RESEARCH NOTE

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 nine 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.

Keywords Human · Posture · Feedforward · Feedback · Reaching

Introduction

During standing, feedforward postural activity of trunk and lower limb muscles is necessary when reaching forward 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 (aPAs) 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).

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, 2009) and is thought to be mediated by the brainstem (Stapley and Drew 2009). In humans, the onset of the initial automatic postural response (APR) 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).

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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 (electromyographic) 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 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 toward (forward) the reach target at different times during the movements. These perturbations caused body sway toward 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. The mean age was 20.2 ± 1.1 years, mean height 1.80 ± 0.06 m, and they were 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 setup

Subjects stood barefoot on two 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 four lower limb muscles was recorded at 1,080 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 (third-order zero-lag Butterworth filter), demeaned, rectified, and low-pass filtered at 40 Hz (first-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 direction with a peak acceleration 590 cm/s^2 (0.6 g), velocity 40 cm/s, and total ramp duration 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 20 ± 3 ms 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 post hoc.

Experimental procedures

Upon an auditory cue, subjects executed reach-to-point movements toward a shoulder-height target, a thin wooden dowel 1 cm in diameter mounted on a tripod, at a distance of 130% of 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 toward 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 sways, 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 was randomized. For both forward and backward RP trials, perturbations occurred randomly at eight different delays (25, 65, 105, 145, 185, 225, 265, and 305 ms) after the onset of movement thus making 16 conditions (8 delays × 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 eight delays in the RP condition were sorted into four 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, and 75–100%). Thus, for the RP conditions, trials were placed into four groups (RP1, RP2, RP3, and RP4, respectively).

Postural response latencies were measured trial-by-trial as the time between platform onset and the onset of the compensatory EMG bursts. SOL 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 high-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 a 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. 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: $F(4,756) = 5.6$, $p > 0.05$; R and forward RP conditions: $F(4,747) = 8.7$, $p > 0.05$). 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 ($\pm$14) ms. During perturbed reaching (RP), movement times ranged from 233 ($\pm$4) to 495 ($\pm$23) ms (mean of 291 $\pm$ 9 ms) when backward perturbations occurred, and 220 ($\pm$5) to 482 ($\pm$16) ms (mean of 305 $\pm$ 11 ms) when forward perturbations did. Consistent with the initiation of forward body displacement during preparatory postural adjustments, SOL and MG muscles 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, and SOL became active toward the end
of reaching.

Similar to prior studies, postural perturbations elicited
clear bursts of muscle activity on averages 106 and 132 ms
after the onset of the disturbance in the P and PA/E con-
ditions. MG and SOL were activated for backward per-
turbations while TA and VL were activated for forward
perturbations. During backward perturbations, MG showed
a discrete burst and shut down quickly afterward, increas-
ing 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 sus-
tained activation lasting beyond the end of platform dis-
placement (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 dif-
ferences in latency across the six conditions were found for
the SOL muscle. For the MG muscle, post hoc analysis
(significant main effect: $F(5,683) = 38$, $p < 0.05$) showed
that the P/AE condition was slightly delayed. However,
latencies were at most 10 ms longer. For forward perturba-
tions (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 signifi-
cantly earlier in all RP conditions compared to P or P/AE
conditions (main effect: $F(5,647) = 29.7$, $p < 0.05$). How-
ever, 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, $F(5,699) = 22.4$, $p < 0.001$;
TA, $F(5,684) = 50.1$, $p < 0.001$). All RP values signifi-
cantly 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 per-
turbation, except for TA during the P/AE condition
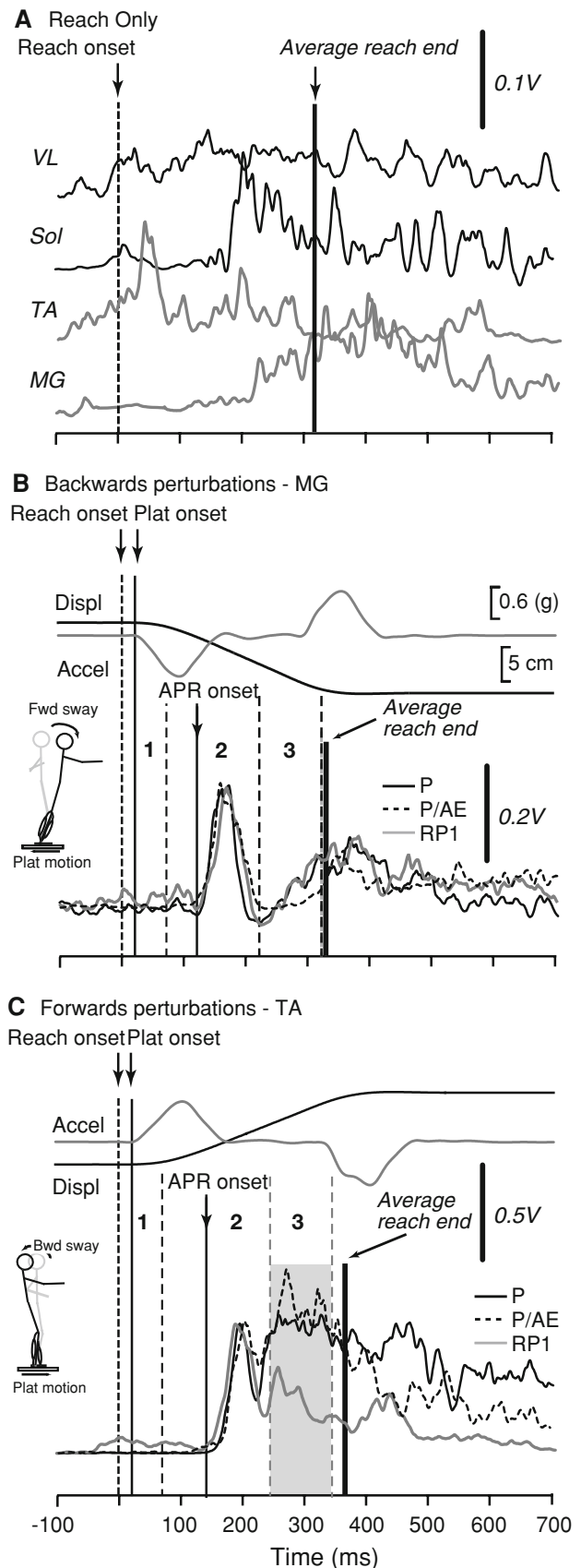(Fig. 2c; main effect: $F(5,686) = 14$, $p < 0.05$).

Fig. 2 Mean (±1 SD) APR latencies for backward (**a**) and forward (**b**) perturbations in SOL, MG, TA, and VL muscles for the experimental conditions P, RP, and P/AE. Statistical differences are shown between measures in RP and P/AE with respect to the P condition (*$p < 0.05$). Muscle abbreviations as in Fig. 1. Mean (±1 SD) EMG activity during two 100 ms periods after the onset of postural perturbations in the three experimental conditions (P, RP, and P/AE) of the MG (**c**) and TA muscles (**d**) during backward and forward perturbations, respectively (*$p < 0.05$, **$p < 0.01$). 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
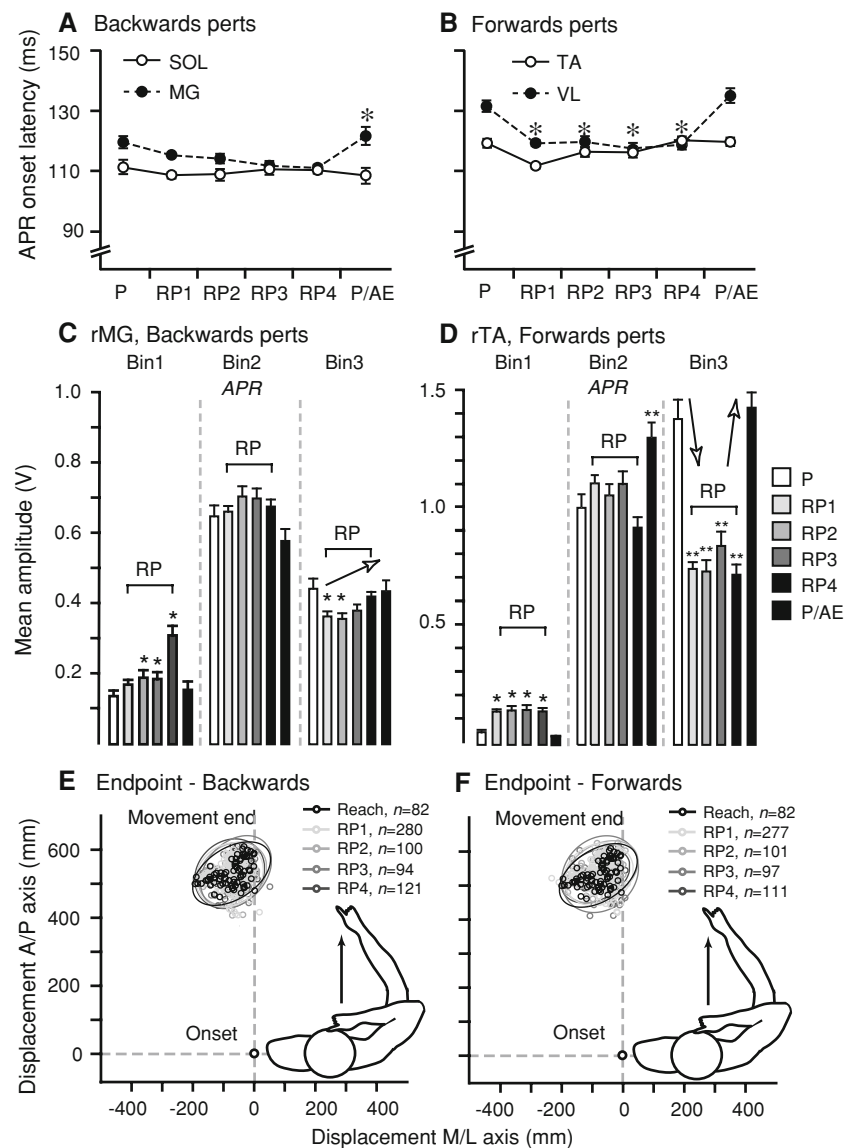
During the later postural response (bin 3), the amplitude of muscle activity depended upon condition. The activity in bin 3 was largely unaffected by platform deceleration for all RP conditions (see Fig. 1b and C for RP1). For backward perturbations, MG activity was significantly lower in early reach compared to quiet standing and showed a general trend toward 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 ($F(5,699) = 134$, $p < 0.001$) 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 (Fig. 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 APRs 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 backward. During RP conditions, the forward sway would therefore aid the action of reaching forward toward the target but would be, to some extent, neutralized by the platform displacing the body backward. 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, and 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 toward 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 toward 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 Fig. 1b, 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 the findings of Schillings et al. (2000) 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, 2006; Schepens et al. 2008), but also to the compensatory postural responses to unexpected perturbations of balance (Stapley and Drew 2009). The robust appearance of the initial APR 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 bin 1 (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.

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