Interactions With Compliant Loads Alter Stretch Reflex Gains But Not Intermuscular Coordination

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1Department of Biomedical Engineering, Northwestern University, Evanston; 2Department of Physical Medicine and Rehabilitation, Northwestern University, and 3Sensory Motor Performance Program, Rehabilitation Institute of Chicago, Chicago, Illinois; 4Department of Mechanics, China Agricultural University, Beijing, China; and 5Health and Rehabilitation Research Centre, Auckland University of Technology, Auckland, New Zealand

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Perreault EJ, Chen K, Trumbower RD, Lewis G. Interactions with compliant loads alter stretch reflex gains but not intermuscular coordination. J Neurophysiol 99: 2101–2113, 2008. First published February 20, 2008; doi:10.1152/jn.01094.2007. The human motor system regulates arm mechanics to produce stable postures during interactions with different physical environments. This occurs partly via involuntary mechanisms, including stretch reflexes. Previous single-joint studies demonstrated enhanced reflex sensitivity during interactions with compliant environments, suggesting reflex gain increases to enhance limb stability when that stability is not provided by the environment. This study examined whether similar changes in reflex gain are present throughout the limb following perturbations that simultaneously influence multiple joints. Furthermore, we investigated whether any observed modulation was accompanied by taskspecific changes in reflex coordination across muscles, a question that cannot be addressed using single-joint perturbations. Reflexes were elicited during the maintenance of posture by perturbing the arm with a three degrees of freedom robot, configured to have isotropic stiffness of either 10 N/m (compliant) or 10 kN/m (stiff). Perturbation characteristics were matched in both environments. Reflex magnitude was quantified by the average rectified electromyogram, recorded from eight muscles crossing the elbow and shoulder. Reflex coordination was assessed using independent components analysis to compare reflex activation patterns during interactions with stiff and compliant environments. Stretch reflex sensitivity increased significantly in all muscles during interactions with the compliant environment and these changes were not due to changes in background muscle activity. However, there was no significant difference in the reflex coordination patterns observed during interactions with the stiff and compliant environments. These results suggest that reflex modulation occurred through altered use of fixed muscle coordination patterns rather than through a change in reflex coordination.

INTRODUCTION

The human motor system regulates arm mechanics to produce stable postures during interactions with different environments. This is accomplished by coordinating muscle activity via feedforward and feedback pathways. Feedback pathways can generate involuntary or reflexive changes in muscle activation following external perturbations of posture. Such stretch-sensitive reflexes can alter limb impedance (Carter et al. 1990; Kearney et al. 1997; Sinkjaer 1988) and regulation of reflex sensitivity may provide a mechanism for conditioning the involuntary response to changing environmental mechan-
interactions with compliant environments. The rationale for this hypothesis was that this increase would be suitable for increasing limb impedance in tasks that required the subject to generate increased limb stability. The second goal was to quantify whether any observed changes in reflex activation were accompanied by changes in reflex coordination that were appropriate for the changed mechanical properties of the environment. Because muscles spanning multiple joints play an important role in the regulation of limb stability (McIntyre et al. 1996) and also contribute more to the regulation of limb mechanics during interactions with compliant environments (Franklin and Milner 2003; Perreault et al. 2001), we anticipated that multijoint muscles also may be selectively excited during the compliant task. This second goal is important for understanding the specificity of stretch reflex modulation with respect to the mechanical properties of the environment and cannot be addressed using single-joint studies.

**METHODS**

These experiments were conducted on nine subjects with no upper limb or neurological impairments and ages ranging from 23 to 36 yr. Eight subjects participated in the main protocol. Two of these subjects and one additional person participated in control experiments. All protocols were approved by the Northwestern University Institutional Review Board (IRB protocol 1322-003) and required informed consent of the subjects.

**Equipment**

Reflex responses were elicited using a three degrees of freedom (3DOF) robotic manipulator (HapticMaster; Moog FCS, Nieuw-Vennep, The Netherlands) to apply displacement perturbations to each subject's arm (Fig. 1A). Subjects were attached to the manipulator using a custom-fitted fiberglass cast. The cast fixed the wrist in a neutral position and extended approximately one third of the distance from the wrist to the elbow. A low-mass, custom gimbal mounted between the end of the robot and the cast ensured that the robot from the wrist to the elbow. A low-mass, custom gimbal mounted on the neutral point at which no spring forces are generated and Xd is the desired position command sent to the robot position servo. In these experiments, the robot was configured as a critically damped, second-order system with a 3D isotropic stiffness of 10 N/m (compliant) or 10 kN/m (stiff) and a mass of 3 kg. As a reference, the endpoint stiffness of the human arm is on the order of 200 N/m for low levels of voluntary muscle activity (Perreault et al. 2001). Perturbations applied to the arm were matched in both environments. This was accomplished by first applying perturbations in the stiff environment, using the data collected from these experiments to estimate the multiple-input, multiple-output transfer functions between the commands to the robot servomotors (Xd) and the resulting interaction forces (Fend) and then using these estimates to generate a perturbation signal (Xp) that would match the servomotor commands in the stiff and compliant environments. This process allowed continuous perturbations to be applied during each experimental trial, without the need for rapidly switching the impedance of the robot. It is important to note that perturbation matching was achieved via feedforward correction of the command signal Xp. Feedforward compensation cannot be used to match disturbance rejection in the stiff and compliant environments. Thus our approach implicitly assumes that the subject response to the perturbation does not differ in the two virtual environments during the time period of interest. The control experiments subsequently described explicitly evaluate whether this assumption influenced our results.

**FIG. 1.** Experimental setup. A: 3 degrees of freedom (3DOF) robotic manipulator used to simulate the stiff and compliant mechanical environments and to apply displacement perturbations to the arm. B: block diagram of the admittance control algorithm used in all experiments. M, B, and K represent the isotropic inertial, viscous, and elastic parameters simulated by the controller, respectively. Hend(s) represents the impedance of the subject's arm. C: sequence of perturbations applied to the arm. Randomly timed ramp-and-hold perturbations were applied along the coordinate axes show in A. Perturbations along each direction were applied at separate times. D: electromyograms (EMGs) elicited during a typical trial.
Surface electromyograms (EMGs) were recorded from eight muscles in the upper limb (Table 1). These were used to measure background muscle activity prior to each perturbation and reflexively elicited changes in muscle activation in response to the perturbation. Bipolar electrodes (model #272; Noraxon USA, Scottsdale, AZ) and standard skin preparation techniques were used. EMGs were amplified by a Bortec AMT-16 system (Bortec Biomedical, Calgary, AB, Canada), which has a bandwidth of 10–1,000 Hz, an input impedance of 10 GΩ, and a common-mode rejection ratio of 115 dB at 60 Hz. The amplified signals were antialias filtered at 500 Hz using custom fifth-order Bessel filters and then sampled at 1,250 Hz with an 18-bit analog to digital converter (NI PCI-6289; National Instruments, Austin, TX). A common clock was used to synchronize data from the EMG and robotic systems. Once collected, data were resampled at 1,000 Hz before further processing.

Protocols

A series of maximum voluntary contractions (MVCs) were performed at the start of each trial. These data were used later to normalize EMGs recorded from each muscle. Standard muscle testing procedures were used to isolate the activity of each target muscle during these MVCs (Delagi and Perotto 1979); a separate isometric contraction was performed for each target muscle. Each contraction lasted for about 2 s and two repetitions were performed. The maximum EMG for each muscle was defined as the maximum value recorded across the entire set of muscle tests.

Reflexes were elicited using a randomly timed series of ramp-and-hold perturbations applied to the arm (Fig. 1A). Perturbations were applied in six directions corresponding to positive and negative hold perturbations applied to the arm (Fig. 1, A). Each perturbation had a duration of 60 ms, which was long enough to elicit consistent long-latency reflexes (Lewis et al. 2005), and a maximum velocity of 500 mm/s. The interval between successive perturbations was uniformly distributed between 250 and 1,250 ms. Each trial lasted about 75 s and contained six to seven perturbations in each of the six measurement directions. Two trials were collected for each experimental condition and subjects were required to rest for ≥2 min between trials.

The subjects’ task in these experiments was to maintain a constant endpoint force and a fixed arm posture, while not reacting to the applied perturbations. Target forces were set at 0, ±5, and ±10% MVC along the X-axis, which corresponded to pushing (−X) or pulling (+X) along a line at the intersection of the horizontal and sagittal planes passing through the glenohumeral joint. Subjects were assisted in maintaining the target force and position through visual feedback on a computer display. The visual display used a vector representation to indicate the direction and magnitude of the applied force during interactions with the stiff environment and the location of the hand during interactions with the compliant environment. Data at all voluntary force levels were collected first in the stiff and then in the compliant environments to allow the perturbations to be matched in each environment, as described earlier. The order in which the force targets and perturbation directions were presented was randomized.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Abbreviation</th>
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<tbody>
<tr>
<td>Brachioradialis</td>
<td>BRD</td>
</tr>
<tr>
<td>Biceps Brachii</td>
<td>BI</td>
</tr>
<tr>
<td>Triceps Long</td>
<td>TRI_{long}</td>
</tr>
<tr>
<td>Triceps Lateral</td>
<td>TRI_{lat}</td>
</tr>
<tr>
<td>Anterior Deltoid</td>
<td>AD</td>
</tr>
<tr>
<td>Middle Deltoid</td>
<td>MD</td>
</tr>
<tr>
<td>Posterior Deltoid</td>
<td>PD</td>
</tr>
<tr>
<td>Pectoralis Clavicular</td>
<td>PECT_{clav}</td>
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A control experiment was performed in three subjects to evaluate the assumptions implicit in our perturbation-matching algorithm. In this experiment, perturbations in the compliant environment were matched to those in the stiff environment by switching the stiffness of the controller 1 ms prior to perturbation onset. Stiffness was switched to the value used in the stiff environment experiments and was maintained at that level for 520 ms. Each perturbation was applied independently and subjects were allowed to return to the target before another perturbation was applied. Using this method, it was possible to exactly match the perturbation characteristics in each environment, even in the presence of a changing subject response. This method of matching the perturbations also allowed us to conduct the compliant trials before the stiff trials to verify that the order imposed in the primary experiment did not influence the observed results. These control experiments were conducted using voluntary force targets at +5 and +10% MVC, and displacements along both directions of the Y-axis.

Analysis

Electromyograms were used to quantify the magnitude of the stretch reflex elicited in each muscle. The mean was removed from all EMG records and then these data were rectified before further processing. EMGs for each muscle were normalized by the mean rectified value (0.5-s average) recorded during the MVCs performed at the start of each experimental session. Endpoint displacement and EMG data were segmented and aligned according to the velocity of the imposed perturbation; separate segments were obtained for each perturbation direction. Data from each edge of the ramp-and-hold displacement were used, resulting in a total of 24–28 responses for each perturbation direction, which were averaged. The use of data from both edges of the imposed displacement resulted in variations in the initial hand location, prior to perturbation onset, of 30 mm for each imposed velocity; these differences in initial hand posture were found to have no discernable influence on the measured reflex EMG, which is primarily velocity sensitive. For the control experiment data, only the initial edge of the perturbation was used since the control paradigm did not incorporate a bidirectional displacement during interactions with a compliant environment. Reflex latencies in each muscle were estimated as the time after perturbation onset where the rectified EMG exceeded 3SDs of the background muscle activation (Lewis et al. 2005); all results were verified by visual inspection. The magnitude of the reflex EMG in each muscle was quantified by the average rectified value. Two time windows were considered: 20–50 ms, corresponding approximately to short-latency pathways, and 50–100 ms, corresponding to longer-latency pathways.

To compare reflex sensitivity during interactions with the stiff and compliant environments, it is necessary to ensure that comparisons for each subject are made at matched levels of background muscle activity (Smeets and Erkelens 1991; Stein et al. 1995). For example, it is not possible to compare the reflexes shown in Fig. 2A because the reflex magnitudes measured in the stiff and compliant environments were obtained at different levels of background EMG. Thus it is not possible to determine whether the increased responses measured in the compliant environment are due to changes in reflex sensitivity or changes in background muscle activity. To control for background activity, reflex magnitudes were compared in conditions only where there was an overlap in background activity between the data collected in the stiff and compliant environments. Overlap was determined by considering the average background activity recorded during 5 and 10% MVC contractions; pushing and pulling contractions were compared separately. Figure 2B illustrates a data set in which there was overlap during voluntary pushing conducted in both environments. When overlap was detected, reflexes elicited in the two environments were compared using linear interpolation to estimate the
change in reflex magnitude at the midpoint of the region of average background activity overlap (Fig. 2B).

An additional goal of this study was to quantify the patterns of reflex coordination elicited in response to the applied perturbations and to determine whether any observed patterns were consistent across tasks and subjects. This was done using a dimensionality-reduction technique to assess whether there were common coordination patterns across all perturbation directions and voluntary force levels. Reflex coordination patterns were estimated using an independent component analysis preceded by a principal component analysis (ICA/PCA), as implemented in the *runica* function from the EEGLAB Toolbox (Delorme and Makeig 2004). This technique was selected based on previous work demonstrating that it provides robust estimates of EMG coordination patterns (Tesch et al. 2006). It first uses PCA to reduce the dimensionality of the data set and then ICA to estimate the independent components (ICs) from the reduced data. This two-stage technique has been shown to reduce the influence of noise and to prevent overlearning during the estimation of the independent components (Hyvarinen et al. 2001).

EMG data from 0 to 100 ms after perturbation onset were used to estimate the reflex coordination patterns through the end of the long-latency time period considered earlier. Prior to running the ICA/PCA analysis, the data were compressed by averaging the rectified EMG within each 10-ms window, creating 10 data points for the EMG measured in each muscle. Confidence intervals on the ICs were estimated using a bootstrap technique with 100 replications (Press 1986). A muscle’s contributions to an IC were considered to be significant if its weight was significantly different ($P < 0.05$) from the weight estimated when the ICA/PCA algorithm was applied to the same data, except with the reflexes measured in each muscle shuffled randomly and independently in time (Cheung et al. 2005).

Similarity between two sets of ICs, A and B, was quantified by determining how much of the data variance in set A could be accounted for by the ICs estimated for set B, and vice versa. The multiple correlation coefficient ($R^2$) was used for this quantification (Ljung 1999). A number of alternative approaches have been used to compare the similarity of estimated muscle coordination patterns, including: correlation between individual patterns, subspace similarity, and Euclidean distance (Hart and Giszter 2004; Kargo and Nitz 2003; Tresch et al. 2006). All produce useful estimates of the similarity between estimated patterns A and B, but do not consider the variance of the data described by the components of these patterns. In contrast, the technique used in this study provides a measure of similarity between A and B that considers the variance of the data described by the ICs in each set. This de-emphasizes the contributions of ICs that do not contribute much to the total data variance. Statistical comparisons were made using a jackknife analysis with 100 repetitions (Politis 1998). In each repetition, a random sample of 50% of the available trials was used to estimate the ICs and the remaining 50% of the data were used for cross-validation of the fit accuracy. This allowed accurate estimations of the mean fit accuracy for each subject.

**RESULTS**

**Perturbation characteristics**

Perturbation characteristics between the stiff and compliant environments were well matched (Fig. 3). Across all subjects, the average difference of the mean perturbations did not differ significantly for matched experimental conditions ($\Delta = 0.03 \pm 1.4$ mm, $P = 0.7$); this mean difference was measured between 90 and 100 ms after perturbation onset, the end of the EMG analysis period. The lack of significance indicates that there was no systematic bias in the perturbations delivered in the two environments. Due to the fact that a feedforward control algorithm was used to match the perturbations in the compliant environment to those in the stiff environment, there was increased variability within an experimental trial for perturbations delivered in the compliant environment. Variability was quantified by the SD of the perturbation amplitudes across all trials and subjects. This also was measured at the end of the EMG analysis window (90–100 ms), since the variability increased with increasing time from the perturbation onset. The SD of the perturbations delivered in the stiff environment was 0.16 mm and that for the trials delivered in the compliant environment was 3.56 mm, a difference that was highly significant ($P < 0.0001$, two-sample $F$-test).

**FIG. 3.** Displacement perturbations delivered in the stiff and compliant environments. Individual traces are shown in gray and averages throughout a typical trial are shown in black. Average perturbations were matched in both environments, but increased variability was noted for perturbations delivered in the compliant environment.
Stretch reflex characteristics

Reflex responses were elicited as subjects interacted with the stiff and compliant environments. As expected, the observed patterns of reflex activity varied with perturbation direction, the level of voluntary force, and the mechanical environment with which the subjects interacted. Typical responses from a single subject are shown in Fig. 4. These data were collected as the subject exerted forces in the $-X$ direction at 5% MVC. This required extension moments about the elbow, resulting in large triceps reflexes for perturbations that stretched this muscle group. Large responses also were noted in the BI, AD, PD, and PECT$_{clav}$, for specific perturbation directions. In contrast, small or absent responses were noted in certain muscles, such as the MD and BRD (perturbations in $Y$ and $Z$). Low levels of background muscle activity as well as small changes in muscle length for a specific perturbation direction likely contributed to small reflexes in any given trial.

There was a broad range of reflex latencies observed in each muscle (Table 2). The shortest latencies were consistent with the monosynaptic stretch reflex (Lewis et al. 2005, 2006), but the median latency for each muscle was significantly longer than would be expected from this pathway. This difference may be due to contributions from slower afferents, integration from multiple polysynaptic spinal pathways (Bonasera and Nichols 1996), or supraspinal pathways (Palmer and Ashby 1992), a distinction that was not addressed in this study.

Consistent with the observed latencies was the finding that the largest reflex EMG occurred in the period about 50–100 ms following perturbation onset. Across all perturbation conditions and subjects, the average EMG magnitude in the 50- to 100-ms period was fivefold larger than that in the 20- to 50-ms period. The difference in EMG magnitude between these time periods was highly significant ($P < 0.001$), as determined from a paired-sample, Wilcoxon signed-rank test.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Fastest 10%, ms</th>
<th>All Data, ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>BRD</td>
<td>22.7 ± 3.4</td>
<td>40.0 ± 13.5</td>
</tr>
<tr>
<td>BI</td>
<td>21.9 ± 3.7</td>
<td>39.6 ± 14.4</td>
</tr>
<tr>
<td>TRI$_{long}$</td>
<td>25.5 ± 3.1</td>
<td>47.5 ± 14.5</td>
</tr>
<tr>
<td>TRI$_{lat}$</td>
<td>20.1 ± 3.6</td>
<td>41.2 ± 14.8</td>
</tr>
<tr>
<td>AD</td>
<td>26.5 ± 3.2</td>
<td>46.2 ± 12.4</td>
</tr>
<tr>
<td>MD</td>
<td>27.6 ± 3.5</td>
<td>50.3 ± 14.0</td>
</tr>
<tr>
<td>PD</td>
<td>23.0 ± 3.4</td>
<td>43.1 ± 12.6</td>
</tr>
<tr>
<td>PECT$_{clav}$</td>
<td>21.6 ± 2.6</td>
<td>37.1 ± 10.6</td>
</tr>
</tbody>
</table>

Values are means ± SD.

Modulation of reflex sensitivity with changes in environmental mechanics

There were significant increases in the stretch reflex recorded in all muscles as subjects interacted with the compliant environment. Typical changes in the elicited reflexes are also shown in Fig. 4. The thick traces correspond to responses...
measured in the compliant environment and the thin traces to responses measured in the stiff environment. Increases in the elicited reflexes were seen in most muscles when the mechanical environment was compliant relative to those observed when it was stiff. The degree of modulation depended strongly on the background activity prior to perturbation onset and the direction of the imposed perturbation. The strongest modulation was observed in both heads of the triceps, which contributed to the voluntary pushing force in this task and therefore had relatively large background activities. Across all muscles, observed changes included increased reflex magnitude in the compliant environment and the emergence of reflexes in the compliant environment that were not present in the stiff environment. In this subject, examples of the former include the BI, PD, and PECTclav reflexes elicited in response to perturbations along the Y-axis; examples of the latter include the BRD and PD responses to perturbations along the X-axis.

Changes in the stretch reflex related to the mechanical properties of the environment were observed in all muscles and all subjects. Group responses are shown in Fig. 5. This figure illustrates the increased stretch reflex during interactions with the compliant environment relative to those in the stiff environment for perturbations in each of the six directions. Magnitudes were computed as the average rectified EMG in the 50–100 ms following perturbation onset, where the elicited reflexes were largest. The change in reflex magnitude is plotted at each level of voluntary force. Data points significantly different from zero indicate significant reflex modulation. Points above the dashed line in each figure indicate increased reflex EMG in the compliant environment and points below the dashed line indicate decreased reflex EMG, usually corresponding to increased inhibition, in the compliant environment. Significance was assessed to a level of \( P < 0.05 \) using a general linear model with the level of voluntary force considered as a fixed factor and each subject as a random factor. Only EMGs that contained measurable reflex responses (3SD above background) are included in Fig. 5 and the corresponding statistical analysis. This excluded muscle responses in trials.

![Fig. 5](image-url)Changes in reflex EMG at each level of voluntary force. Data are group responses. The figures at the top of each data column indicate the direction of the applied perturbation; these are colored to match the data below. Each row corresponds to a different muscle. Each plot indicates the change in reflex magnitude (50–100 ms) in the compliant environment relative to the stiff environment. Reflexes are normalized by the background muscle activity prior to the perturbation to partially account for background dependent changes in reflex sensitivity. The error bars correspond to 95% confidence intervals, computed using a generalized linear model with zero offset and each subject treated as a random factor. Data above the dashed line in each figure indicate increased reflex responses in the compliant environment and data below the dashed line indicate decreased reflex EMG in the compliant environment. Statistically significant modulation, observed in each muscle, is indicated by the asterisks above each voluntary force condition. Statistical significance corresponds to plotted values significantly different from zero \( (P < 0.05) \).
where the specific combination of the imposed perturbation and voluntary background activity was not sufficient to elicit a reflex, since it is not appropriate to quantify the degree of reflex modulation when no reflexes are present. Statistically significant changes in reflex magnitude were observed in 97 of the 240 possible conditions (8 muscles × 5 force levels × 6 perturbation directions). The most distal muscles, BRD and TRl_at, had a pattern of modulation that depended strongly on the level of voluntary force generation. The TRl_at had a modulated stretch reflex only during voluntary pushing; the BRD was modulated during voluntary pushing and pulling, although in a manner that depended on the direction of the applied perturbation. It is interesting to note that the BRD modulation following perturbations in the +X and −Y directions corresponded to excitatory responses during muscle shortening. In contrast to these muscles acting at the elbow, the more proximal shoulder muscles exhibited a modulation pattern that was less dependent on the voluntary forces generated by the subjects. Rather, all four shoulder muscles (AD, MD, PD, PECTclav) were modulated across the range of voluntarily generated forces. This may result from the fact that the voluntary forces used in these experiments did not require the generation of net torques about the shoulder.

In contrast to these longer-latency results, less modulation was observed in the 20- to 50-ms period after perturbation onset. Significant modulation was observed in fewer conditions (18 of 240 conditions) and the magnitude of the observed modulation in these significant conditions was less than that observed for the longer-latency period (P < 0.001; Wilcoxon rank-sum test). For this reason, the remainder of the analysis comparing reflex magnitudes in the stiff and compliant environments will consider only reflex EMG in the longer-latency time period.

Controlling for changes in background muscle activity

There were modest changes in background muscle activity between the two tasks (Fig. 6). This activity represents the EMG recorded from each muscle prior to the onset of the imposed displacements. Most changes in background reflected an increase in muscle activity during interactions with the compliant environment. Because the net force generated by the subject was controlled in the two tasks, these changes in muscle activity correspond to an increase in muscle cocontraction when subjects interacted with the compliant environment. Statistically significant increases in background EMG during interactions with the compliant environment were observed in five of eight muscles; a decrease in muscle activity was observed only in the BI at 10% MVC in the pushing direction. The average change in EMG magnitude across all statistically significant conditions was an increase of 1.3 ± 0.7% MVC.

The observed reflex modulation was not due to differences in background activity during interactions with the stiff and compliant environments. Even though small, environmentally dependent changes in background activity were noted, it was possible to compare reflex responses at matched levels of background in 436 of the 768 possible conditions [6 perturbation directions × 8 muscles × 8 subjects × (voluntary pushing + pulling contractions)], using the technique described in METHODS. Only comparisons at matched levels of background are contained in the following text. Typical results for two muscles, the AD and PECTclav, are shown in Fig. 7. These data represent group results across our subject pool. During interactions with the compliant environment, the AD and PECTclav exhibited statistically significant increased reflex EMG during lateral perturbations, corresponding to muscle stretch, and significantly reduced reflex EMG during medial perturbations, corresponding to muscle release; significance was assessed using a Wilcoxon signed-rank test to determine whether the net change in the reflex response was significantly different from zero. The ▲ symbols correspond to trials requiring a voluntary pushing force and the ▼ symbols correspond to the trials requiring a voluntary pulling force. It is interesting to note that the degree of reflex modulation was not dependent on the direction of the voluntary forces exerted by the subjects, but only on the direction of the applied perturbation. This finding was consistent across all muscles. Statistically significant reflex modulation at matched levels of background muscle activity was observed in each of the eight monitored muscles (Table 3). The most consistent modulation was observed for perturbations in the Y direction; in this direction, modulation was observed in all muscles.

Most observed patterns of reflex modulation appear to be consistent with an increased excitation following muscle stretch and increased inhibition following muscle shortening. Although changes in muscle length resulting from the applied perturbations were not measured, the direction of these changes can be estimated for most muscles in a subset of the perturbation directions. For example, the shoulder flexors were likely stretched by perturbations in the +Y direction and shortened by perturbations in the −Y direction. Similar con-

![FIG. 6. Changes in background EMG at each level of voluntary force. Data are group responses. Each row corresponds to a different muscle. Each plot indicates the change in EMG (50-ms window before perturbation onset) in the compliant environment relative to the stiff environment. The error bars correspond to 95% confidence intervals, computed using a generalized linear model with zero offset and each subject treated as a random factor. Data above the dashed line in each figure indicate increased background EMG in the compliant environment and data below the dashed line indicate decreased background EMG in the compliant environment. Significant differences (P < 0.05), observed in each muscle, are indicated by the asterisks above each voluntary force condition.](http://jn.physiology.org/doi/10.1152/jn.00210.2007)
methodology allowed the perturbation variability to be smooth and reported to be undetectable by the subjects. This compliant environment. The change in controller stiffness was to be stiff immediately prior to the perturbations applied in the compliant environment. This was assessed by the control experiments with the compliant environment. Significance for each condition was assessed using a Wilcoxon signed-rank test.

Conclusions can be drawn for the shoulder extensors in response to perturbations along the Y-axis and for muscles crossing the elbow in response to perturbations along the X-axis. For these cases, most responses corresponded to increased excitation during muscle lengthening and increased inhibition during muscle shortening (Table 3), which is consistent with an increased reflex contribution to limb impedance during interactions with the compliant environment. Only the BRD, which had increased excitatory responses during perturbations in the +Y and −Y directions, did not follow this pattern. This may have occurred to counter the enhanced reflexes in the TRI muscles, which are antagonists at the elbow.

Controlling for perturbation variability

The observed changes in reflex sensitivity were not due to increased variability of the perturbations applied in the compliant environment. This was assessed by the control experiments, in which the stiffness of the manipulator was switched to be stiff immediately prior to the perturbations applied in the compliant environment. The change in controller stiffness was smooth and reported to be undetectable by the subjects. This methodology allowed the perturbation variability to be matched in the stiff and compliant environments. In both environments, the SD across all perturbations applied to all subjects was 0.38 mm at a time period 90–100 ms after perturbation onset; no significant difference was detected between the variance of the perturbations delivered in each environment ($P = 0.997$, two-sample $F$-test).

Even with matched perturbation variability, reflex modulation was observed in all subjects. Comparisons of the reflex modulation observed in the primary and control protocols are shown for a typical subject in Fig. 8. Data are shown for select muscles that had significant reflexes in conditions tested during the control experiments. Both the magnitude of reflex activation within each muscle and the pattern of activation across muscles were similar in both protocols. A post hoc analysis of the control data illustrated in Fig. 8 revealed that the background EMGs prior to perturbation onset were significantly larger only for the PECTclav. Across all muscles and voluntary force conditions tested in the three control subjects (8 muscles × 2 voluntary forces × 3 subjects = 48 total combinations), there were 42 instances in which the background muscle activity in the compliant environment was less than or statistically indistinguishable from that recorded in the stiff environment. Of these instances, 28 exhibited clear increased reflexes in the compliant environment, suggesting that the reflex modulation observed in these control experiments was not due to increased cocontraction of the target muscle and its antagonists during interactions with the compliant environment. Together, these results demonstrate that the perturbation

**TABLE 3. Muscles exhibiting significant reflex modulation at matched levels of background activity**

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Perturbation Direction</th>
<th>X</th>
<th>Y</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>BRD</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>BI</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>TRI_long</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>TRI_lat</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>AD</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>MD</td>
<td>−</td>
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<tr>
<td>PECTclav</td>
<td>−</td>
<td>+</td>
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</table>

$P < 0.05; \bullet P < 0.01$, where $\bullet = +$ indicates enhanced excitation and $\bullet = -$ indicates enhanced inhibition.

**FIG. 8.** Typical results from the control experiment. All data are from a single subject (8) who was exerting voluntary pulling forces (+X direction) at 5% MVC. Perturbations were applied only along the Y-axis, as shown in the top row of data. The direction of the perturbation is colored to match the reflex EMGs shown below. Thin traces correspond to data collected in the stiff environment and thick traces to data collected in the compliant environment. EMGs on the left were collected in the primary experiment and those on the right in the control experiment. The observed increases in reflex EMG during interactions with the compliant environment were similar in both protocols.
variability and the order in which the environments were presented in the primary experiment did not influence the observed changes in reflex sensitivity.

**Assessment of reflex coordination**

The patterns of reflex activity elicited across muscles during the 30 different experimental conditions for each subject (5 loads × 6 perturbation directions) could be described well using four ICs. Figure 9 illustrates how the multiple correlation coefficient increased with the number of coordination patterns used to describe the data. Results show the mean and SD across subjects for the stiff and compliant environments. Four coordination patterns had an average $R^2$ of 0.94 ± 0.02% across all subjects and both environments. As a result, four coordination patterns were used for the remainder of the analysis.

Reflex coordination patterns were similar during stiff and compliant tasks. Figure 10 shows the estimated coordination patterns for a single subject in both tasks. The numbers to the right of each pattern indicate the relative variance described by each pattern, for the data collected in each environment. Note that these numbers consider the variance in the data only after the initial PCA step in the ICA/PCA algorithm. The confidence intervals for the coordination patterns estimated from the stiff environment data tended to be larger than those estimated from the compliant environment data due to the smaller reflexes elicited in the stiff environment. Nevertheless, there was a striking similarity for the coordination patterns observed in each environment, especially for the first, second, and fourth ICs estimated for this subject.

Similarity of the coordination patterns for each subject was quantified by computing how well the coordination patterns estimated from data collected in one environment could predict the data collected in the second environment, which we refer to as the cross-prediction accuracy. The accuracy of the cross-predictions was compared with that of the self-predictions, obtained by fitting the data in each set using the ICs estimated from that set. To provide equivalent comparisons, the predictions were evaluated on cross-validation data not used to estimate the ICs. A jackknife procedure with 100 replications was used to provide robust estimates of the mean fit accuracy for each subject. The average $R^2$ across all subjects was 0.89 ± 0.06 for the cross-predictions and 0.91 ± 0.04 for the self-predictions. The difference between these values was small and did not reach statistical significance ($P = 0.15$; paired $t$-test, $n = 16$). These results suggest that similar patterns of reflex coordination were elicited as subjects interacted with the stiff and compliant environments.

**Common patterns of reflex coordination across subjects**

Coordination patterns for the tested experimental conditions also were similar across subjects. This was examined by pooling data from all subjects collected in both environments and quantifying how fitting accuracy increased with the number of coordination patterns considered. Four patterns were able to account for 88.1 ± 0.6% of the data variance across all subjects and tasks. Figure 11 shows the coordination patterns that were consistent across subjects. The first two coordination patterns accounted for 67% of the observed data variance. These contributed to activation of muscles controlling primarily shoulder flexion (IC1) and elbow extension (IC2). The third pattern accounted for 18% of the data variance, which contributed mainly to shoulder flexion. The fourth pattern was the most variable, as indicated by its large error bars for most muscles. Only two muscles had activations that were significantly different from zero and these contributed mainly to shoulder extension and abduction. This pattern accounted for 14% of the data variance across all conditions.

**DISCUSSION**

This study examined whether stretch-sensitive reflexes elicited in response to multijoint perturbations are modulated by the mechanical properties of the environment with which a subject interacts. Our results demonstrated significant task-dependent modulation of the reflexes elicited within individual muscles. The observed modulation corresponded to an increase in reflex sensitivity during interactions with compliant environments, which is consistent with an increased reflex contribution to limb impedance during interactions with low-impedance environments. We also demonstrated that increased reflex sensitivity was not accompanied by a corresponding change in reflex coordination. Rather, the groups of muscles that were activated synergistically during interactions with the stiff environment also tended to be activated synergistically during interactions with the compliant environment.

**Modulation of reflex sensitivity**

Increased reflexes were observed in all muscles following perturbations delivered in the compliant environment, even at matched levels of background muscle activity. This result is consistent with previous single-joint studies. Akazawa et al. (1983) were among the first to demonstrate that stretch reflexes are modulated according to the mechanical properties of the environment. They found increased reflexes in the flexor pollicis longus, a thumb flexor, during interactions with compliant and unstable loads compared with those elicited during interactions with stiff loads. Consistent results were reported by Doemges and Rack at the wrist (Doemges and Rack 1992b) and index finger (Doemges and Rack 1992a) and by Dietz et al.
(1994) at the elbow. In contrast, De Serres and Milner (1991) reported unchanged stretch reflexes in wrist muscles during interactions with elastic and isotonic loads, which are similar to the mechanical environments simulated in the studies just referenced as well as in the present work. One important difference in the De Serres study is that measurements were made isometrically, possibly providing subjects with insufficient sensory information regarding the mechanical properties of the environment. In contrast, Doemges and Rack (1992a,b) and Dietz (1994) required subjects to move and thereby acquire sensory information about the characteristics of the mechanical interface. Subjects in our experiments had a similar experience from interactions with continuous rather than individual perturbations. Even in our control experiments that used discrete perturbations, subjects interacting with the compliant environment were required to return to the initial posture voluntarily prior to the onset of each perturbation. In previous studies demonstrating reflex modulation, sensitivity increased during interactions with compliant loads. Our results are the first to demonstrate that this occurs throughout the limb in response to multijoint perturbations.

Multiple mechanisms may contribute to the observed modulation. The first is increased activation of gamma motoneurons, which would increase muscle spindle sensitivity (Prochazka et al. 1985). Increased spindle sensitivity would be expected to increase short- and long-latency reflexes. However, increased excitability in both components of the reflex response was not observed in this study or in previous works (Dietz et al. 1994; Doemges and Rack 1992a,b). Although reflexes in each muscle were compared at matched levels of background activity for that muscle, it was not possible to control background activity throughout the limb. Since cocontraction can increase during interactions with compliant environments (Franklin and Milner 2003), increased afferent input from heteronymous pathways may have contributed to increased reflex sensitivity. Hore et al. (1990) examined this possibility at the wrist by anesthetizing antagonist muscles and found that modulation, although reduced, still occurred. Their results suggest that other mechanisms, possibly in addition to heteronymous pathways, can contribute to reflex modulation. In a multijoint study, changes in the background activity of nontarget muscles may also alter the heteronymous reflex contributions through changes in limb impedance and corresponding changes in muscle length resulting from the imposed endpoint displacements. Because the changes in background activity observed in this study were modest relative to the observed reflex modulation (Figs. 5 and 6), this does not seem to be a likely explanation for our results.
although the present experiments cannot be used to directly test this possibility, especially since changes in reflex gain can be quite steep near threshold. Cortical modulation may also have contributed to the enhanced longer-latency reflexes, either directly or via descending changes to spinal circuitry (Prochazka 1989). Evidence for direct cortical modulation was provided by Evarts and Fromm (1978) who found increased discharge in pyramidal tract neurons following wrist perturbations when animals were performing precision tasks relative to discharge recorded during posture maintenance. Recent results by Kimura et al. (2006) demonstrated that reflex modulation during movements through directional force fields could be abolished using appropriately timed transcranial magnetic stimulation to the cortex, also suggesting that cortical pathways can contribute to task-dependent reflex modulation. Such mechanisms likely contributed to the modulation observed in this study.

**Reflex coordination**

The patterns of reflex activity across all recorded muscles did not depend on the mechanical properties of the environment, suggesting that the observed modulation resulted from coordinated changes in the activation to groups of muscles rather than individual muscles. This finding is counter to our initial expectations. Previous studies have demonstrated that muscles spanning multiple joints play an important role in the regulation of limb stability (McIntyre et al. 1996) and that these muscles contribute substantially to the regulation of limb mechanics during interactions with compliant environments (Franklin and Milner 2003), but not stiff environments (Perreault et al. 2001). We thus expected to observe increased reflex activation of multijoint muscles in the compliant task. However, the observed lack of task-specific muscle activation patterns is consistent with previous studies demonstrating that a small number of muscle coordination patterns, or synergies, can describe the patterns of muscle activation across a wide range of tasks (Cheung et al. 2005; d’Avella et al. 2006; Hart and Giszter 2004; Kargo and Giszter 2000; Ting and Macpherson 2005; Tresch et al. 1999). Furthermore, our results indicate that short-term adaptations to changing mechanical environments can occur through modulation of existing reflex patterns rather than the generation of novel patterns that may be optimized for the task. It remains to be seen whether this strategy is also used for more specific tasks that may demand muscle coordination patterns counter to those observed in this study. The use of preferentially unstable environments (Franklin et al. 2007) may help to address this issue.

Consistent reflex coordination patterns were observed across all subjects. Although these patterns may indicate a general coordination strategy used by the nervous system, such an assessment was not the focus of this study and cannot be tested rigorously from the collected data. Our analysis simply estimated a set of ICs to describe the observed reflex activation patterns. The finding that four ICs were able to describe the activation patterns in the eight recorded muscles across 60 different experimental conditions indicates the presence of a coordinated reflex response. However, this coordination inevitably describes properties of the neuromuscular system and the task that system was performing. Determining whether the coordination patterns identified in this study are fundamental building blocks of the reflex system would require determining how they generalize across a wider range of tasks. Our results suggest that such a study can now be conducted without the need to include environmental mechanics as a controlled experimental variable.

**Functional implications**

The observed increase in reflex sensitivity during interactions with compliant environments is consistent with increased reflex contributions to limb impedance (Houk 1979; Nichols and Houk 1976). A direct assessment of reflex contributions to impedance in humans would require a methodology for assessing how reflexively elicited changes in muscle activation alter limb mechanics (Allum et al. 1982; Carter et al. 1990; de Vlugt et al. 2002; Kearney et al. 1997; Perreault et al. 2000; Sinkjaer 1988; Zhang and Rymer 1997). Such techniques have not yet been applied to multijoint systems, in part due to difficulties associated with blocking reflex transmission in multiple muscles or developing computational techniques for estimating reflex contributions to systems with significant inertia. Nevertheless, for perturbations that had a definitive influence on muscle length, reflex modulation served to increase opposition to imposed length changes in most muscles.

During interactions with compliant environments, reflex modulation may provide an involuntary mechanism for enhancing limb stabilization when the mechanical environment cannot be used for that purpose. It has been suggested that reflexes would be an inappropriate mechanism for regulating limb stability due to the neural delays. However, such arguments have been made considering linear systems analyses, and simulations incorporating some of the nonlinearities known to be present in the neuromuscular system have demonstrated that much larger reflex gains may be possible (Stein et al. 1995). Moreover, it is important to note that involuntary responses, including the stretch reflex, do not constitute the only mechanism by which limb impedance and stability can be regulated; they simply represent the first neural response to perturbations of posture. Changes in voluntary muscle activation work in concert with involuntary responses to ensure limb stability (Hasan 2005) and both can contribute to the regulation of impedance and stability during postural tasks (Bennett et al. 1994). Finally, recent studies have demonstrated different motor unit recruitment patterns during interactions with stiff and compliant environments (Mottram et al. 2005) and changes in afferent feedback may contribute to those differences, although how this may influence limb stability remains to be studied.

In summary, our results demonstrate that the reflex response to perturbations of multijoint posture is modulated by the mechanical properties of the environment with which an individual interacts. The observed modulation was consistent with an increase in the reflex contribution to limb impedance during interactions with compliant environments. These findings complement previous single-joint studies and extend those results to more natural perturbations that effect simultaneous changes in the posture of multiple joints. The use of multijoint perturbations also allowed us to investigate task-dependent changes in reflex coordination across muscles throughout the limb. We observed no changes in the patterns of reflex coordination during interactions with the stiff...
and compliant environments, suggesting that the short-term adaptations addressed in this work reflect a change only in reflex gain, not reflex coordination.

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