res*. 2004; 159:301–309. [PubMed: 15480608]
- Diener HC, Horak F, Stelmach G, Guschlbauer L, Dichgans J. Direction and amplitude precuing has no effect on automatic posture responses. *Exp Brain Res*. 1991; 84:219–223. [PubMed: 1855560]
- Dufosse M, Macpherson JM, Massion J. Biomechanical and electromyographical comparison of two postural supporting mechanisms in the cat. *Exp Brain Res*. 1982; 45:38–44. [PubMed: 7056336]
- Gahery Y. Associated movements, postural adjustments and synergies: some comments about the history and significance of three motor concepts. *Arch Ital Biol*. 1987; 125:345–360. [PubMed: 3326536]
- Horak FB, Diener HC, Nashner LM. Influence of central set on human postural responses. *J Neurophysiol*. 1989; 62:841–853. [PubMed: 2809706]
- Horak, FB.; Macpherson, JM. Postural orientation and equilibrium. In: Rowell, LB.; Shepherd, JT., editors. *Handbook of Physiology Section 12: Exercise: Regulation and Integration of Multiple Systems*. Oxford Univ Press; New York, NY: 1996. p. 255-292.
- Horak FB, Nashner LM. Central programming of postural movements: adaptation to altered support-surface configurations. *J Neurophysiol*. 1986; 55:1369–1381. [PubMed: 3734861]
- Jacobs JV, Horak FB. Cortical control of postural responses. *J Neural Transm*. 2007; 114:1339–1348. [PubMed: 17393068]
- Leonard JA, Brown RH, Stapley PJ. Reaching to multiple targets during stance: The spatial organization of feed-forward postural adjustments. *J Neurophysiol*. 2009; 101 (4):2120–2133. [PubMed: 19211658]
- Lockhart DB, Ting LH. Optimal sensorimotor transformations for balance. *Nature Neuroscience*. 2007; 10:1329–1336.
- Massion J. Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol*. 1992; 38:35–56. [PubMed: 1736324]
- Muller MLTM, Redfern MS, Jennings JR. Postural prioritization defines the interaction between a reaction time task and postural perturbations. *Exp Brain Res*. 2007; 183:447–456. [PubMed: 17690875]
- Nashner LM. Fixed patterns of rapid postural responses among leg muscles during stance. *Exp Brain Res*. 1977; 30:13–24. [PubMed: 590411]
- Nashner LM. Adapting reflexes controlling the human posture. *Exp Brain Res*. 1976; 26:59–72. [PubMed: 964327]
- Nashner LM, Cordo PJ. Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. *Exp Brain Res*. 1981; 43:395–405. [PubMed: 7262232]
- Redfern MS, Muller MLTM, Jennings JR, Furman JM. Attentional dynamics in postural control during perturbations in young and older adults. *J Gerontol A Biol Sci Med Sci*. 2002; 7:B298–303. [PubMed: 12145355]

- Schepens B, Drew T. Independent and convergent signals from the pontomedullary reticular formation contribute to the control of posture and movement during reaching in the cat. *J Neurophysiol.* 2004; 94:2217–2238. [PubMed: 15175364]
- Schepens B, Drew T. Descending signals from the pontomedullary reticular formation are bilateral, asymmetric and gated during reaching movements in the cat. *J Neurophysiol.* 2006; 96:2229–2252. [PubMed: 16837662]
- Schepens B, Stapley PJ, Drew T. Neurons in the pontomedullary reticular formation signal posture and movement both as an integrated behavior and independently. *J Neurophysiol.* 2008; 100 (4):2235–2253. [PubMed: 18632892]
- Schillings HM, van Wezel BM, Mulder T, Duysens J. Muscular responses and movement strategies during stumbling over obstacles. *J Neurophysiol.* 2000; 83:2093–2102. [PubMed: 10758119]
- Stapley PJ, Drew T. The pontomedullary reticular formation contributes to the compensatory postural responses observed following removal of the support surface in the standing cat. *J Neurophysiol.* 2009; 101 (3):1334–1350. [PubMed: 19118108]
- Welch TD, Ting LH. A feedback model reproduces muscle activity during human postural responses to support-surface translations. *J Neurophysiol.* 2008; 99 (2):1032–1038. [PubMed: 18094102]
- Welch TD, Ting LH. A feedback model explains the differential scaling of human postural responses to perturbation acceleration and velocity. *J Neurophysiol.* 2009; 101 (6):3294–3309. [PubMed: 19357335]

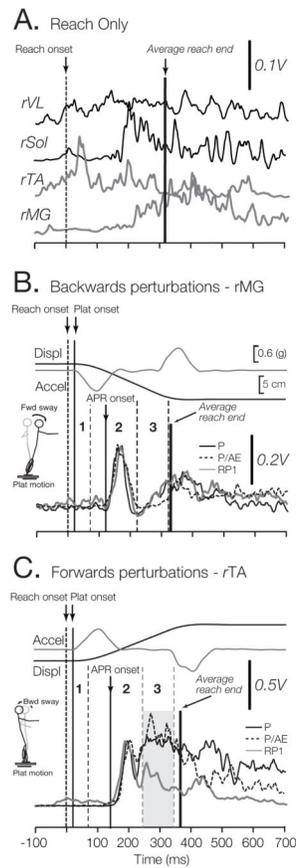


Figure 1.

A. Average muscle activity (\pm 1SD) in the right vastus lateralis (VL), soleus (SOL), tibialis anterior (TA) and medial gastrocnemius (MG) during unperturbed reaches for subject 2. B. Average muscle activity of the MG for perturbation only (P), perturbations with the arm extended (P/AE) and reaching with perturbations occurring at delay 1, 25 ms after reach onset (RP1) for the same subject as in A (S2). C. As in B, but for the TA muscle. For B and C, traces are aligned to the onset of the perturbation in all 3 conditions and average reach end represents the average time taken to perform the reach for all trials in the RP1 condition for the subject shown.

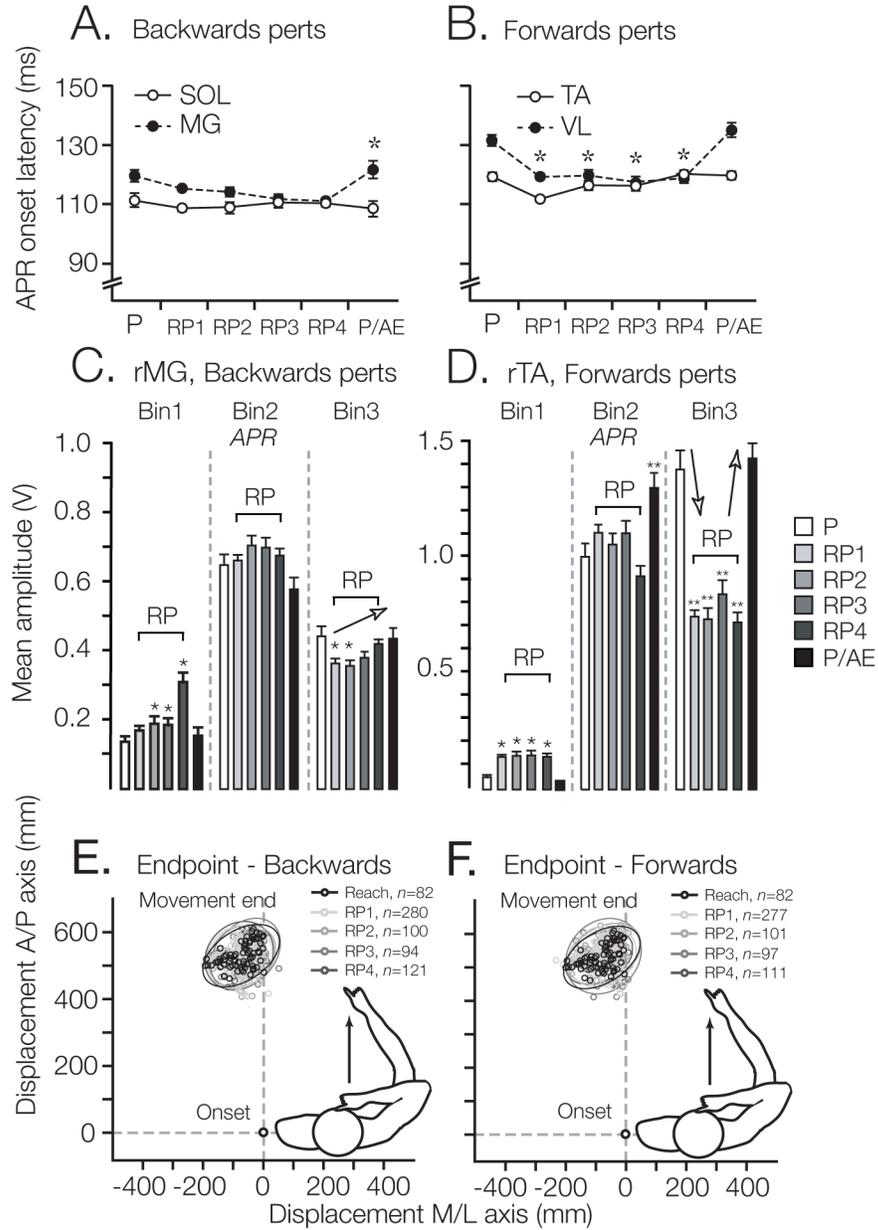


Figure 2. Mean (\pm 1SD) automatic postural response (APR) latencies for backward (A) and forward perturbations (B) in SOL, MG, TA and VL muscles for the experimental conditions P, RP and P/AE. Statistical differences are shown between measures in the RP and P/AE with respect to the P condition ($*=p<.05$). Muscle abbreviations as in Fig. 1. Mean (\pm 1SD) EMG activity during two 100 ms periods after the onset of postural perturbations in the 3 experimental conditions (P, RP and P/AE) of the MG (C) and TA muscles (D) during backward and forward perturbations, respectively ($*=p<.05$, $**=p<.01$). End finger position for RP conditions in relation to the reach only (R) condition for all trials and all subjects

studied during backward (E) and forward (F) perturbations. For each condition, end-point ellipses have been drawn representing the 95% confidence level.