Neuromuscular Adaptation During Skill Acquisition on a Two Degree-of-Freedom Target-Acquisition Task: Isometric Torque Production

Jonathan Shemmell, Matthew Forner, James R. Tresilian, Stephan Riek, Benjamin K. Barry, and Richard G. Carson
Perception and Motor Systems Laboratory, School of Human Movement Studies, The University of Queensland, Brisbane, Australia
Submitted 2 July 2004; accepted in final form 2 June 2005

Shemmell, Jonathan, Matthew Forner, James R. Tresilian, Stephan Riek, Benjamin K. Barry, and Richard G. Carson. Neuromuscular adaptation during skill acquisition on a two degree-of-freedom target-acquisition task: isometric torque production. J Neurophysiol 94: 3046–3057, 2005. First published June 8, 2005; doi:10.1152/jn.00670.2004. In this study we attempted to identify the principles that govern the changes in neural control that occur during repeated performance of a multiarticular coordination task. Eight participants produced isometric flexion/extension and pronation/supination torques at the radiohumeral joint, either in isolation (e.g., flexion) or in combination (e.g., flexion–supination), to acquire targets presented by a visual display. A cursor superimposed on the display provided feedback of the applied torques. During pre- and postpractice tests, the participants acquired targets in eight directions located either 3.6 cm (20% maximal voluntary contraction [MVC]) or 7.2 cm (40% MVC) from a neutral cursor position. On each of five consecutive days of practice the participants acquired targets located 5.4 cm (30% MVC) from the neutral position. EMG was recorded from eight muscles contributing to torque production about the radiohumeral joint during the pre- and posttests. Target-acquisition time decreased significantly with practice in most target directions and at both target torque levels. These performance improvements were primarily associated with increases in the peak rate of torque development after practice. At a muscular level, these changes were brought about by increases in the rates of recruitment of all agonist muscles. The spatiotemporal organization of muscle synergies was not significantly altered after practice. The observed adaptations appear to lead to performances that are generalizable to actions that require both greater and smaller joint torques than that practiced, and may be successfully recalled after a substantial period without practice. These results suggest that tasks in which performance is improved by increasing the rate of muscle activation, and thus the rate of joint torque development, may benefit in terms of the extent to which acquired levels of performance are maintained over time.

INTRODUCTION

With repeated performance (practice) of a motor task one’s performance typically improves, in the sense that one’s ability to achieve the task goal is enhanced in some way. For example, one may make fewer errors, take less time, and/or perform with less effort (Flament et al. 1999; Lackner and Dizio 1994; Lay et al. 2002). Because motor tasks, by definition, are achieved to perform actions that require both greater and smaller joint torques than that practiced, and may be successfully recalled after a substantial period without practice. These results suggest that tasks in which performance is improved by increasing the rate of muscle activation, and thus the rate of joint torque development, may benefit in terms of the extent to which acquired levels of performance are maintained over time.

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
come more similar after practice, allowing the electromyographic traces of a large number of synergistic muscles to be described by a small number of waveforms. This would provide evidence that the CNS increasingly simplifies the problem of control as skill is acquired by reducing the number of separate commands it sends to activate muscles. This hypothesis is based on previous observations that agonist muscles (including partial agonists) are recruited synchronously before the onset of practiced movements and antagonist muscles are recruited synchronously during movement deceleration (Sergio and Ostry 1995). These observations provide evidence of similarities in the timing of activity in muscles with functionally similar roles.

Significant changes in the magnitude of muscle activity are most likely to be observed in monofunctional muscles in circumstances in which the activation of bifunctional muscles represents an impediment, rather than an aid, to the solution of task goals. Indeed, it was proposed previously (MacConaill and Basmajian 1977) that, at least in the context of single degree-of-freedom (df) movements, the development of expertise is accompanied by an attenuated level of engagement of multifunctional muscles. Based on this idea and evidence of the adaptive nature of muscle synergies demonstrated in previous studies (Barry et al. 2005a; Jamison and Caldwell 1993; Macpherson 1991; Sergio and Ostry 1995), we predict that the amount of activity in bifunctional muscles will be reduced in actions for which their line of action is incongruent with the intended combination of joint torques.

The ability to generalize learned patterns of muscle activation is also important in the context of daily activities because it provides us with the opportunity to improve performances on a wide range of actions through practice on a subset of those tasks. In the current experiment, we are interested in determining whether the modification of muscle activation patterns through practice at one level of torque can enhance performance in similar tasks performed with higher or lower torque demands than those practiced. We predict that skill acquired by practice will be readily transferred to tasks in which the required magnitude of torque production is modified.

In the current study, we therefore seek to determine the nature of changes in muscle synergy organization that mediate the decreases in target-acquisition time that result from practice of a task requiring the isometric generation of torque in two degrees of freedom: flexion/extension about the elbow and pronation/supination of the forearm. Specifically, we will test the hypothesis that the role of bifunctional muscles is reduced after practice in tasks for which their activation produces torque that is incongruent with task goals. Additionally, we will determine whether the number of underlying waveforms that can describe the electromyographic (EMG) patterns of synergist muscles acting about the elbow and forearm are reduced after practice, thus increasing the simplicity of CNS control.

**METH O DS**

**Participants**

Eight right-hand–dominant (Oldfield 1971) participants between the ages of 20 and 45 yr (seven males and one female) were involved in this experiment. Participants gave their informed consent before involvement in the study. All experimental procedures were approved by the Medical Ethics Committee of The University of Queensland and conformed with the Declaration of Helsinki.

**Apparatus**

Participants were seated in a height-adjustable chair 65 cm from a computer display positioned at eye level. The dominant arm was placed in the pendant position with the elbow flexed at 90° and the forearm in a neutral position. The elbow joint was held stationary in a padded brace by a Velcro strap and the hand grasped a manipulandum. Padded clamps were located above and below the hand to minimize the force required to grip the manipulandum (Fig. 1). A molded thermoplastic restraint was attached around the wrist to prevent motion at this joint. The positions of all adjustable elements of the apparatus were recorded for all participants during their first experimental session and remained constant for all subsequent sessions.

**Force/torque recordings**

The manipulandum was instrumented with a multiple df force/torque transducer (Delta ATI, Industrial Automation, Perth, Australia). Force (flexion/extension) and torque (pronation/supination) were sampled at 2,000 Hz at an analog-to-digital interface (AT-mio-16E-10, National Instruments, Austin, TX) and stored on a personal computer. Labview (v. 5.0, National Instruments) was used to write the custom experimental control and data-acquisition routines.

**Electromyographic recordings**

The EMG activity of eight muscles was recorded during the pre- and posttests as well as during the first, third, and fifth days of training. Bipolar (AgCl) surface electrodes (diameter 5 mm) were used to obtain recordings from 1) brachioradialis [BRAD], 2) triceps brachii (lateral head) [TRI], 3) pronator teres [PT], 4) flexor carpi radialis [FCR], and 5) extensor carpi radialis [ECR]. The electrodes were placed approximately 2 cm apart on the muscle belly, nearly parallel to muscle fibers, and recordings were tested by asking participants to perform test contractions according to procedures outlined by Delagi (1980). The EMG activity of the 6) long [BB(LI)] and 7) short head [BB(S)] of biceps brachii, and 8) brachialis [BRA] was recorded using fine-wire (75 micron) bipolar hook electrodes, inserted into the muscle 2 cm apart by 27-gauge needles. The needles were removed before recording. The EMG signals were amplified (500–10,000 times; P511 amplifiers, Grass Instruments, Berkshire, England).

**FIG. 1.** Vertical cursor movement on the visual display was controlled by the production of elbow flexion and extension torques (measured as the vertical force at the force/torque transducer multiplied by the distance between the transducer and the elbow joint). Pronation and supination torques moved the cursor horizontally. Participants were fitted with an elbow restraint to reduce movement at this joint. A thermoplastic wrist brace (not shown) was also fitted to limit movement of the wrist. Visual display was positioned 1 m from the participants, approximately at eye level.
UK), band-pass filtered (30–1,000 Hz), sampled at 2,000 Hz, and stored in the manner described previously.

To provide a means of normalizing the amplitude of the EMG signals across the experimental sessions, maximal M-waves were evoked in all muscles by electrical stimulation (Digitimer DS7A: pulse width 0.5 ms) of the brachial plexus at Erb’s point, before the commencement of each session. The stimulation intensity was increased in steps from an imperceptible level until the magnitude of the EMG responses no longer increased. The intensity of stimulation was then increased by a further 20%, and the responses to eight supramaximal stimuli were recorded at intervals varying randomly between 6 and 8 s.

**Torque feedback**

The torques produced in pronation/supination and flexion/extension were presented to the participants in real time as the position of a cursor on a computer display. Flexion of the elbow resulted in a cursor movement vertically upward; elbow extension caused the cursor to move vertically downward; pronation of the forearm moved the cursor to the left and supination to the right. The amount of cursor movement generated for each unit of applied torque differed for each participant and was proportional to the maximal voluntary torque (MVT: the amount of torque produced during a maximal voluntary contraction) for each direction. Pronation and supination torques were measured directly from the torque transducer. Torques in flexion and extension were obtained by multiplying the force measured in the vertical plane by the distance between the center of rotation of the elbow and the transducer.

**Familiarization**

Before the commencement of training, all participants completed a familiarization session. To determine the mapping between torque and movement of the cursor on the visual display, MVTs were recorded in flexion (FLX), extension (EXT), pronation (PRO), and supination (SUP). The participants were asked to produce and hold a maximal contraction for 3 s. During this procedure, the participants were given visual feedback of the torque produced in the other df, and were instructed to keep this torque as close to zero as possible. Trials in which this level became >0.5 Nm were repeated after a period of rest.

The participants subsequently performed eight familiarization trials in each of the eight torque combinations that were to be used during the practice sessions. Unlike the experimental task (described below), the torque produced in each df was presented as a bar graph. The target torque level for each df was indicated by line superimposed on the graph. When the applied levels of torque fell within the target area (target torque ±5% MVT) there occurred a change in the color of the bar.

**Target-acquisition task**

Targets representing combinations of torques in 2-df movements (FLX/PRO, FLX/SUP, EXT/PRO, EXT/SUP) were positioned such that a constant visual distance was maintained between the center of the screen and each target. The vertical (\( T_{F/E} \)) and horizontal (\( T_{P/S} \)) torques required to reach the targets were calculated as

\[
T_{F/E} = MVT_{F/E} \times M_{PROP} \times \sin(\theta)
\]

\[
T_{P/S} = MVT_{P/S} \times M_{PROP} \times \cos(\theta)
\]

where \( MVT_{F/E} \) is the flexion or extension MVT (whichever was relevant for the target in question) for an individual participant and \( MVT_{P/S} \) is the pronation or supination MVT. \( M_{PROP} \) is the proportional multiplier for each torque level (0.2 and 0.4 for pre- and posttests; 0.3 for practice and retention sessions). \( \theta \) is the angle between the target and the positive horizontal visual axis (Fig. 2).
The dependent variables obtained from these data further determined for each trial as the point at which the torque produced in either df first exceeded 5% of the associated MVT after presentation of the target. All trials were visually inspected to ensure that this criterion eliminated false onset identification. A target was acquired when the torque produced by the participant fell within 5% of the associated MVT and was held within that limit for 100 ms. For the data analysis, target acquisition was defined as the beginning of the 100-ms hold period. All kinetic variables were calculated between movement onset and target acquisition.

Because the participants were instructed to acquire the targets as rapidly as possible, target-acquisition time (the time in seconds from torque onset to target acquisition) was the primary measure of performance. The peak rate of torque development was obtained as the first temporal derivative of the normalized (with respect to the MVT in the corresponding direction) resultant torque vector. A time-normalized measure of the extent to which trajectories deviated from straight paths to each target was determined by calculating the root mean squared (RMS) error between the normalized torque trajectory and the vector defined between zero torque (the initial condition) and the target. The values were expressed as a proportion of the torque range in the dimension orthogonal (in torque space) to that of the target. For example, the directional error for PRO and SUP targets were normalized to the torque range of the FLX/EXT axis. Normalizing ranges for diagonal targets were determined by calculating the angle of the target in torque–space and normalizing to the torque range in the dimension orthogonal (in torque space) to that of the target (described in Davis and Vaughan 1993), and the calculation of the principal components, the attrition of components with eigenvalues below the criterion, the application of a varimax rotation (described in Davis and Vaughan 1993), and the calculation of the component scores (also referred to as eigencurves; Thomas et al. 2005).

**Statistical analysis**

The median values of the 16 trials performed in each condition were used as the basis of all statistical analyses. Each dependent measure was analyzed separately using a repeated-measures time (pre- and postpractice) by target position ANOVA. Planned comparisons were used to assess whether the outcome measures obtained after practice differed from those recorded before practice. In assessing the changes that occurred during the practice period, the outcome measures obtained during sessions 2–5 were compared individually to the values obtained during the first practice session. The measures obtained during the retention session were compared with those recorded during the final (fifth) practice session. To assist in the interpretation of the tests of significance, the effect size index for ANOVA ($f$) was calculated following Cohen (1969). A small effect size is considered by convention to be indicated by an $f$ value of $<0.25$, a medium effect size by an $f$ value of between 0.25 and 0.4, and a large effect size by an $f$ value of $>0.4$. In the text, all data are presented as means ± SD.

**RESULTS**

**Performance variables**

Participants modified the manner in which they developed torque during the acquisition of each target after practice (representative data are shown in Fig. 2). The nature of such changes, however, differed across the eight target directions. The dependent variables obtained from these data further demonstrate the nature of changes in the torques produced before and after practice.

Before practice, acquisition times were longest for targets that required combinations of extension torque with either pronation or supination torque (Fig. 4). The acquisition times for pronation (20%: $0.30 ± 0.1$ s; 40%: $0.65 ± 0.56$ s) and supination (20%: $0.30 ± 0.07$ s; 40%: $0.53 ± 0.53$ s) targets were significantly lower than the average acquisition time across all target directions ($P < 0.05$). No reliable practice-
related changes in performance were evident when participants produced torque solely in extension or pronation at 20% of their MVTs, or when extension and supination torques were combined at 40% of their MVTs. In all other conditions however, acquisition times were substantially lower after practice ($P < 0.05$; $f > 0.4$). During the postpractice session, targets requiring supination torque were acquired most rapidly, whereas those requiring extension torque in combination with either supination or pronation torque were acquired most slowly. Targets that required extension torque in isolation were also among those acquired most slowly at 20% MVT ($0.33 \pm 0.1$ s).

The decreases in target-acquisition times observed at both torque target levels were associated with increases in the peak rate at which torque was generated (Fig. 5). Before practice, the rate of torque production was highest when pronation and supination targets were acquired. Peak rates in all other directions (Flx, Flx/Sup, Flx/Pro, Ext, Ext/Sup, Ext/Pro) were significantly lower than those achieved in pronation and supination ($P < 0.05$; $f > 0.4$), but not reliably different from each other (mean peak rate across these six targets: $1.2 \pm 0.09%$ of MVT/s). After practice, peak rates of cursor movement were 40–60% larger in each target direction (all $P < 0.05$ and $f > 0.4$), although the variation in this measure across target positions did not change as a result of practice.

Electromyographic variables

The greatest levels of activity in each muscle were generally observed when the required torques corresponded to the principal muscle moments (Fig. 6). The brachialis muscle for example, was most active during pure flexion actions and those combining flexion and pronation. Consistent with previous observations (Jamison and Caldwell 1993; Sergio and Ostry 1995), however, the same muscle displayed lower levels of activation when flexion and supination torques were combined, despite having a line of action that would allow it to contribute positive work in this context.

The level of activity in the short head of the biceps brachii displayed no change after practice for targets defined at 20% MVT, but increases were exhibited in Flx/Sup, Sup, and Ext/Sup at 40% MVT ($P < 0.05$; $f > 0.4$). Conversely, the long head of biceps brachii displayed increases in the same directions (Flx/Sup, Sup, and Ext/Sup) as well as during pure flexion at the lower level of torque but not at the higher level of target torque (Fig. 6). The brachialis and brachioradialis muscles exhibited very similar patterns of activation across the task workspace, being active primarily during flexion actions, and combinations of flexion and pronation (Pretest values: Flx, $4.29 \pm 4.27\%$ of MaxM; Flx/Pro, $4.39 \pm 3.46\%$ of MaxM).

After practice, levels of activation in brachialis were lower during supination and combinations of flexion and supination ($P < 0.05$; $f > 0.4$), for targets at 20% MVT, and during flexion at 40% MVT ($P < 0.05$; $f > 0.4$). The activation of triceps brachii was generally higher during combinations of extension and supination than during pure extension and combinations of extension and pronation. The level of engagement of this muscle increased after practice during pure extension at 20% MVT ($P < 0.05$; $f > 0.4$), but decreased during Ext and Ext/Sup at 40% MVT ($P < 0.05$ and $f > 0.4$).

The rate of onset of muscle activity was always greatest when each muscle was engaged as an agonist (Fig. 7). Both heads of the biceps brachii, for example, were recruited most rapidly during combinations of flexion and supination torque. Likewise, the monofunctional elbow flexors, brachialis and brachioradialis, were recruited most rapidly during pure flexion actions and during combinations of flexion and pronation, when biceps brachii activity was reduced. After practice, the rate of activation of all muscles was greater than that observed initially, during actions in which they acted as agonists ($all P <$

![FIG. 4](image1)

**FIG. 4.** Target-acquisition times achieved during the pre- (dashed lines with diamond symbols) and posttests (solid lines with square symbols) with targets requiring 20% (A) and 40% (B) of MVTs. Filled posttest symbols represent differences between pre- and posttest values that were both statistically reliable ($P < 0.05$) and had a large effect size ($|f| > 0.4$).

![FIG. 5](image2)

**FIG. 5.** Peak rates of cursor movement in each target direction, expressed as the percentage of the relevant MVT moved per second. Data are shown for pre- (dashed lines, diamond symbols) and posttest (solid lines, square symbols) sessions, and for targets that required 20% (A) and 40% (B) of participants’ MVTs. Filled posttest symbols represent differences between pre- and posttest values that were both statistically reliable ($P < 0.05$) and had a large effect size ($|f| > 0.4$).
0.05; $f > 0.4$). The extent of these changes was similar for each muscle, with the rates of agonist muscle recruitment after practice being around 100% greater than those observed before practice. In contrast, during actions for which each muscle acted as an antagonist, the rates of initial activation generally showed no change after practice. This presumably reflects the relatively minor role played by antagonist muscles during rapid isometric contractions.

For each participant, the number of principal components that accounted for a significant amount of variability in the EMG traces was small (one to nine) in comparison to the number of muscle and target combinations (eight muscles $\times$ eight targets $= 64$ combinations) that they represented (Fig. 8). This represents a substantial reduction in the number of neuromuscular degrees of freedom to be controlled. Additionally, the number of significant PCs was reduced after practice at both levels of torque. Some participants' EMG data produced an equal number of PCs before and after practice, but there were no instances in which more PCs were required after practice compared with before practice. Correspondingly, the average amount of variance accounted for by the first PC increased from $67 \pm 19\%$ at 20% MVT and $77 \pm 5\%$ at 40% MVT, to $78 \pm 15$ and $84 \pm 7\%$, respectively, after practice.

Before practice, the first PC at 20% MVT was associated with a curve that increased rapidly before reaching a plateau level, whereas the second PC had a more transient initial pulse with a steeper trajectory (Fig. 9A). The third PC reflected peaks of muscle activation both before and after the onset of movement, whereas the fourth PC reached a peak very late in the movement. The fifth PC demonstrates activity through the entire trial and, given the small amount of variance it accounted for, most likely reflects low-level activity in a small number of muscles. The first PC was altered after practice as the initial rate of rise became steeper and the peak was
followed by a gradual reduction in activity that lasted until the end of the waveform. The second PC remained essentially unchanged whereas the third PC after practice was characterized by a single peak occurring slightly after movement onset and a gradual reduction thereafter, similar to PC1. The fourth significant PC after practice demonstrated a steady rise from around 200 ms before movement onset to a peak beginning at movement onset that was sustained for 100 ms before being reduced around 30% and held until the end of the waveform.

The fact that all of the significant PCs after practice were characterized by a peak in activation close to the onset of movement demonstrates that antagonist contraction was not required to decelerate the movement of the cursor in this task. The relatively small contribution of antagonist muscles (Fig. 6) was instead used concurrently with agonist muscle activation, presumably to achieve the correct balance of torques.

---

**FIG. 7.** Mean rate of onset of activity in the 8 recorded muscles is shown for targets that required 20% (left column) and 40% (right column) of participants’ MVTs for pre- (dashed lines, diamond symbols) and posttest sessions (solid lines, square symbols). Filled symbols indicate that reliable increases in the rate of recruitment were generally observed when muscles acted agonistically in either one or 2 dfs but not when muscles acted antagonistically. Filled posttest symbols represent differences between pre- and posttest values that were both statistically reliable ($P < 0.05$) and had a large effect size ($|f| > 0.4$).

**FIG. 8.** Mean number of significant principal components (PCs) across subjects is shown with error bars indicating the SD from the mean in each case. Asterisks represent differences between pre- and posttest values that were statistically reliable ($P < 0.05$).
The first PC at 40% MVT was similar to the first PC at 20% MVT extracted before practice in that it rose rapidly before movement onset and remained close to its peak level for the duration of the trial. The shape of this PC remained comparable in shape after practice, although a slight increase in the initial rate of rise was observed (Fig. 9B). The second PC at 40% MVT was very similar in shape to the second PC extracted at the lower target torque level and remained consistent in shape after practice. The third prepractice PC reflected a pulse in muscle activity that began 150 ms before movement onset and peaked at movement onset, whereas the fourth contained one peak at around 80 ms before movement onset and a second peak that rose from above baseline levels to a maximum at 190 ms after movement onset. A third of these PCs was replaced by a single significant waveform (PC3) after practice, which contained one peak 80 ms before movement onset and another around 100 ms after movement onset.

The extent to which an individual muscle is activated in the manner described by the first PC in each target direction can be determined by examining the loading of each EMG trace onto the first PC (Fig. 10). The same method can be used to determine the extent to which EMG traces are described by each additional PC. To reduce the complexity of the Fig. 10, only the loadings for the first PC are presented at each target torque level. Loadings of note on subsequent PCs are noted in the text.

Despite the relative complexity of Fig. 10, three important features of the PC loadings are clearly observable. First, the pattern of loadings is similar at both target torque levels, indicating that a comparable subset of muscles is being driven in a manner described by the first PC. Second, the differences in individual muscle loadings become greater after practice, indicating that the first PC becomes a better descriptor for the activation of some muscles and a worse descriptor for others. Not shown in the data presented is the fact that muscles that did not load highly onto the first PC generally demonstrated the highest loadings onto the second PC at both levels of torque.

The extent to which an individual muscle is activated in a particular muscle on the first PC (or any PC) based on its functional role as an agonist or antagonist. Neither is it the case that a specific subset of muscles loads to an equal extent on any PC in each target direction. For example, both agonist (BBL, BRA, and BRAD) and antagonist (TRI) muscles load to a similar extent on PC1 during pure elbow flexion. The fact that both agonist and antagonist muscles load positively onto the first and second PCs shows that whereas antagonist muscles in this task are not strongly activated (see Fig. 6), they are activated concurrently with agonist muscles before movement onset.

**Kinematic adaptations exhibited during practice and in retention**

Target-acquisition times were significantly lower in six of the eight target directions (Flx/Sup, Ext/Sup, Ext, Ext/Pro, Pro, and Flx/Pro) during the final practice session than during the initial practice session (Fig. 11A). These performance improvements were associated with reliable increases in peak movement speed in each target direction (Fig. 11B). Participants also decreased the extent to which cursor trajectories deviated from a straight path in Flx/Sup (Fig. 11C). The decrease in trajectory deviation in Flx/Sup was associated with significant changes in the timing of agonist muscle activity ([BRA] Day 1: −10 ± 24 ms, Day 5: −52 ± 19 ms; [FCR] Day 1: −81 ± 43 ms, Day 5: −13 ± 25 ms). The amount of target overshoot remained unchanged in most target directions, increasing only when pure elbow flexion was required (Fig. 11D).

In two of the eight target directions (Flx/Sup and Ext), the acquisition times produced during the retention test were significantly different from those observed in the final practice session. The acquisition of the Flx/Sup target was performed less rapidly after the nonpractice period (final practice session: 0.32 ± 0.03 s; retention test: 0.38 ± 0.09 s), whereas the Ext target was acquired more rapidly (final practice session: 0.39 ± 0.13 s; retention test: 0.32 ± 0.12 s). Most of the kinematic features of the respective actions were also preserved after the
nonpractice period. The peak rates of cursor movement that were produced during the retention session were not significantly different from those produced during the final practice session (Fig. 11B). The amount of directional deviation produced in each target direction during the retention session also remained similar to that produced in the final practice session.

The combination of flexion and supination torques was the only action for which the amount of trajectory deviation during the retention session was significantly greater than that observed during the final practice session. The extent to which participants overshot each target was also similar to that observed in the final practice session with the exception of pure...
pronation actions, in which the extent of target overshoot was significantly reduced in the retention test (Fig. 11D, $P < 0.05$; $f > 0.4$).

**DISCUSSION**

The results of this study demonstrate that during practice of an isometric goal-directed torque-production task, decreases in target-acquisition time are associated primarily with increases in the rate of agonist muscle recruitment. The observed increase in the rates of agonist recruitment was reflected at the kinetic level by an increase in the peak rate of joint torque development in each target direction. The decreases in acquisition time observed after practice were similar in proportion for each action, despite there being a large degree of variability in the acquisition times achieved across the eight target directions. Increases in the rate of agonist muscle recruitment produced performances that generalized successfully to magnitude-scaled variants of the practice task and were easily recalled after a period without practice. Some changes in the contribution of individual muscles were also evident after practice. These changes were primarily expressed as increases in the activity of bifunctional agonist muscles (both heads of the biceps brachii and extensor carpi radialis) in both single and dual df actions. The contribution of monofunctional agonists was generally either maintained near prepractice levels (e.g., brachialis at 20% MVT and brachioradialis at 20 and 40% MVT) or was reduced as a consequence of practice (e.g., triceps brachii at 40% MVT).

A major issue addressed by this paper is that of the extent to which the CNS is able to simplify the problem of controlling multiple muscles by driving groups of muscles together as synergists. By performing a principal component analysis on the EMG data obtained from each recorded muscle in each target direction, we obtained an indication of the extent to which such a simplification may occur. The reduction of activation patterns from 64 (eight muscles in each of eight target directions) to fewer than five in many cases is striking evidence that a simplification of neuromuscular control is occurring (Fig. 8). Additionally, the fact that the number of significant principal components was reduced after practice for every participant and at both target torque levels strongly suggests that further simplification of the control problem is an important aspect of skill acquisition. These results are supported by previous studies that have identified a small number of underlying waveforms that describe the activation of a large number of muscles during the human gait cycle (Davis et al. 1991; Ivanenko et al. 2004).

A reduction in the number of waveforms that describe the activation profiles of many muscles is analogous to the original idea proposed by Bernstein (1967) that the number of degrees of freedom that must be controlled by the CNS is reduced during even the performance of novel tasks. As skill is acquired, it seems that the CNS becomes more selective with respect to the particular muscles that are driven by each of the underlying waveforms (Fig. 10). We found that it was not the case that muscles with similar mechanical actions loaded equally onto each PC, suggesting that synergistic groupings are based on task-specific functions (such as steady force production and stabilization) of each muscle rather than their lines of action about the joint complex. When performing an elbow flexion task at 40% MVT, for example, most of the eight muscles loaded most heavily onto the first PC, which showed a rapid increase in activity followed by a plateau beginning at movement onset. The short head of the biceps brachii, however, loaded almost exclusively onto the second PC, which provided a more pulsatile contraction that was reduced after movement onset. The separation of even two heads of the same muscle is a clear indication that synergistic groups are not formed based purely on mechanical criteria. In this case it is conceivable that the additional pulse of activity in the short head of the biceps brachii was produced to provide stabilization to the cursor during movement onset, although it is difficult to intimate the precise functions of each activation waveform.

The generalization of acquired skill to unpracticed areas of the workspace was successful in all target directions, regardless of whether targets represented larger or smaller joint torques than those practiced. The fact that performance improvements were observed in both generalization conditions (i.e., generalization to torque targets of higher and lower magnitude than those practiced) demonstrates that patterns of muscular activity and joint torque development acquired with practice can be scaled in magnitude to improve performance on tasks that require dissimilar levels of joint torque. The magnitude of the performance improvements was larger when the targets were presented in unfamiliar areas of the workspace (i.e., at 40% MVT) than when they were presented in familiar workspace areas (i.e., at 20% MVT). The percentage decrease in acquisition times for smaller torque targets than those practiced (20% MVT) was 16.14 $\pm$ 7.6%, compared with 26.58 $\pm$ 6.4% for higher torque targets (40% MVT). This observation appears to be contrary to the common observation that familiarity with a task workspace facilitates motor learning (Shadmehr and Mussa-Ivaldi 1994). It is possible that the success of skill generalization to actions requiring greater levels of torque than were experienced during practice was attributable, at least in part, to an enhanced facility for torque production. A number of studies have demonstrated evidence of increases in muscle strength after the repetition of tasks that require moderate levels of torque production (around 40% of maximum levels) (Barry and Carson 2004; Faigenbaum et al. 1999; Ohta et al. 2003).

We have observed previously that increases in the rate of agonist recruitment transfer effectively from programs of resistance training to a target-acquisition task similar to that used in the current experiment (Barry et al. 2005b). In a series of experiments carried out by Barry et al. (2004, 2005a,b), increases in the rate of biceps brachii recruitment were observed after training in which the participants were required to produce coupled torques in elbow flexion and forearm supination that represented a moderate (40%) to high (100%) proportion of their maximum capacity. The increases in agonist recruitment rate observed in this experiment are consistent with changes induced by resistance training in similar tasks and it may be hypothesized therefore that the neural mechanisms through which these changes take place are also similar.

Carroll et al. (2002) showed that the functional motor changes induced by a program of resistance training are mediated by adaptations in the firing properties of spinal motoneurons. Specifically, the gain of corticospinal pathway was altered such that a greater level of muscular activation was
produced with the same amount of cortical input after training. The effects of changing the firing properties of spinal motoneurons are likely to be expressed on each occasion that the adapted motoneurons are used. The generalized nature of such adaptations is therefore quite distinct from the highly context dependent effects that result from motor learning. An adaptive mechanism that modifies the operational characteristics of spinal motoneurons may therefore be responsible for the success of skill generalization and retention observed during the current study.

Interestingly, the single action for which performance improvement was mediated by both increases in the rate of torque development and the decrease of directional deviation (Flx/Sup) demonstrated significant increases in target-acquisition times after the nonpractice period. The regression of performance in this action was associated with the return of directional deviation to levels observed during the initial practice session. It appears therefore that such performance adaptations were less stable than those that were brought about purely by increases in the rate of torque development. The distinction between these two practice-related performance adaptations is consistent with previous evidence that has suggested the existence of separate neural mechanisms that produce modifications in the speed and accuracy of movements (Hikosaka et al. 2002). In this study, we used cursor path deviation as a measure of the extent to which the production of joint torques is appropriately coordinated for the task. This assumption follows from work demonstrating that straight effector trajectories are a central feature of human limb movements (Flanagan and Rao 1995; Flash and Hogan 1985; Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994) and is supported by data from the current study that demonstrate an association between a decrease in path deviation during coupled flexion and supination, and changes in the relative timing of agonist muscle activation. We consider it likely that improvements in the coordination of joint torques or muscle forces represent a relatively complex method of adaptation (in that many variables must change) compared with increases in the rate of agonist muscle recruitment. Serrien et al. (2002) demonstrated that interference during the consolidation period in a bimanual coordination task occurred as a function of coordinating complexity. It is unknown at this stage whether the complexity of adaptive mechanisms governs their stability in the same manner on discrete, unimanual tasks, although the current results would support this supposition.

In summary, the performance improvements observed during the current experiment were primarily associated with increases in the rate of agonist muscle recruitment and, consequently, in the rate of torque development in each target direction. Task-related increases in the contribution of bifunctional muscles were observed in both single and dual df variants of the task, suggesting that changes in the organization of muscle synergies during practice were designed to facilitate the rate of increase in agonist recruitment. We demonstrated that the control of isometric tasks involving many muscles may be simplified by grouping muscles into synergies that are each driven with a distinct control command. It also appears likely that the CNS attempts to reduce the number of muscle synergies during skill acquisition, thus further simplifying the control problem. Increasing the rate of recruitment of all agonist muscles during practice appears to be a method of adaptation capable of improving performance on this type of isometric task set and offers benefits over other potential modes of adaptation (synergistic reorganization) in terms of the generalization and retention of acquired skill.

**References**


