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RESEARCH ARTICLE

Muscle cocontraction following dynamics learning

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Abstract Coactivation of antagonist muscles is readily observed early in motor learning, in interactions with unstable mechanical environments and in motor system pathologies. Here we present evidence that the nervous system uses coactivation control far more extensively and that patterns of cocontraction during movement are closely tied to the specific requirements of the task. We have examined the changes in cocontraction that follow dynamics learning in tasks that are thought to involve finely sculpted feedforward adjustments to motor commands. We find that, even following substantial training, cocontraction varies in a systematic way that depends on both movement direction and the strength of the external load. The proportion of total activity that is due to cocontraction nevertheless remains remarkably constant. Moreover, long after indices of motor learning and electromyographic measures have reached asymptotic levels, cocontraction still accounts for a significant proportion of total muscle activity in all phases of movement and in all load conditions. These results show that even following dynamics learning in predictable and stable environments, cocontraction forms a central part of the means by which the nervous system regulates movement.

Keywords Motor learning · EMG · Impedance control

Introduction

Muscles in the human motor system have the unique characteristic, that as force generating devices, they actively work only in a single direction. Hence, for each single mechanical degree-of-freedom, at least two antagonistic muscles are necessary to control motion. The ways in which these antagonistic muscles are recruited in different tasks is a fundamental problem in understanding human motor control. Two distinct control mechanisms have been identified in motor control studies. In one case, the nervous system reciprocally activates sets of antagonist muscles and produces torques at a desired joint. Alternatively, antagonistic muscles are recruited at the same time. When cocontraction is balanced there is no kinematic effect, but there are resulting changes in the mechanical impedance of the musculoskeletal system. Reciprocal control and muscle cocontraction have been studied extensively. However, the relative contribution of each to different motor tasks is not well understood nor is manner in which cocontraction varies with the specific requirements of the task.

It has been shown that subjects use cocontraction control to offset the effects of destabilizing forces both under static conditions (Darainy et al. 2004) and during reaching movements (Burdet et al. 2001; Franklin et al. 2003a). Cocontraction control has been documented in the early stages of motor learning. It was shown that the cocontraction of muscles declines as learning progresses, both when subjects learn stable dynamics (Franklin et al. 2003b; Thoroughman and Shadmehr 1999) and for unstable dynamical tasks (Milner and Cloutier 1993). Little is known about the characteristics of cocontraction following

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motor learning in stable environments. Apart from a general decline in cocontraction following learning, the manner in which cocontraction during movement is tuned to specific requirements of the task is unknown. In the present study, we have assessed the role of muscle cocontraction following adaptation to stable environmental dynamics in two situations. We have first examined the degree to which cocontraction during movement is modulated with the strength of the external force field. The modulation of cocontraction with the level of external force would be consistent with the idea that cocontraction control is part of the way in which the nervous system compensates for the effects of external dynamics. A second focus is whether cocontraction is differentially tuned to offset the effects of loads associated with movements in different directions. Different muscle pairs are involved in moving in different directions and accordingly different patterns of muscle coactivation may be necessary to optimally support these movements. Apart from demonstrations under static conditions (Gribble and Ostry 1998; Gomi and Osu 1998), it is unknown whether the nervous system is capable of modulating the balance of cocontraction over different muscle pairs to counteract the forces involved in different movement directions.

In the present study we have assessed the role of muscle cocontraction after extensive practice. We have used a center-out reaching task with a clockwise velocity-dependent curl field to gauge this effect (Shadmehr and Mussa-Ivaldi 1994). Two primary directions of movement were chosen for this study. Reaching movements in one direction required mostly elbow rotation (elbow movement condition) while movements in the second direction involved primarily shoulder rotation (shoulder movement condition). In each direction, subjects trained with two levels of force-field strength consecutively. We obtained a measure of muscle cocontraction using a technique described previously—the minimum normalized muscle activity for each antagonist pair of muscles (Thoroughman and Shadmehr 1999; Gribble et al. 2003). This is a measure of co-occurring activity that is shared by an antagonist muscle pair and provides an estimate of cocontraction. We observed that even following adaptation and after considerable training, the cocontraction level varied with the strength of the force-field. We also observed that movement direction had a substantial influence on the pattern of cocontraction. Moreover, the cocontraction associated with these effects accounted for a substantial and remarkably constant portion of total muscle activation. These results show that even during wholly stable interactions with the environment, cocontraction is modulated with the level of the force-field and also with the direction of movement. These findings suggest that coactivation control is an integral component of the motor control system and is applied broadly even after learning.

Methods

Subjects and apparatus

Ten male subjects, between 19 and 28, participated in this study. All subjects were right-handed and had no history of neuromuscular disorder. Experimental procedures were approved by the McGill University Ethics Committee. Subjects were seated in front of a two degree-of-freedom planar robotic arm (Inmotion2, Interactive Motion Technologies Inc.) and held the handle in their right hand. For each subject, the height of the seat was adjusted to produce an abduction angle at the shoulder of 85°. The seat position was also adjusted to have a shoulder angle of 45° relative to the frontal plane, and an elbow angle of 90° relative to the upper arm, as the start point for all movements. To decrease friction, the subject's hand was supported on the surface of a glass table by an air-sled. Hand position was measured with optical encoders at the robot joints.

Experimental task

The experimental session was divided into a familiarization phase and an experimental phase. The electrodes were placed just prior to the experimental phase. In the familiarization phase of experiment, subjects were trained to make 15 cm reaching movements in 600 ± 50 ms to two visual targets that were positioned just below the surface of the glass table. No forces were applied during this part of the experiment (null condition). One visual target was placed lateral to the subject at the left of the start point. The reaching movement to this target involved shoulder flexion (on average 21°) and to a lesser extent elbow extension (6°). We will refer to this as the shoulder movement condition. A second target was placed in a diagonal direction, forward and to the right of the start point. Movement to this target primarily involved elbow extension (30°, combined with 6° shoulder flexion) and will be referred to as the elbow movement condition.

Subjects were asked to move as straight as possible and audio–visual feedback of movement duration was provided at the end of each trial. In familiarization phase, two blocks of 50 trials each were carried out to each of the targets. Subjects had full view of the arm at all times during the experiment. Each trial started with a short beep and subjects were asked to reach the target in a single movement. They were also told that their reaction time was not the focus of the study and accordingly was not included in the measured movement duration. Following movement, when the hand stopped inside a 1 cm diameter circular target zone, visual feedback of their movement duration was displayed on a monitor beside the robot. They also heard audio feedback at the same time. The robotic arm then moved the subjectÕs hand back to the start point and after a 500 ms delay the next trial began.

Six shoulder and elbow muscle sites were identiÞed and prepared for electrode placement. The muscles of interest were two single-joint shoulder muscles (pectoralis clavicular head and posterior deltoid), two muscles acting at the elbow (the double-joint muscle biceps long head and single-joint triceps lateral head) and two bi-articular shoulder and elbow muscles (biceps short head and triceps long head). A variety of test maneuvers were carried out to determine electrode placement. EMG signals were ampliÞed and analog Þltered between 20 and 450 Hz (Delsys, Bangoli 8).

In the experimental phase of study, subjects were randomly divided into two groups of Þve subjects each. The Þrst group was tested Þrst with movements to the lateral target (shoulder movement condition) and then repeated the same procedure with movements to the diagonal target (elbow movement condition). The second group of subjects did the same task but in opposite order. Five blocks of reaching movements were carried out to each target. Blocks 1 and 2 involved 50 trials each and were carried out under null conditions (only Block 2 was recorded). Block 3 involved 150 trials under low force-Þeld conditions (see below). A fourth block (Block 4) also involved 150 trials under high force-Þeld conditions. A Þnal block of 50 trials was carried out under null conditions to test for aftereffects. EMG data and kinematics were recorded simultaneously.

Clock-wise velocity-dependent forces were used during force-Þeld trials. Equation 1 shows the forces that were applied to the subjectÕs hand.

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = \beta \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix} \quad (1)$$

In this equation f_x and f_y are the commanded force to the robot, v_x and v_y are hand velocities in Cartesian coordinates and β gives the Þeld strength. β was set at 7 N s/m for the low force-Þeld condition and 17 N s/m for the high force-Þeld condition. In 20% of randomly chosen force-Þeld trials, the robot motors were turned-off and subjects were tested under null conditions (catch trials).

Data analysis

Position signals were sampled at 200 Hz, low-pass Butterworth Þltered at 20 Hz and numerically differentiated to produce the velocity signals. EMG signals were sampled at 1,000 Hz and digitally band-bass Þltered between 20 and 450 Hz. EMG signals were then full-wave rectiÞed and the root-mean-square of the signal was calculated over a sliding window of 100 ms. A measure of baseline EMG activity was removed from all signals on a per muscle basis. The measure was obtained by recording a single 30-s trial at the beginning of the experimental phase, during which the subject rested at the center of workspace and did nothing. For each trial, the EMG signals and kinematics data were time-aligned at movement start. Movement onset was scored at the time that tangential hand velocity exceeded 20 mm/s. Movement end was also scored when the hand tangential velocity fell below the 20 mm/s. Kinematic error was used to assess learning and was deÞned on a trial-by-trial basis, as the maximum perpendicular distance (PD) between the hand trajectory and a straight line that connected movement start and end.

We also assessed performance by computing a learning index (Hwang et al. 2003), LI, a measure that takes into account both force-Þeld trials and catch-trials and, hence, corrects for possible differences in performance due to differences in the action of the force Þeld. The LI is deÞned as:

$$LI = \frac{|PD_{catch}|}{|PD_{catch}| + |PD_{ff}|} \quad (2)$$

where PD_{ff} is the maximum perpendicular distance from a straight line under force Þeld conditions and PD_{catch} is the same measure for catch trials. The learning index ranges from 0.0 early in training to an upper limit of 1.0 under conditions of complete adaptation.

Following the removal of baseline activity, measures of EMG were normalized on a muscle-by-muscle basis for each subject separately. The normalization serves to equate EMG magnitudes of antagonist muscles under static conditions. As a normalization factor we used the mean muscle activity from the high force condition during a 200 ms window from 500 to 300 ms before movement onset (averaged over the 300 trials in both movement directions). As a control, we repeated the normalization procedure using the mean EMG activity in a 200 ms window starting 300 ms after the end of movement. We also repeated the normalization procedure based on measures of maximum voluntary cocontraction that were recorded prior to the experimental measurements. In both cases, the results obtained were qualitatively similar to those reported above.

We have not used the more usual technique of normalizing EMG relative to maximum voluntary contraction (MVC). In order to obtain a normalized measure of muscle cocontraction (as opposed to individual muscle contraction), we needed a reference that equated for EMG levels in antagonist muscles when the arm is cocontracted in statics. Conventional MVC measures are obtained for each muscle separately and MVC values for antagonist muscle pairs are unlikely to result in static equilibrium.

We obtained a measure of cocontraction as follows. On each trial and for each antagonistic pair of muscles (for example, biceps long head and triceps lateral head), the minimum normalized muscle activity (from the two EMG signals) was calculated at each point in time (Thoroughman and Shadmehr 1999; Gribble et al. 2003). This measure of cocontraction was calculated over the course of movement to yield a cocontraction trajectory for all trials in the null, low force and high force conditions.

We also computed a measure of reciprocal activation for each trial and each pair of antagonist muscles. The measure of reciprocal activation was the total activity in each muscle pair minus the activation in each muscle due to muscle cocontraction. The total activity in each muscle pair was thus the sum of reciprocal activation plus two times muscle cocontraction (reflecting the contribution of cocontraction to the measured activity of each individual muscle). The contribution following learning of muscle cocontraction to total muscle activity was calculated as follows (averaged over the final 25 trials in each experimental condition, not including catch-trials and the immediately following trial):

$$C = \frac{2\text{coc}}{2\text{coc} + \text{recip}} \quad (3)$$

where C is the proportion of total muscle activity due to cocontraction, coc is the contribution of each muscle to cocontraction and recip is the total reciprocal activation as defined above.

For purposes of statistical analysis, each individual cocontraction trajectory was divided to four parts, 250 to 50 ms before movement onset, 50 ms before movement onset to maximum tangential hand velocity, maximum velocity to end of movement and a 200 ms interval immediately following movement end. Repeated measures ANOVA and Bonferroni corrected post hoc tests were used to evaluate statistical differences.

We also classified muscles according to their role in movement and cocontraction measures were divided on this basis. We refer to the cocontraction activity of antagonistic muscles that are involved in the generation of movement as prime mover cocontraction, and the cocontraction activity of antagonistic muscles at the largely stationary joint as stabilizer cocontraction. Previous studies have demonstrated that activity in biarticular muscles is closely related to movement and torque at the elbow (Gomi and Osu 1998; Gribble and Ostry 1998). Therefore, we have grouped double joint muscles with elbow muscles for purposes of this analysis. Thus, we grouped together as stabilizers, the shoulder cocontraction values in the elbow movement condition and the elbow and biarticular cocontraction values in the shoulder movement condition. We grouped as prime movers, shoulder cocontraction in the shoulder movement condition and elbow and biarticular cocontraction in the elbow movement condition.

We tested six additional subjects in a control study that involved only the shoulder movement condition, and was conducted without catch trials. Subjects first completed 450 trials under null conditions followed by 450 further trials in the high force condition. EMG and movement kinematics were recorded as described above. We verified that performance had reached asymptotic levels by dividing the experiment into bins of 25 trials each. A repeated measures ANOVA assessed differences in both cocontraction and movement curvature over the course of the null and force-field trials in the control study.

Results

The aim of this study was to assess the role of cocontraction following adaptation to a novel dynamic environment. In order to quantify learning we calculated the maximum perpendicular deviation (PD) of the hand from a straight line connecting movement start and end. Figure 1a shows the mean PD (±SE) for the shoulder movement condition over the course of the four blocks of the experiment (50 trials under null-field, 150 trials under low force-field conditions, 150 trials under high force-field conditions and 50 final after-effect trials). The occurrence of catch-trials shown in red was random in the actual experiment however for visualization purposes they are plotted at equal intervals. It can be seen that movements are straight during null field trials. When the force-field is unexpectedly introduced, the hand path deviates from a straight line but with practice the deviation is reduced. As in other studies of force-field learning even at asymptote some curvature remains (Lackner and Dizio 1994; Caithness et al. 2004). The hand path is deviated in the opposite direction during catch trials and the magnitude of the after-effect increases as a function of load. Following the completion of the low force condition subjects rest for 5 min and then start the high force condition in which the direction of force-field remains the same but the magnitude is increased. As in the low force condition, the hand initially deviates from a straight line. Curvature is reduced with practice, however, the effect of the force-field is not fully removed and some residual curvature is observed that is greater in magnitude than in the low force condition. The final block of the experiment involves 50 trials under null field conditions. Here one can observe a considerable after-effect that gradually returns to null field levels. Figure 1b shows the perpendicular deviation for the elbow movement task. The effect is qualitatively similar to that observed in the shoulder movement condition.

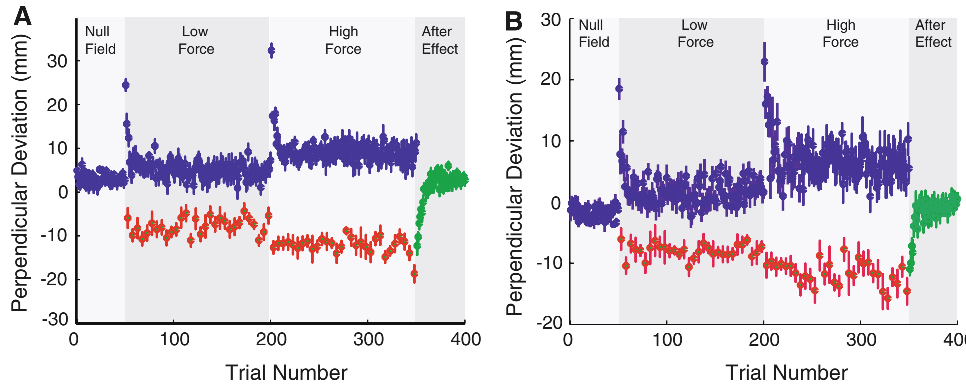

Fig. 1 Maximum perpendicular deviation (PD) during the four phases of the experiment. Mean values across subjects (±SE) are shown. a Shoulder movement condition. b Elbow movement condition. PD reaches at asymptotic levels well before the end of training

Figure 1 shows that performance reached asymptotic levels in all conditions. This was examined quantitatively by assessing changes in perpendicular deviation over the course of the final 50 trials of training. For this purpose, we divided the last 50 trials of the low and high force conditions into five bins of ten trials each (catch trials were excluded). A repeated measures ANOVA found no differences in mean curvature over this set of 50 trials ($P = 0.30$), although, as noted above curvature was reliably higher in the high force condition ($P < 0.01$). This analysis thus shows that performance had reached asymptotic levels long before the end of training.

The larger perpendicular deviation that is observed in high force-field trials at the end of the learning phase is accompanied by larger perpendicular deviation in catch-trials in this condition. Thus, while limb deflections due to the presence of the force-field are greater, the amount of learning as assessed by the magnitude of the catch trial curvature is greater as well. To assess possible differences in the amount of motor learning with force-field strength, we calculated a learning index, LI, for both the low force and the high force conditions (Hwang et al. 2003). The computation was carried out on a per subject basis using PD measures for final 10% of trials in each condition. Differences in the LI were tested using a two-way repeated-measures ANOVA. We found that the LI was similar in low and high force conditions ($P = 0.19$), averaging 0.65 and 0.61 for the shoulder movement condition and 0.71 and 0.66 for the elbow movement condition ($P = 0.24$ for shoulder vs. elbow movement). This suggests that in each movement direction subjects learned approximately the same percentage of the force-field regardless of its actual magnitude.

Figure 2 shows performance under null field conditions for a representative subject. Mean shoulder and elbow rotation are shown along with the EMG activity of six shoulder and elbow muscles. The data are time aligned to movement start and the highlighted area shows the period of movement. There is a clear burst of phasic muscle activity in agonist muscles before the onset of movement (triceps lateral and long head for elbow movement and pectoralis for shoulder movement). This phasic burst is preceded and followed by coactivation of antagonistic muscles.

To analyze changes in EMG activity that accompany force field learning, we removed catch trials and the following force-field trial from statistical analyses. Normalized EMG activity for the final 25 trials in the null, low force, and high force conditions was used to calculate the shoulder, elbow and biarticular cocontraction. To ensure that there were no changes to EMG activity during these intervals as a result of variation in movement kinematics, we examined the maximum tangential hand velocity during these trials in the three conditions that we measured. In the shoulder movement condition, maximum hand velocity was 41 ± 2, 40 ± 2 and 41 ± 3 cm/s for null, low and high force conditions, respectively. In the elbow movement condition, maximum hand velocity for the same three conditions was 43 ± 2, 45 ± 5 and 47 ± 3 cm/s, respectively. A two-way repeated measures ANOVA showed no reliable differences in hand velocity for the different force conditions ($P = 0.06$). Therefore, changes in EMG pattern are not present as a byproduct of velocity change.

Muscle cocontraction was calculated over the course of movement as the minimum normalized muscle activity for each antagonistic muscle pair and averaged over the final 25 trials in each condition, that is, at asymptotic performance levels following learning. Each resulting cocontraction trajectory was divided into four parts, 250–50 ms before the onset of movement, 50 ms before movement to maximum tangential velocity, maximum tangential velocity to movement end and the 200 ms interval following the end of movement. Figure 3 shows the mean (±SE) normalized cocontraction of shoulder, elbow and biarticular muscles in each of these four intervals, respectively. Cocontraction for the shoulder movement condition is shown in green while dark blue represents cocontraction for the elbow movement condition.

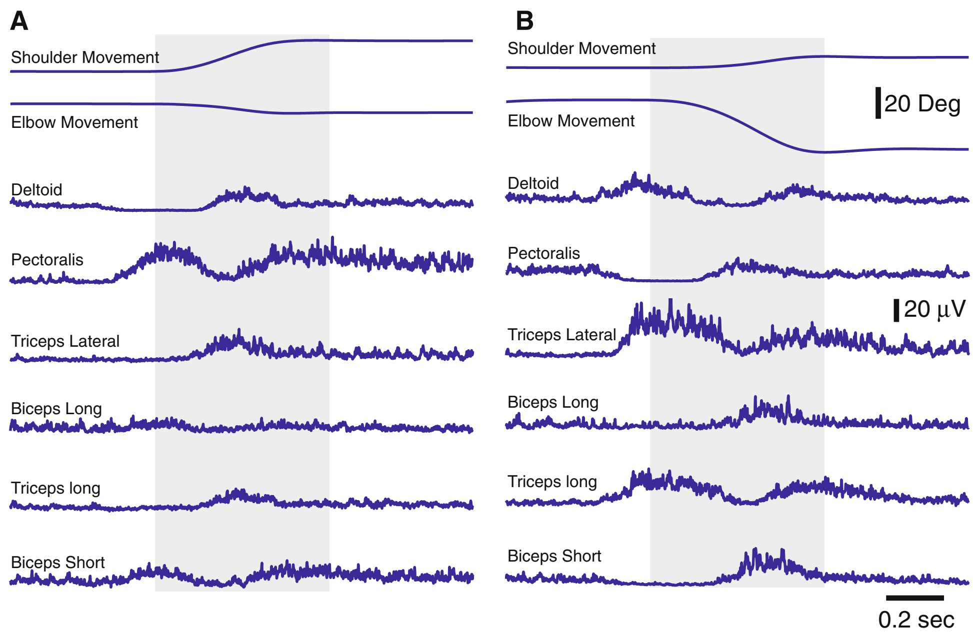

Fig. 2 Shoulder and elbow rotation and mean EMG activity of six shoulder and elbow muscles for a representative subject. a Shoulder movement condition. b Elbow movement condition

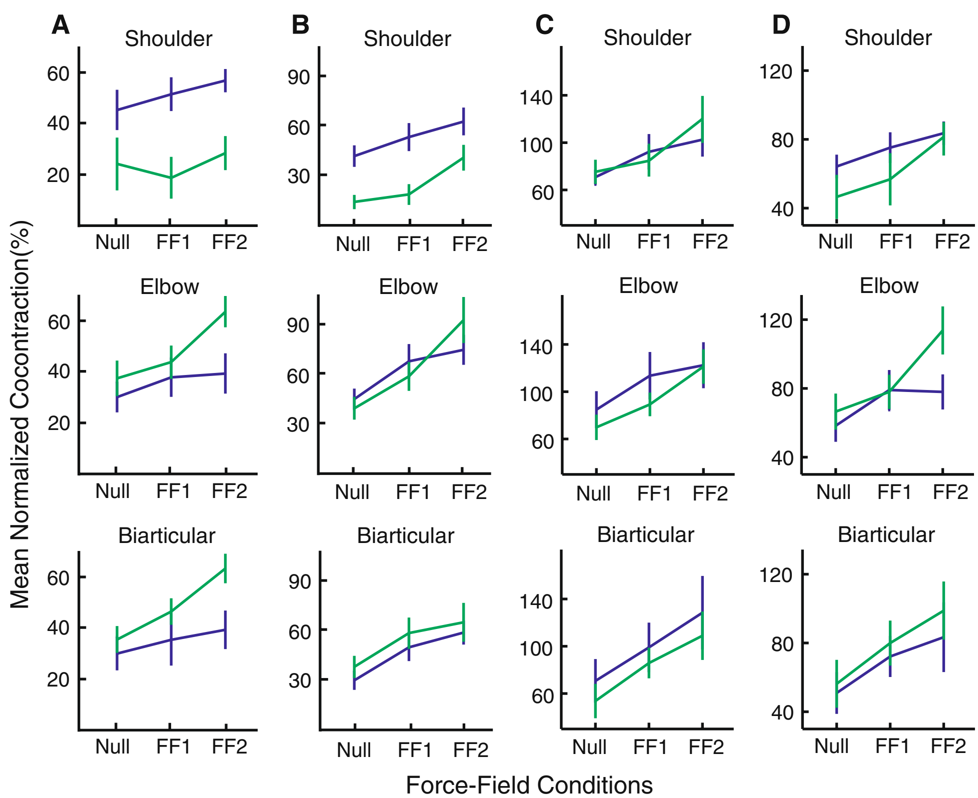

Fig. 3 During wholly stable interactions with the environment, cocontraction is modulated with the level of the force-field and also with the direction of movement. Mean across subjects (±SE) of shoulder, elbow, and biarticular cocontraction for shoulder movement direction (*green*) and elbow movement direction (*dark blue*). Note that for visualization purposes different scales have been used. a From 250 to 50 ms before movement. b A measure of 50 ms before movement to maximum velocity. c Maximum velocity to movement end. d A measure of 200 ms following movement end

A four-way repeated measure ANOVA followed by Bonferroni corrected post hoc tests was used to compare the mean changes in muscle cocontraction. For this particular analysis we divided muscles based on their role in the movement. We will refer to muscles at the largely stationary joint as stabilizers and muscles involved in generating limb displacement as prime movers. The analysis showed that cocontraction increased with magnitude of the force-field ($P < 0.001$). Cocontraction magnitudes at each force level were found to be reliably different from one another by post hoc tests ($P < 0.02$ in all cases). Cocontraction magnitudes also varied over the course of the movement (P < 0.001). Cocontraction was lowest in the intervals preceding peak velocity and increased reliably to a maximum in the deceleration phase of movement (P < 0.05 in both movement directions). The cocontraction level at the end of movement was not reliably different from that in the deceleration phase (P = 0.08).

The relative magnitude of cocontraction in stabilization versus movement related muscles also varied during movement (P < 0.01). In the period prior to movement (Fig. 3a) and in the interval from movement start to peak velocity (Fig. 3b), post hoc comparisons showed that cocontraction magnitudes were reliably greater for muscles involved in joint stabilization than for muscles involved primarily in generating the movement (P < 0.01 and < 0.05, respectively). In the two subsequent intervals, from peak velocity onward, cocontraction levels were similar for stabilization muscles and prime movers (P = 0.24, 0.07 respectively).

Muscle cocontraction accounted for a substantial portion of total activity in each muscle pair even following learning. Figure 4a shows a representative example of muscle activity in the shoulder movement condition (null field). The records display an interval from 500 ms before movement start to 500 ms after movement end. The activity for each muscle pair is shown separately. Flexor muscles are shown in green, extensors are in blue and the common portion due to cocontraction is the light blue shaded region.

We quantified the proportion of total muscle activity due to cocontraction, C, for each of the four time intervals shown in Fig. 3. Figure 4b shows this ratio in each of the four movement phases and the three force-field conditions (averaged over muscle pairs). Overall it can be seen that cocontraction accounted for approximately half of the measured muscle activity, except in the acceleration phase of movement where the contribution is less. It can also been seen the proportion of activity due to cocontraction is relatively constant in the different force conditions tested here and in different movement directions. Thus while both phasic muscle activity and cocontraction increase with level of the force-field the overall proportion is for the most part unchanged.

Differences in C were assessed using a three-way repeated measures ANOVA followed by Bonferroni corrected post hoc tests. We found a significant change in the proportion of muscle activation due to cocontraction over the four time intervals of the movement (P < 0.001). Cocontraction during the acceleration phase of movement was reliably less than in the three other intervals (P < 0.001 in each case). Overall, cocontraction was found to account for 53, 36, 57 and 56% of the total activity in these intervals, respectively. The lowest value, in the acceleration phase of the movement, is due to the large phasic muscle activation associated with initiation of limb movement. We found that the proportion of cocontraction did not differ with force level (P = 0.06). However there were reliable

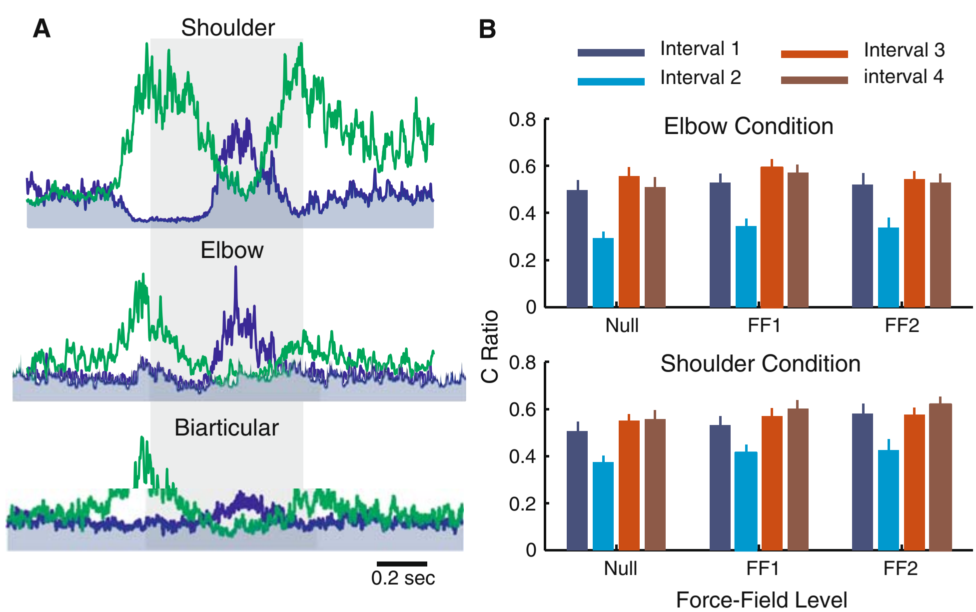

Fig. 4 Cocontraction accounts for a substantial proportion of total muscle activity. a Representative example of muscle activity in the shoulder movement condition for an individual subject (averaged over 20 null field trials). Agonist muscles are shown in *green*, antagonist muscles are in *dark blue*. The *darker shaded area* shows the defined cocontraction activity for each muscle pair. The *vertical highlighted band* indicates the period of movement. b Mean across subjects (±SE) of the relative contribution of cocontraction to total muscle activity (C ratio), averaged over muscles. The figure shows the four movement intervals at each of the three force-field levels

differences in the proportion of cocontraction with movement direction (P < 0.01). A greater proportion of cocontraction overall was observed in the elbow movement condition but the differences were small (52.5 vs. 48.5%). There were two other statistically reliable differences. Cocontraction during the acceleration phase of movement accounted for less of the total in the shoulder condition (32.5 vs. 40.5%). Similarly the proportion of cocontraction at the end of movement was less in the shoulder condition (53.7 vs. 59.3%) (P < 0.02 in each case).

Figure 5 shows changes in cocontraction over the course of learning. The mean (±SE) cocontraction level is given during the interval from 250 to 50 ms before the onset of movement (the other parts of the cocontraction trajectory show a similar pattern). Null Þeld trials are shown in dark blue, cocontraction in the low force condition is shown in green (with catch trials and the Þrst trial following the catch trial removed) and cocontraction in the high force condition is shown in light blue. A repeated measures ANOVA revealed a reliable difference between the mean cocontraction activity of the Þrst 10% of trials (the very Þrst trial was excluded) and the last 10% of trials (P < 0.05) in each condition. However, there is still substantial cocontraction even in the plateau phase of learning.

We veriÞed that EMG activity was at asymptotic levels by assessing changes in the cocontraction level over the last 50 trials of force-Þeld learning. As in our earlier assessment of movement curvature, we divided cocontraction measures over the last 50 force-Þeld trials in each of the high and low force conditions into Þve bins of ten trials each (catch trials and the following force-Þeld trial are excluded). Over the course of these trials we found no statistically reliable differences in cocontraction activity (P > 0.4, repeated measures ANOVA). Cocontraction had thus reached asymptotic levels long before the end of training. In summary, the present study Þnds persistent cocontraction throughout all phases before and after learning a novel task.

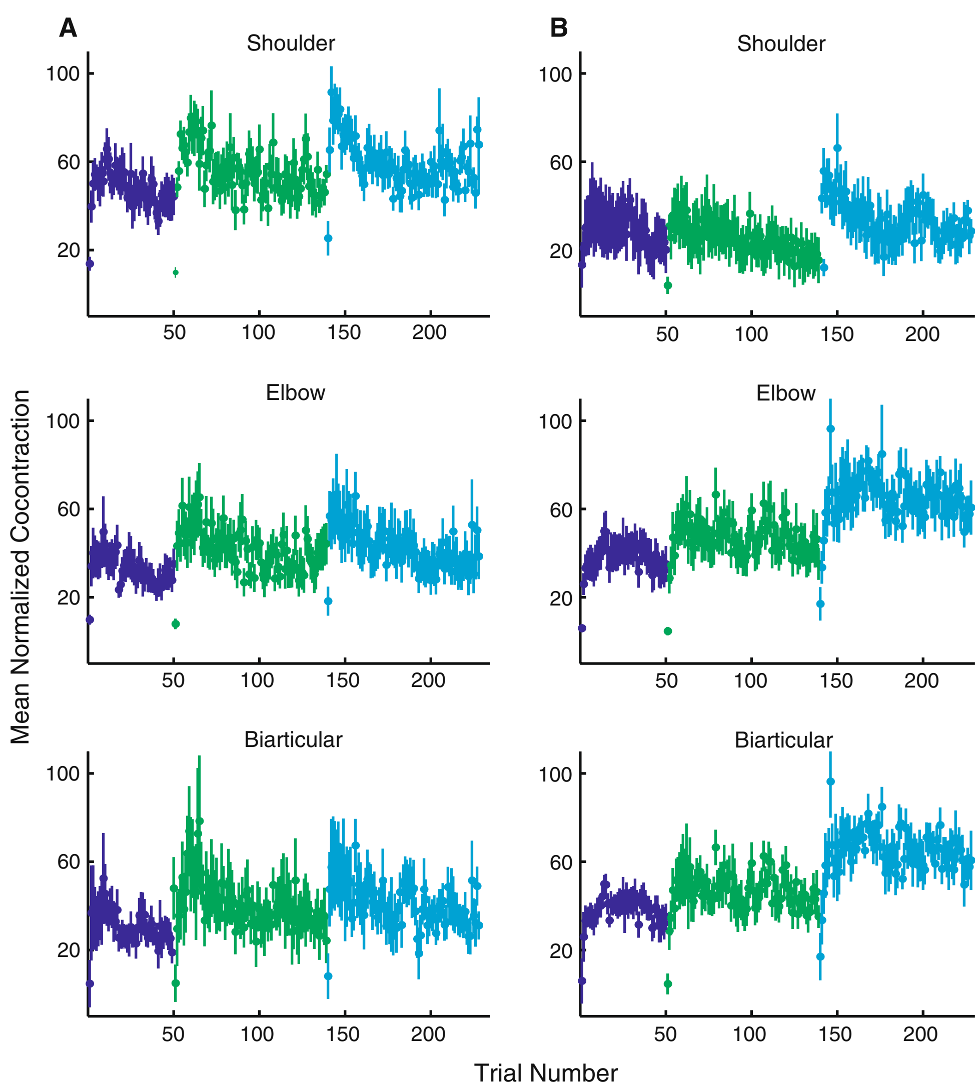

Fig. 5 Cocontraction declines with learning but there is persistent cocontraction even at asymptotic performance levels. Mean across subjects (±SE) of shoulder, elbow, and biarticular muscle cocontraction from 250 to 50 ms before movement. Null is in *blue*, low force is in *green* and high force is in *light blue* (catch trials and the Þrst force-Þeld trial afterwards are removed). a Shoulder condition. b Elbow condition

We conducted a control study with six new subjects to rule out the possibility that either insufÞcient learning or the presence of catch-trials were the source of the persistent cocontraction. The new subjects were tested over the course of 450 null movements and 450 high force condition movements, without any catch-trials. Figure 6a shows normalized cocontraction, over the interval 250 ms before movement start to 200 ms after movement end, averaged over muscle pairs and subjects. Cocontraction is seen to be at asymptotic levels at the end of each phase of the experiment and greater in magnitude in the high force condition. We examined this quantitatively by dividing the cocontraction measures in both null and force Þeld conditions into Þve bins of 25 trials each that were spaced evenly throughout the 450 trial interval. Differences were assessed using a two-way repeated measures ANOVA. We found that cocontraction was reliably greater under high force conditions ($P < 0.001$). Using Bonferroni corrected pairwise comparisons, we found no differences in cocontraction over the Þnal four bins, that is, following the Þrst 100 training trials ($P > 0.1$ in all cases). This shows that even after a longer period of training without catch trials subjects consistently use cocontraction as part of the control that underlies movement.

Figure 6b shows that the proportion of total muscle activity due to cocontraction remains high regardless of the force-Þeld condition. Indeed, even in the absence of catch trials, cocontraction accounts for the same proportion of total muscle activity (in range of 50%). There were no reliable differences over the Þnal 25 trials in the null and force-Þeld conditions in the proportion of activity due to cocontraction ($P = 0.09$). The mean (±SE) of C ratio in the null condition was 0.45 ± 0.03 while the same value for the force-Þeld condition was 0.55 ± 0.05. Figure 6c shows that learning as assessed by maximum perpendicular deviation reaches null Þeld levels within about 100 trials. A repeated measures ANOVA, divided as above into bins of 25 trials, indicated no differences in movement curvature over the Þnal 350 training movements ($P > 0.1$).

The order in which subjects performed the task requires comment. In all cases, null Þeld trials were followed by low force trials and then by high force trials. Although subjects were given 5Ð10 min rest breaks between the three conditions, the possibility remains that muscle fatigue played a role in the observed results. We tested for muscle fatigue quantitatively. It is known that during isometric contraction the median of the EMG power spectrum shifts toward lower frequencies. Recently timeÐfrequency analysis has been used to assess muscle fatigue in cyclic dynamic contractions (Bonato et al. 2001). It has been shown that as a muscle fatigues the Instantaneous median frequency (IMDF) shifts toward lower values. To test for fatigue in the present study we compared the mean IMDF of the last ten trials in each condition. A three-way repeated

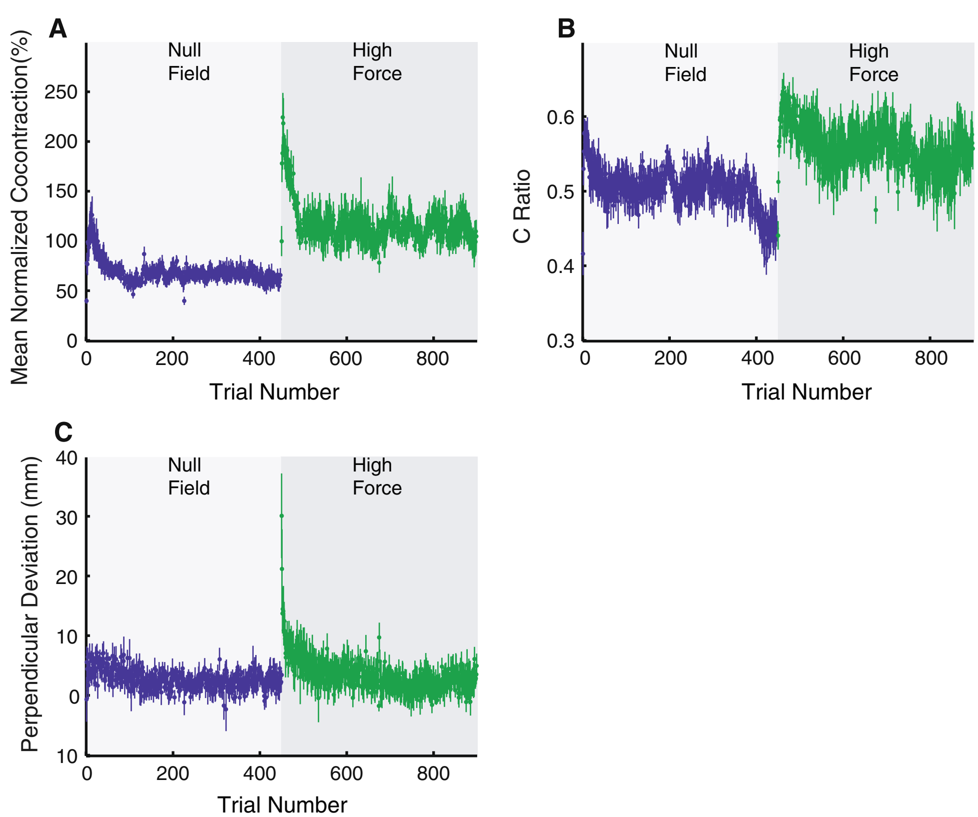

Fig. 6 Cocontraction remains high after extensive training in the absence of catch-trials. a Mean normalized cocontraction across subjects and muscle pairs (±SE) over the interval 250 ms before movement start to 200 ms after movement end. The level of cocontraction is greater in the high force condition. b Mean C ratio (proportion of total muscle activity due to cocontraction) averaged over subjects and muscle pairs (±SE). In both null and high force conditions, cocontraction accounts for about 50% of total muscle activity. c Mean perpendicular deviation (±SE) over the course of training. Performance in the high force condition approaches null Þeld levels within about 100 trials

measures ANOVA (two directions of movement, three different force-Þeld conditions, six muscles) found no differences in the mean IMDF for the three force-Þeld conditions (P = 0.16). Muscle fatigue can thus be ruled out as a potential source of the present results.

Discussion

We have assessed characteristics of antagonistic muscle cocontraction over the course of dynamics learning. Subjects were given extensive practice in producing reaching movements to two visual targets. Each subject was tested in a null Þeld followed by two force-Þeld conditions, a low force and then a high force condition. Muscle coactivation, as assessed by the overlap of agonist and antagonist muscle activity was observed in all phases of movement and throughout the course of training and accounted for a substantial proportion of total muscle activation even following learning. Importantly, cocontraction characteristics varied with the speciÞc details of the task. In particular, cocontraction varied in magnitude with the strength of the force-Þeld and also varied with movement direction. In each direction, cocontraction changed over the course of movement such that before movement start and up to peak velocity, cocontraction in muscles involved primarily in joint stabilization was higher than in the prime movers. Following peak velocity cocontraction activity patterns in stabilizer muscles and prime movers was similar.

It has been suggested that a combination of feedforward and impedance control are involved in adaptation to both stable and unstable dynamical environments (Franklin et al. 2003b). A number of studies have evaluated patterns of muscle activity in the early stages of learning (Franklin et al. 2003b; Thoroughman and Shadmehr 1999). These studies report an initial increase in activity for all muscles followed by a decrease in cocontraction as learning progresses. The data from the present study (Fig. 5) show a similar decline. The present study extends the previous Þndings by showing that the cocontraction which remains following motor learning is tuned to the requirements of the task such that it varies in magnitude in a systematic fashion both with force level and movement direction. Moreover, we observe that the relative contribution of cocontraction to total muscle activity remains essentially the same following learning at all force levels. This shows that cocontraction control is involved in all phases of learning and that the nervous system maintains a fairly constant balance of cocontraction and reciprocal activation.

The relative level of cocontraction is more or less constant over different phases of movement as well. Except for the acceleration phase of the movement (from just before movement start to maximum velocity), we found that cocontraction quite consistently accounted for 50Ð60% of total muscle activity. The reason that cocontraction percentages were not higher in the intervals just before and just after movement is the presence of phasic muscle activity both prior to movement onset and persistent activity following movement end (Suzuki et al. 2001). In the present dataset, the onset of phasic activity is clearly evident by 200 ms before the start of movement and is likewise present for several hundred milliseconds after the end of the movement (see Fig. 4a). This accounts for the fact that the observed proportion of cocontraction in these intervals (250Ð50 ms before movement start and in the 200 ms following movement end) is comparable to that observed during movement.

The directional tuning of muscle cocontraction and corresponding directional changes to hand stiffness have been reported previously (Burdet et al. 2001; Darainy et al. 2004; Franklin et al. 2003b; Gomi and Osu 1998; Perreault et al. 2002). However, the studies in which this directional tuning has been observed, have involved either adaptation to an unstable dynamic environment or biofeedback of muscle cocontraction that is presented to the subject. The present results (Fig. 3, panels a, b) show that different patterns of shoulder and elbow cocontraction, and hence presumably, different underlying neural commands, are involved for different movement directions even when the interaction of the hand with the environment is stable.

Cocontraction magnitudes were greater at the stationary joint. This difference presumably arises as a consequence of the biomechanics of the experimental design. The force-Þeld here produces torques that act primarily about the stationary joint. The observed difference in cocontraction between the stationary and moving joint may well reßect the need for greater stability under these conditions.

The way in which muscle cocontraction has been assessed in this study merits comment. The rationale for using overlap in EMG levels of antagonistic muscles as a measure of cocontraction is that the activity that is common to both muscles results in changes in impedance without producing accompanying changes in net joint torque. However the measurement of cocontraction in this manner also has certain limitations. First cocontraction as assessed in this way may in part reßect phasic muscle activation. This component is of course absent when cocontraction is assessed under stationary conditions. Nevertheless, even if the measured cocontraction in the present study derives in part from phasic activation, it acts to increase impedance and in this sense its effects are similar to those observed for coactivation under static conditions. A second caveat is that cocontraction in the present study is estimated over time by computing the minimum normalized EMG activity of antagonistic muscle pairs. For each muscle, EMG activity is normalized relative to the observed EMG level under static conditions well before the movement onset. However, the normalization that serves to cancel out each opposite muscle torque under static conditions may require modification during movement. For example, changes in muscle moment arms along with length and velocity dependent differences in muscle force generating abilities (and the activity of other synergistic muscles) may influence torque and the actual level of muscle cocontraction. It is worth noting that measures taken in the interval preceding movement onset (Fig. 3a) are not contaminated by changes in muscle length and velocity. Similarly, measures from muscles that are primarily involved in joint stabilization are less affected.

We also wish to comment on a potential concern regarding the muscle activity level that we have used for EMG normalization. If EMG values in the interval used for normalization were small relative to those observed during movement, the effects of measurement error or noise could be greatly exaggerated. In the present study, EMG signals were normalized relative to the mean muscle activity in the high force condition during a 200 ms window before movement onset. The mean normalization factor (over subjects and muscles) was 11 µV whereas the mean baseline muscle activity was 1.7 µV. Muscle activity in the interval used for normalization was thus almost 6.5 times the baseline activity level. By way of comparison, maximum EMG activity for the null field movements shown for a representative subject in Fig. 2 was around 40 µV. Our normalization factor is thus large in relation to background signal levels and well within the range of signals that is applied to for normalization. It is thus unlikely that this procedure increases the effects of measurement error or noise.

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