

## RESEARCH ARTICLE

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# A multimuscle state analysis of adult motor learning

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**Abstract** We introduce a new EMG state analysis to test two competing hypotheses about the role of muscle coactivity in learning a complex, multijoint reaching movement. Following Bernstein, one hypothesis is that as a task is learned, coactivity should decrease as degrees of freedom are released and limb stiffness is reduced. An alternative hypothesis is that as movement speed increases with learning, muscle coactivity should increase, possibly to stabilize joints against high inertial forces. Three participants performed a vertical reaching movement identical to that used by Schneider et al. We monitored the activity of four arm and shoulder muscles as participants completed 100 practice trials. Each frame of EMG activity was assigned to one of 16 possible combinations of the four monitored muscles based on an on-off activation threshold. This analysis yielded a time-based summary of muscle coactivity during the movement and across practice trials. Results of the state analysis supported the second hypothesis. As participants decreased their movement times over practice, coactivity increased – participants used more three- and four-muscle coactivity states. Changes were especially dramatic during the braking phase of the Up and Down portion of the vertical movement. When participants performed deliberately slow movements after speeded practice, three- and four-muscle coactivity was suppressed. We suggest that increased use of muscle coactivity may serve to counteract unwanted rotational forces generated during fast movements.

**Key words** Motor learning · Muscle coactivity · EMG · Movement speed

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## Introduction

In their everyday activities, humans use a dazzling array of complex movements that are dynamically adapted to changing task demands. All of these movements require coordinating multiple muscles spanning multiple joints. Furthermore, such coordination patterns are *learned*. In this paper, we use a new method for analyzing EMG waveforms to examine how multimuscle activity changes as adults learn a complex, multijoint task.

Over the past several decades, researchers have made considerable progress in characterizing the muscle patterns underlying simple single-joint movements such as elbow flexions (e.g., Corcos et al. 1989; Gottlieb et al. 1989a, 1989b; Mustard and Lee 1987; Wierzbicka et al. 1986). Our understanding of the muscle patterns underlying multijoint movements is much less far advanced, although recent studies are closing this gap (e.g., Almeida et al. 1995; Buneo et al. 1994; Flanders 1991; Flanders and Herrmann 1992; Gottlieb et al. 1996). One reason for this disparity is the complexity of multijoint movements. Even a simple reach involves dozens of muscles spanning the shoulder, elbow and wrist joints, including several muscles which span two joints.

A second challenge when studying multijoint movements is the redundancy of the neuromuscular system. The muscles of the arm generally contribute to force generation across a broad array of movement directions and at different times during a movement (Buchanan et al. 1986; Flanders 1991; Flanders et al. 1994; Flanders and Soechting 1990). Constraints are required, therefore, to select and coordinate the directional contributions of the many muscles involved in a complex arm movement.

One way to constrain this redundancy is to link muscles together into a muscle synergy – a temporally coherent and task-dependent grouping of muscles controlled by the CNS as one degree of freedom (Bernstein 1967; Kugler et al. 1980). For instance, Flanders and Soechting (1990) found that medial deltoid and posterior deltoid showed tightly coupled activity when participants produced isometric forces at the wrist in some directions.

For other force directions, medial deltoid and anterior deltoid showed tightly coupled activity. The activity of these muscles was tightly coupled despite the different mechanical actions of the individual muscles. In addition, the coupling changed as the posture of the arm and direction of force changed. These results demonstrate that muscles are functionally linked by the CNS relative to task parameters such as movement and force direction (Buchanan et al. 1986).

But how are these coactivity synergies learned? Bernstein (1967) proposed that, early in learning, redundancy might be constrained by freezing out degrees of freedom via muscle coactivity. Later in learning, these restrictions could be relaxed, allowing reductions in coactivity in favor of more specific multimuscle sequencing. Finally, multimuscle activity could become more economical as people use passive forces such as reactive and inertial forces. For instance, during the braking of slower movements, active muscle contraction might be replaced by the passive stretch properties of muscles (Lestienne 1979).

One hypothesis that emerges from these ideas is the following: muscle coactivity should *decrease* with skill learning as degrees of freedom are freed up and limb stiffness is reduced. While this hypothesis has not been explicitly tested, data from Moore and Marteniuk (1986) provide some support for this claim. Moore and Marteniuk (1986) found that agonist and antagonist activity overlapped considerably early in learning relative to later learning trials in a forearm extension task. Such overlap would increase joint stiffness, possibly freezing out degrees of freedom and stabilizing the movement.

Nevertheless, data from several other single-joint learning tasks show that as *speed* increases during learning, agonist/antagonist overlap becomes *more* likely. This may be due to an increase in the amount of antagonist activity (Hobart et al. 1975) or to an increase in the amplitude of both the agonist and antagonist accompanied by an earlier onset of the antagonist (Corcos et al. 1993; Darling and Cooke 1987). Changes in coactivity as movement speed increases may serve to stabilize the arm against high inertial forces generated during fast movements (Schneider et al. 1989). From these single-joint data, a second competing hypothesis emerges: muscle coactivity should *increase* with skill learning in *speeded* learning tasks.

#### Measuring changes in multimuscle activity

To date, no studies have investigated these two competing coactivity hypotheses in a multijoint task. We contend that this is due, in part, to limitations in the analysis methods commonly used to measure changes in EMG activity over learning. What is needed to test these hypotheses is a method that captures changes in the *coactivity* of multiple muscles.

Perhaps the most promising method used to study muscle activity in multijoint movements is principal

components analysis (PCA). PCA has strong appeal in that one does not have to identify discrete EMG bursts to analyze patterns of muscle activity. As such, this approach avoids the contentious issue of thresholding EMG waveforms. Nevertheless, PCA has two limitations in the context of the present paper. First, PCA is limited when applied to learning because data must be grouped over trials. Without a priori information about when learning changes occur, such grouping could cut across a period of change, thereby obscuring how muscles change over learning. A second concern is that PCA has been primarily used to extract components from single muscle data. Thus, this method alone cannot determine if muscle coactivity increases or decreases with learning. Soechting and Lacquaniti (1989) used an interesting combination of PCA and cross-correlation to examine multimuscle activity. While this is also a promising method, its complexity would be amplified when applied to complex multijoint movements where the number of PCA waveforms to be compared pairwise could be quite large.

Other methods currently used to analyze EMG data require the selection of single bursts of muscle activity. Then, burst characteristics such as duration and amplitude can be analyzed. Usually, these characteristics are examined individually for each muscle. The method we describe herein requires the selection of single bursts of activity; however, we offer a new way to look at changes in coactivity across multiple muscles based on identifying *coactivity states*. To do this, we identify, for every frame of EMG data, a state vector which indicates whether each muscle is “on” or “off.” The state vector provides an operational definition of coactivity for it indicates which muscle combination is seen at each moment in time. Hadders-Algra et al. (1996) used a related method to identify patterns of coactivity in postural muscles in sitting infants. Our state analysis differs from theirs in its improved temporal resolution. The method used by Hadders-Algra et al. (1996) was not time based – they identified only one predominant coactivity pattern per trial.

#### Specific goals

In the present report, we test two competing coactivity hypotheses using the state analysis. According to the first hypothesis, muscle coactivity should *decrease* over learning as more economical patterns of coactivity are learned. Thus, this hypothesis predicts that over learning, states with only one or two muscles “on” at a time should become more frequent. According to the second hypothesis, muscle coactivity should *increase* with learning as movement speed increases, given the constraints placed on force production during fast movements. Thus, this hypothesis predicts that as speed increases over learning, states with three, four, etc., muscles “on” at a time should become more frequent.

To test these hypotheses, we measured muscle activity in a task first studied by Schneider et al. (1989).

This is one of the few three-dimensional, unconstrained, multijoint learning tasks that have been studied at a neuromuscular level. Here we examine the utility of the state analysis by asking whether this method offers new insights into what participants learn in this task beyond the results reported by Schneider and colleagues.

In their original report, Schneider et al. (1989) investigated how intersegmental dynamics and muscle activity changed as adults practiced a maximal-speed movement with their non-dominant hand. Participants in this study started each movement at a lower target, rounded a T-shaped barrier, entered an upper target, and then moved back down around the barrier to the lower target. Over practice, movement times decreased from about 900 ms to 670 ms. Associated with this speed increase was an increase in biceps and posterior deltoid activity as the hand approached the upper target. This served to slow the hand and speed up the reversal phase of the movement. In addition, Schneider et al. reported a more precise alternation of triceps with biceps and anterior deltoid with posterior deltoid over practice, and a decrease in deltoid burst durations. This suggests that deltoid coactivity decreased with increasing speed, although coactivity was not explicitly quantified.

Given that Schneider et al. (1989) did find changes in muscle activity related to movement speed, we modified their experiment slightly in the present report. At end of the training trials, we added five “slow” trials in which participants were asked to move at a “comfortable, relaxed pace.” This allowed us to compare muscle coactivity on the slow trials with activity early and late in practice to determine if coactivity changes over learning were speed dependent.

## Materials and methods

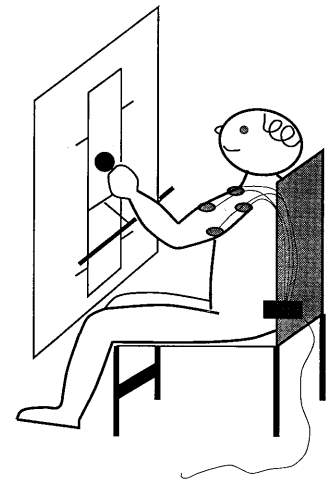
### Participants

Two females and one male ( $25.3 \pm 5.1$  years) participated in this study. All participants were right handed. Participants were recruited from the student population at Indiana University. All participants gave informed consent.

### Apparatus

The details of the experimental apparatus were identical to those used by Schneider et al. (1989). Thus, only some measurement details will be repeated here. Participants sat in a straight-backed chair facing a plane covered with gray foam padding to eliminate any reflections that might interfere with the motion analysis system (see Fig. 1). To minimize trunk movements, we secured participants to the chair back with a soft, wide fabric band. An upper target was positioned level with each participant's shoulder joint, while a lower target was positioned such that each participant could reach the lower target with a comfortable shoulder and elbow angle. There was a T-shaped barrier midway between these two targets. The stem of the barrier was  $3.5 \times 21.5$  cm, and its cross piece was  $0.3 \times 32$  cm. At the center of the Plexiglas sheet was a  $7 \times 80$ -cm slit that restricted the left-right motion of the participants as they entered the upper or lower targets. Thus, we constrained participants' hand paths near the two targets and

Fig. 1 Experimental apparatus



around the barrier. Otherwise, participants' movements were unconstrained.

Behind each target, we placed a photocell that emitted a beam of light (approx. 4 mm radius) across the center slit in the Plexiglas. The signal from these photocells was sent through a tone generator which was converted from analog to digital at 1500 Hz using a Watscope A/D converter. Participants moved to the upper and lower targets by breaking these light beams with a small, circular metal plate (3.7 cm radius) connected to a wooden-dowel handle. Given the size of the metal plate relative to the size of the light beams, this task did not require a high degree of accuracy. Interrupting each beam produced an audible clicking noise and changed the tone frequency sent to the Watscope. Thus, signals from the photocells could be analyzed later to determine precisely when participants arrived at and left the lower and upper targets. A four-camera Watsmart motion-analysis system was used to record participants' movements. Four infrared-emitting diodes (IREDS) were placed on each participant, one below the third metacarpophalangeal joint and one at the joint centers of the wrist, elbow, and shoulder.

Surface muscle activity was recorded at 1500 Hz over the bellies of the following arm muscles: posterior deltoid (PD), anterior deltoid (AD), biceps (BI), and the long head of the triceps (TRI). Muscle activity was recorded using Therapeutics Unlimited model D-100 preamplified surface electrodes. Signals from these preamplified electrodes were sent through a Therapeutics Unlimited EMG 544 amplifier and then converted on-line from analog to digital using a Watscope A/D converter.

### Procedure

Each participant performed 3 *baseline* trials, 100 successful *practice* trials, 5 successful *slow* trials, and then 3 additional *baseline* trials. Each block of *baseline* trials consisted of two trials during which participants remained completely motionless with arms resting in their laps, and one trial during which participants held the paddle in the lower target. The *practice* and *slow* trials consisted of a movement with the non-dominant (left) hand from the lower target, up around the barrier to the upper target, and then down around the barrier back to the lower target, holding the paddle steady in the lower light beam for 2–3 s at the end of the movement. A trial was unsuccessful when the participant either missed one of the targets (failed to break the light beam), bumped the barrier, or failed to hold the paddle in the lower light beam at movement termination. *Practice* and *slow* trials differed in the instructions we gave to participants. For the *practice* trials, we asked participants to move as quickly as possible, while for the *slow* trials we asked participants to move at a comfortable, relaxed pace. During the block of *practice* trials, participants' muscle activity

**Table 1** Thresholds (SD) (mV) for each participant and muscle

Participant	Muscle	Threshold (SD)	SD as %Max
KJ	PD	33.3 (2.1)	0.27
	AD	38.2 (3.6)	1.01
	BI	33.6 (2.9)	0.21
	TRI	45.5 (4.7)	0.47
LS	PD	31.0 (3.3)	0.37
	AD	38.5 (6.6)	0.71
	BI	31.6 (2.5)	0.37
	TRI	56.4 (10.4)	3.47
SK	PD	29.7 (4.3)	0.79
	AD	30.0 (2.7)	0.35
	BI	29.5 (5.3)	1.51
	TRI	55.0 (8.2)	2.98

was recorded on *three randomly selected trials of every block of ten successful trials*. Thus, we analyzed *30 out of 100 practice trials* for each participant.

The experimenter began each *practice* or *slow* trial by giving the participant a 3-2-1 countdown. The participants were allowed to begin moving any time after the experimenter completed the countdown. We emphasized that reaction time was not critical, and, in general, participants began moving within 1 s after the countdown. After each trial, the experimenter gave participants feedback about their movement speeds using a standard stopwatch.

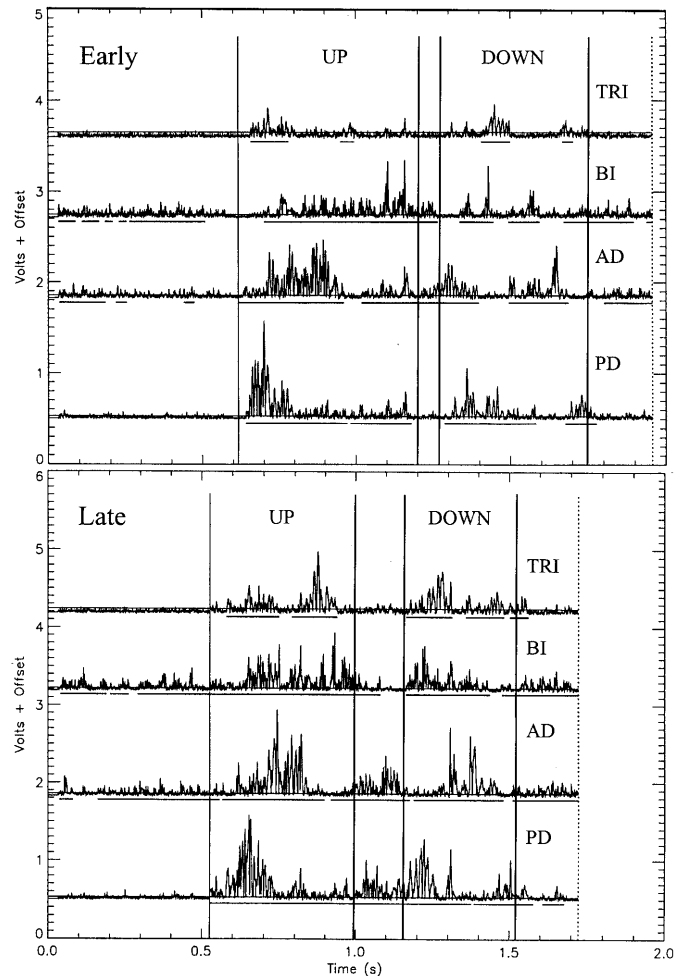
#### Methods of analysis

Data from the upper and lower light beams were used to divide each movement into three phases: Up phase (when the paddle left the lower target and entered the upper target), Reversal (when the paddle entered and then left the upper target), and Down phase (when the paddle left the upper target and entered the lower target). The light beams were also used to measure movement times on each trial. Finally, the light beam data were examined to make sure participants successfully completed each trial. One participant, SK, missed the upper target on recorded practice trials 2 and 9. These trials were eliminated from all further analyses for this participant.

EMG data were analyzed in five steps. First, we subtracted the mean and full-wave rectified each EMG signal. Second, each EMG signal was transformed into an on-off signal. To determine on-off activity, a 50-ms window was moved frame by frame across each EMG waveform. If the averaged EMG activity within a window exceeded a noise threshold, then the center value of that window was assigned a 1 (on).

A noise threshold was computed for each muscle using the 6 s of EMG data from the motionless baseline trials before and after each practice session (see DeLuca 1993). After first inspecting the baseline trials to make sure there was no spiking activity or EMG bursts, the threshold for each muscle was computed by averaging the maximum values across 1-s bins. The thresholds and standard deviations for each participant and muscle are presented in Table 1. This table also shows standard deviations expressed as a percentage of maximal activity. It is clear from Table 1 that the baseline levels of noise were relatively stable across bins (low standard deviations) and varied within a small percentage of the signal range. In addition, threshold values were similar across participants, demonstrating that the amount of noise in the recording equipment was small and stable across collection sessions.

In the third step of our EMG analysis, we identified the phasic EMG activity associated with movement onset. This was a concern since participants often had some tonic muscle activity before movement initiation as they maintained a hovering posture at the lower target (see BI and AD activity prior to the Up phase in Fig.



**Fig. 2** Exemplar plots of rectified EMG activity for one early (recorded trial 6) and late (recorded trial 20) practice trial. The top waveform in each plot was recorded from the triceps, followed by biceps, anterior deltoid, and posterior deltoid activity. Vertical lines denote the Up and Down phases. Horizontal lines below the wave forms indicate when each muscle was “on”

2). When we examined the EMG activity associated with movement onset, we noted that PD generally initiated the upward movement with a clear burst (see also Schneider et al. 1989). TRI initiation also occurred, although much less frequently. Thus, EMG onset was based on the PD or TRI burst that just preceded the triggering of the lower light beam at the start of the Up phase.

Next, we determined the *muscle coactivity* state associated with each frame of EMG activity. This state analysis is a modification of an analysis first used to study changes in cockroach gait (Cocatre-Zilgien and Delcomyn 1993). Once EMG waveforms have been transformed into on-off signals (0=off, 1=on), the state of the neuromuscular system at any point in time can be characterized by a vector consisting of a 0 or 1 for the activity of each recorded muscle. In the present study, we measured the activity of four arm muscles. Thus, there were  $2^4$  or 16 possible muscle states ranging from [0000] – no muscles active – to [1111] – all muscles active. For example, if only the PD were active for a particular frame, the state vector for that frame would be [1000]. If both PD and BI were active, the state vector would be [1010]. The frequency of occurrence of each state and the timing and ordering of state sequences over repetitions of an action can then be analyzed both qualitatively and quantitatively, revealing *which* muscles work together and *when* they work together over learning.

**Table 2** Coactivity states that met the 30% criterion in one bin on at least six trials

Participant	Up phase	Rev phase	Down phase
KJ	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , PD/BI/TRI, PD/BI, AD/BI	PD/BI/TRI, AD/BI	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , PD/BI/TRI <sup>a</sup> , AD/BI <sup>a</sup> , PD/BI
LS	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , PD/BI/TRI, PD/AD/TRI	All 4, PD/AD/BI, PD/BI/TRI	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , PD/BI/TRI <sup>a</sup> , AD/BI <sup>a</sup> , PD/AD
SK	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , AD/BI	PD/AD/BI, AD/BI, PD/AD	All 4 <sup>a</sup> , PD/AD/BI <sup>a</sup> , PD/BI/TRI <sup>a</sup> , AD/BI <sup>a</sup> , PD/AD, PD/BI

<sup>a</sup> Coactivity states common to all three participants within a given movement phase

In the final EMG analysis step, a set of inclusion criteria were developed to select which muscle states to include in all further analyses. Inspection of the state data revealed that many states did not occur at all, and some states occurred quite sporadically. Thus, we identified which states showed some “coherent” activity at roughly the same point in the movement on several trials. To identify coherent activity, state data were normalized to the Up, Rev, and Down movement times. This aligned states that occurred when the hand was in roughly the same spatial location. Next, the Up and Down phases were divided into five equal time bins, while the Rev phase was divided into four equal time bins. For each bin, we identified which states occurred for at least 30% of a bin’s duration. This was equivalent to about 25 ms for the Up and Down phases, and about 12 ms for the Rev phase. *All states that met the 30% criterion in one bin on at least six recorded trials were included in data analysis.*

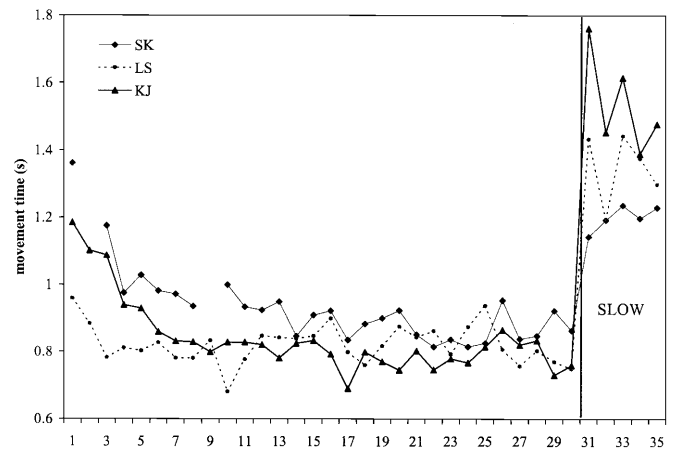
It is important to note that these inclusion criteria were very conservative, consistent with our goal of detecting subtle changes in state activity over learning. Despite these inclusive criteria, however, many coactivity states did not occur at all; participants used only a limited number of the possible combinations. Table 2 shows the seven states that did meet the inclusion criteria during at least one movement phase for one or more participants. Table 2 reveals not only a reduction in the state space, but also a good deal of consistency across participants. Two states – All 4 and PD/AD/BI – met the criteria for all three participants in the Up phase, while four states – All 4, PD/AD/BI, PD/BI/TRI, and AD/BI – met the criteria for all three participants in the Down phase.

## Results

### Movement times

Figure 3 shows that participants decreased their movement times as they practiced the task. Movement times decreased significantly over the recorded practice trials based on a repeated measures ANOVA with practice trials as a within-subject factor ( $F_{(54,27)}=3.70$ ,  $P<0.001$ ). Both KJ and SK, who were the slower movers initially, showed large reductions in movement time across the first 9 recorded practice trials, i.e., across approximately the first 30 trials. LS showed less change – she was moving quickly from the beginning. Finally, all participants increased their movement times during the five slow trials. KJ and LS moved much more slowly during these trials, while SK moved about as slowly as she did during the first few practice trials.

Further analysis indicated that these changes in movement time were not distributed equally over all phases of the movement. A repeated measures ANOVA on each



**Fig. 3** Movement times in seconds for each participant across the practice (recorded trials 1–30) and slow trials. The vertical line indicates when the task instructions were changed. SK is missing data from recorded trials 2 and 9

phase (Up, Rev, or Down) separately revealed a significant decrease in movement time over recorded practice trials in the Up ( $F_{(54,27)}=1.81$ ,  $P<0.05$ ) and Down ( $F_{(54,27)}=2.98$ ,  $P<0.001$ ) phases. There was not, however, a significant decrease during the Rev phase ( $F_{(54,27)}=1.41$ , NS). This is not surprising given that the Rev phase was, on average, quite short (mean MT=112 ms). By contrast, the Up and Down phases lasted, on average, 380 and 457 ms respectively.

In general, these reductions in movement time over practice were comparable to changes reported by Schneider and colleagues (1989). Table 3 shows a comparison of average movement times across trial blocks from the present study and from Fig. 2 of Schneider et al. (1989). The 190-ms reduction in MT across the first 20 recorded practice trials in the present study was comparable to the 150-ms reduction across the first 25 trials in Schneider et al.; however, there was an additional 50-ms reduction in the present study between trials 20 and 30. Across the remainder of the practice trials, participants in the present study showed a slight MT plateau, with gradual reductions thereafter, while participants in Schneider et al. showed a gradual reduction in MT followed by a plateau at the end of practice.

**Table 3** Average movement times (MTs) (ms) from the present study and Schneider et al. (1989). Note: MTs from Schneider et al. were estimated from Fig. 2

Trials	MTs (Spencer and Thelen)	MT differences	Trials	MTs (Schneider et al.)	MT differences
0–10	1100		1, 2, 9, 10	900	
10–20	910	190	–	–	
20–30	860	50	24, 25	750	150
40–50	850	10	44, 45	710	40
70–80	820	30	70, 71	670	40
90–100	790	30	99, 100	670	0

### Single-muscle EMG activity during the early vs late practice trials

To compare our EMG data with data from Schneider et al. (1989), we first describe changes in the activity of single muscles early vs late in practice, using exemplar data from one participant. This description will also highlight how each muscle was being activated to produce the coactivity states described in the next section. Figure 2 shows SK's EMG activity for an early trial (recorded trial 6) and a late trial (recorded trial 20). The underscore beneath each EMG trace indicates when each muscle was "on" across these two trials.

The first indication of a change in muscle activation can be seen approximately halfway through the Up phase in each example. Early in practice, SK used AD activation to move her hand around the barrier to the upper target and a lengthening BI contraction to slow down prior to the reversal. Later in practice, SK added a TRI burst to actively extend her arm toward the target. In addition, there was an increase in PD activity during the Rev phase. This served to both slow the movement and actively reverse the direction of the hand at the upper target.

There were also EMG changes over practice during the Down phase. There was less BI and TRI activity at the beginning of the movement early vs late in practice. The increase in TRI activity in the late example was even more apparent after the hand rounded the barrier (approximately halfway through the Down phase). As in the Up phase for the late trial, there was a second TRI burst that served to actively extend the arm toward the target.

These changes in individual muscle activity early vs late in practice share some similarities with results reported by Schneider and colleagues (1989). For example, these researchers reported an increase in PD and BI activity late in practice as the hand reversed directions at the upper target. This can be clearly seen in Fig. 2. Nevertheless, other results were not observed. Schneider and colleagues reported more precise alternation between BI and TRI as well as AD and PD late in practice. While there is some alternation of AD and PD in the late example from Fig. 2, there are also instances of overlapping bursts. By contrast, the BI and TRI bursts appear to be more overlapping than alternating throughout the late example.

To further compare results across studies, we conducted an analysis of mean burst durations for each mus-

cle. Schneider and colleagues (1989) reported a significant decrease in deltoid burst durations across the practice trials. We did not replicate this finding. A repeated measures ANOVA for each muscle with recorded practice trials as a within-subjects factor showed no significant changes in mean burst durations for any muscle.

### Description of muscle state activity

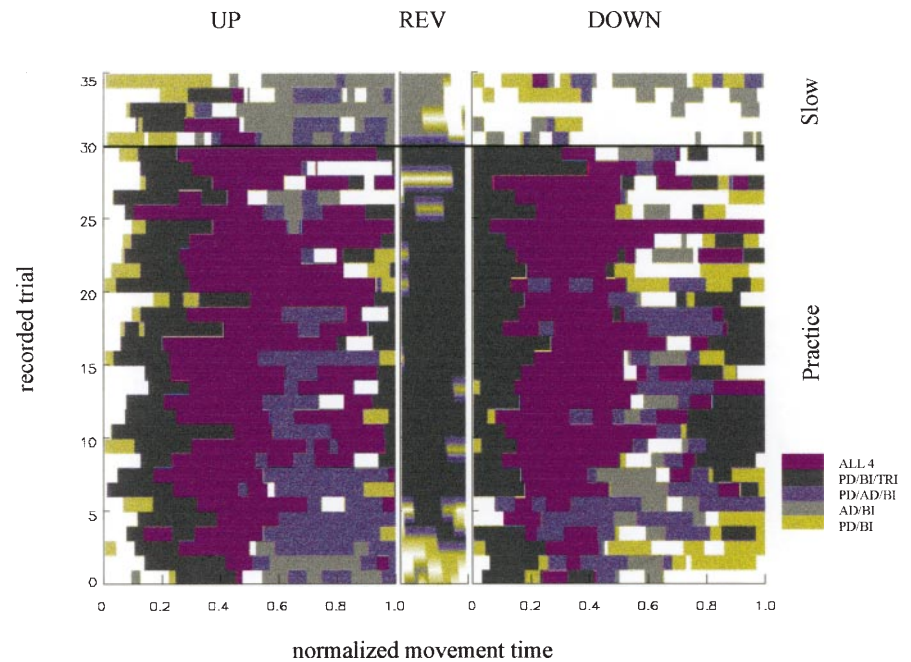
The goal of the muscle state analysis was to test the competing hypotheses about how muscle coactivity would change over practice as speed increased in this complex, multijoint task. Figure 4 illustrates how one participant's (KJ) muscle states changed across the *practice* (recorded trials 1–30) and *slow* trials (recorded trials 31–35). The different colors in Fig. 4 represent the different states that met the inclusion criteria (see "Methods of analysis"). Along the *x*-axis, we have plotted which states occurred as each movement progressed through the Up, Rev, and Down phases. Along the *y*-axis, we have plotted state activity across the different recorded trials. Because movement times were changing across the three movement phases, we normalized state activity to the Up, Rev, and Down movement times (*x*-axis). This served to line up when each state occurred across trials.

In the next three sections, we discuss the state data depicted in Fig. 4 for each phase separately. Within each section, we first highlight the general sequence of state changes characteristic of the phase. Next, we discuss how state activity changed across the *practice* trials. Finally, we discuss how state activity during the *slow* trials compared to activity during practice. We focus on the exemplar data for KJ throughout. It is important to note, however, that the state data for LS and SK were quite comparable.

### Up phase

State activity during the Up phase was dominated by a sequence of four states. There was an initial period of PD/BI/TRI (dark-gray band in Fig. 4) followed by the coactivity of All 4 muscles (purple band), PD/AD/BI (blue band), and then a return to All 4. The sequence of state activity as KJ rounded the barrier (midway through the Up phase) reflects the two-burst TRI activity described in Fig. 2 – All 4 muscles were coactive during the first TRI burst, followed by PD/AD/BI when TRI ac-

**Fig. 4** State activity for one participant across the practice and slow trials (y-axis) as the movement progressed through the Up, Rev, and Down phases (x-axis) (each color represents a different muscle state: purple All 4, dark gray PD/BI/TRI, blue PD/AD/BI, light gray AD/BI, green PD/BI, white no state activity or state activity that did not meet the inclusion criteria). State activity in each phase has been normalized to the Up, Rev, and Down movement times to line up when states occurred across trials. The horizontal line at recorded trial 30 indicates when the task instructions were changed



tivity ceased, followed by All 4 muscle coactivity during the second TRI burst.

Across the practice trials in Fig. 4, several changes in state activity are apparent. While the first band of All 4 coactivity is clearly present early in practice, the second band does not emerge until recorded trial 9. Prior to this trial, the second half of the Up phase was dominated by AD/BI (light-gray band) and PD/AD/BI (blue band). Thus, there was an *increase* in muscle coactivity over practice. This increase mirrors the *decrease* in movement times shown in Fig. 3 – movement times for KJ showed a sharp drop after the first few recorded trials and then began to plateau around recorded trial 9.

One critical question is what happened to muscle state activity when movement speed decreased during the *slow* trials. The data in Fig. 4 illustrate that muscle coactivity *decreased* on these trials and returned to patterns of coactivity present early in practice. The most dramatic change was a decrease in All 4 coactivity, particularly after KJ rounded the barrier. In place of All 4 coactivity, he used a mixture of PD/AD/BI and AD/BI activity.

#### Rev phase

Due to the brief duration of the Rev phase, state activity in this phase generally reflected the activity at the end of the Up phase. The frequent use of PD/BI/TRI activity by KJ at the end of the Up phase continued into the reversal (see dark-gray band in Fig. 4). Early in practice, KJ used some PD/BI (green band) coactivity. During the slow trials, muscle coactivity *decreased*, consistent with data from the Up phase. Specifically, KJ decreased his use of PD/BI/TRI in favor of AD/BI activity (see light-gray band in Fig. 4).

#### Down phase

The state sequence during the Down phase generally mirrored the sequence from the Up phase. The Down phase began with PD/BI/TRI (dark-gray band in Fig. 4), followed by the coactivity of All 4 muscles (purple band), and then PD/AD/BI (blue band). There is a clear difference across the Up and Down phases, however – state activity during the second half of the Down phase was more variable. Across the practice trials, there was a shift in state activity after recorded trial 9 – KJ primarily used PD/BI/TRI (dark-gray band) activity to end the movement. This increase in PD/BI/TRI activity reflects the emergence of the second TRI burst discussed previously. Finally, during the *slow* trials, the coactivity of All 4 muscles decreased dramatically. This state was generally replaced by AD and BI states.

#### Multiple regression analysis of muscle state activity

Participants used several three- and four-muscle coactivity states more frequently as movement speed increased over practice, while several two- or three-muscle states became less frequent. In addition, the change in task instructions produced a rapid reorganization of state activity and a reversion to patterns common early in practice. Thus, movement speed and state activity appear to be closely related. To quantify this relationship, we conducted a multiple regression analysis for each participant and movement phase separately with the Up and Down movement times as criterion variables. We did not conduct regression analyses for the Rev phase because movement times did not show a significant change during this phase over practice. Included as predictors in

**Table 4** Durbin-Watson statistic ( $d$ ) with lower ( $d_L$ ) and upper ( $d_U$ ) limits ( $p < 0.05$ ), and the regression coefficient ( $p$ ) from a first-order autoregression on the residuals from each multiple regression analysis. Lower and upper limits for  $d$  were computed using tables from Johnston (1972)

Participant	Movement phase	$d_L$	$d_U$	$d$	$p$
KJ	Up	1.10	1.87	2.62 (1.38) <sup>a</sup>	-0.33
	Down	1.10	1.87	1.22	0.29
LS	Up	1.16	1.80	2.35 (1.65) <sup>a</sup>	-0.20
	Down	1.10	1.87	1.85	0.06
SK	Up	1.19	1.73	1.37	0.22
	Down	1.00	1.94	1.36	0.14

<sup>a</sup>For convenience, the value of  $(4-d)$  is reported in parentheses

**Table 5**  $R^2$  and  $F$  change statistics for ordered regression analyses predicting movement times from the Up and Down phases. Note: all  $F$  change values specified were significant at  $p < 0.05$

Participant	Phase	Order	$R^2$	$F$ change <sub>(df1, df2)</sub>	Order	$R^2$	$F$ change <sub>(df1, df2)</sub>
KJ	Up	Slow	0.77		Slow	0.77	
		4	0.84	13.72 <sub>(1,32)</sub>	2	0.87	10.98 <sub>(2,31)</sub>
		3	0.87	NS	3	0.90	4.97 <sub>(2,29)</sub>
		2	0.90	4.90 <sub>(2,28)</sub>	4	0.90	NS
	Down	Slow	0.82		Slow	0.82	
		4	0.87	11.79 <sub>(1,32)</sub>	2	0.84	NS
		3	0.89	NS	3	0.85	NS
		2	0.90	NS	4	0.90	13.20 <sub>(1,28)</sub>
SK	Up	Slow	0.51		Slow	0.51	
		4	0.71	20.75 <sub>(1,30)</sub>	2	0.51	NS
		3	0.72	NS	3	0.65	12.03 <sub>(1,29)</sub>
		2	0.72	NS	4	0.72	6.69 <sub>(1,28)</sub>
	Down	Slow	0.31		Slow	0.31	
		4	0.58	19.46 <sub>(1,30)</sub>	2	0.51	3.68 <sub>(3,28)</sub>
		3	0.63	NS	3	0.59	NS
		2	0.64	NS	4	0.64	NS

each regression equation were four sets of variables: a “slow” dummy variable that captured the change in instructions (0=fast, 1=slow) and all of the four-, three-, or two-muscle coactivity states that met the inclusion criteria for each participant and phase (see Table 2).<sup>1</sup> For each included state, we used the proportion of time the state occurred during each movement phase on each recorded trial as the predictive measure.

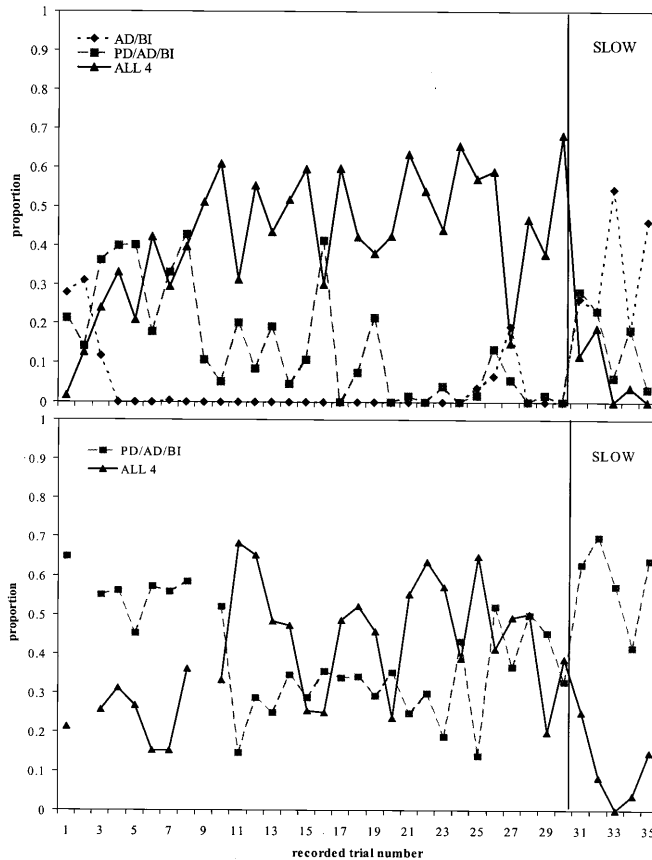
Given that we had no a priori ordering of the sets of predictors, we conducted two regression analyses for each participant and phase. In the first, the sets were ordered slow, 4, 3, and 2. In the second, the sets were ordered slow, 2, 3, and 4. The slow variable was first in both analyses, because our goal was to determine which muscle states contributed significantly to the prediction of movement time above and beyond what could be accounted for by the change in instructions.

Before describing the results, it is important to consider whether the residuals of these analyses showed serial correlation. If serial correlation is present,  $t$ -ratios used for estimating the significance of individual parameters in the regression equation will be seriously inflated (see Ostrom 1990). We examined this issue by computing the Durbin-Watson statistic ( $d$ ) for each regression equation.

The Durbin-Watson statistic tests the hypothesis of no serial correlation ( $H_0$ ) against the hypothesis of positive serial correlation. Values less than a lower limit lead to rejection of  $H_0$ , while values above an upper limit lead to acceptance of  $H_0$ , i.e., no serial correlation. Table 4 shows the Durbin-Watson statistics and associated lower and upper limits for the six regression analyses we conducted. All of the  $d$  values are above the lower limit. Thus, it is likely that serial correlation is not a major problem in our analyses. However, strong conclusions are not possible because all of the  $d$  values are below the upper limit. Therefore, we also tested for the presence of serial correlation by computing the autocorrelation at lag 1 ( $p$ ) for each residual series. If  $p > 0.3$ , serial correlation is likely present and alternatives to least squares estimation should be considered (Griliches and Rao 1969; Hibbs 1974). The  $p$  values for all of our regression analyses were  $< 0.3$  with the exception of one value, which was 0.33 (see Table 4). Thus, our estimates of the regression parameters and their significance tests appear to be valid.

In Table 5 we report the percentage of movement time variance accounted for in each step of the regression analyses ( $R^2$ ) as predictor sets were added in different orders. In addition, Table 5 indicates all the predictor variable sets that accounted for a significant change ( $p < 0.05$ ) in the  $R^2$  value above and beyond the variance accounted for by the slow predictor (see  $F$  change statistics). LS

<sup>1</sup> One equation had only three sets of predictors (slow, 4, 3) – the equation for the Up phase for LS (see Table 3).

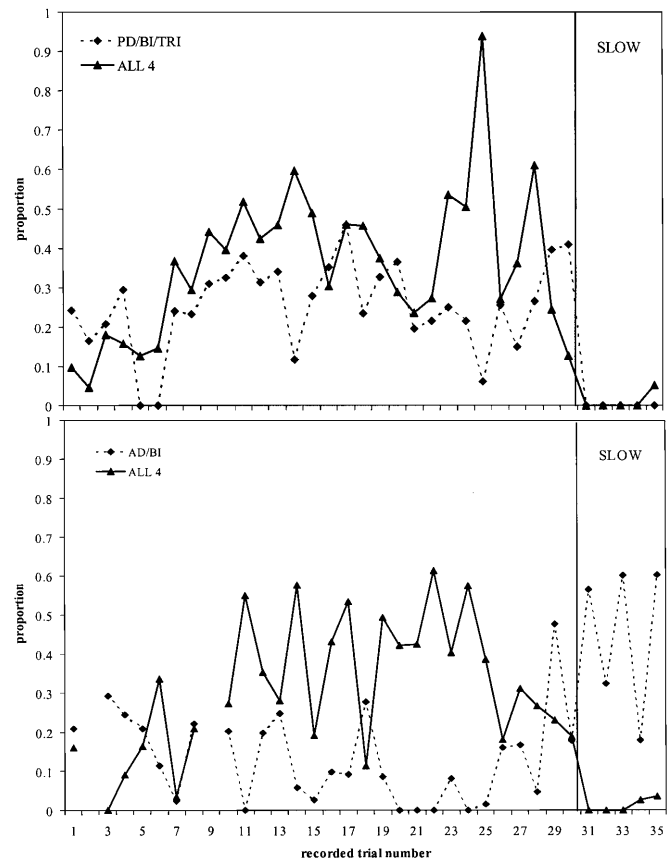


**Fig. 5** The proportion of Up movement time four-coactivity states occurred across the practice and slow trials for KJ (*upper panel*) and SK (*lower panel*). The states plotted in each panel accounted for a significant proportion of Up movement time variance in the regression analyses (see text). The vertical line indicates when the task instructions were changed. SK is missing data from recorded trials 2 and 9

showed few significant regression effects. Thus, her data will be reported in the body of the text.

Overall, muscle state activity accounted for a significant amount of movement time variance for both KJ and SK. Changes in the proportion of four-, three-, and two-coactivity states helped account for 90% of the variance in Up and Down movement times for KJ (see  $R^2$  value in Table 5), 72% of the variance in Up movement times for SK, and 64% of the variance in Down movement times for SK.

The central question of the regression analyses was how specific types of coactivity were related to movement time. Both KJ and SK showed a significant correlation between All 4 coactivity and movement time (see set “4” in Table 5). An examination of the standardized  $\beta$  weights for the regression equations revealed that All 4 state activity was *negatively* correlated with movement times for the Up and Down phases for both participants. A significant negative correlation between All 4 coactivity and movement time was also found for the slow, 4, 3, 2 ordering for LS in the Down phase ( $R^2=0.80$ ,  $F$  change<sub>(1,32)}=5.78). In addition to All 4 state activity, the proportion of two-muscle coactivity was significantly related to movement time. There was a significant  $R^2$  change associated with the ad-</sub>



**Fig. 6** The proportion of Down movement time three-coactivity states occurred across the practice and slow trials for KJ (*upper panel*) and SK (*lower panel*). The states plotted in each panel accounted for a significant proportion of Down movement time variance in the regression analyses (see text)

dition of the two-muscle coactivity states (set “2” in Table 5) to the Up phase regression for KJ and the Down phase regression for SK. For both participants, this was due to a positive correlation between AD/BI coactivity and movement time. Finally, three-muscle coactivity was significantly related to movement time. There was a significant  $R^2$  change associated with the addition of the three-muscle coactivity states (set “3” in Table 5) to the Up phase regression for KJ and SK and the Down phase regression for KJ. In the Up phase, PD/AD/BI activity was positively correlated with movement time, while in the Down phase for KJ, PD/BI/TRI was negatively correlated with movement time.<sup>2</sup>

The states that showed significant positive or negative correlations with Up movement times for KJ and SK are

<sup>2</sup> Some states contributed significantly in only one ordering due to the colinearity of states – an increase in the occurrence of one state was paralleled by a decrease in the occurrence of another state. When this occurs, one regressor is deemphasized in favor of the regressor that contributes most to the change in  $R^2$ . This was not a major concern herein since our goal was to identify *any* coactivity state that accounted for a significant proportion of movement time variance regardless of ordering.

illustrated in Fig. 5. This figure shows the proportion of time each of these states occurred during the Up phase for the recorded practice and slow trials. There is a clear increase in All 4 coactivity up to recorded trial 9 for KJ (upper panel) and trial 11 for SK (lower panel). By contrast, AD/BI and PD/AD/BI decrease across these early practice trials. AD/BI decreases to zero by recorded trial 4 for KJ, while PD/AD/BI decreases across the first 9 trials for KJ and the first 11 trials for SK. These patterns were reversed in the slow trials: All 4 coactivity returned to a low proportion, while AD/BI and PD/AD/BI increased.

During the Down phase, three states showed significant positive or negative correlations with movement times for KJ and SK. The proportion of time these states occurred across the practice and slow trials is shown in Fig. 6. As in Fig. 5, there is a steady increase in All 4 coactivity across the first 14 trials for KJ (upper panel) and the first 11 trials for SK (lower panel). The increase in All 4 coactivity for KJ was accompanied by an increase in the proportion of PD/BI/TRI, while SK showed a gradual decrease in AD/BI coactivity. Finally, as in Fig. 5, these trends reversed during the slow trials: All 4 and PD/BI/TRI coactivity was dramatically reduced, while the proportion of AD/BI increased for SK.

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## Discussion

In this paper, we used a new EMG state analysis to test two competing hypotheses. The first hypothesis predicted that muscle coactivity would *decrease* over learning as more economical patterns of coactivity were learned. The second hypothesis predicted that muscle coactivity would *increase* with learning as movement speed increased. Data from the state analysis clearly support the latter hypothesis.

Two participants in this study showed a significant increase in muscle coactivity across the first 9–11 recorded practice trials (approximately the first 30 trials). KJ and SK decreased the proportion of two- and three-muscle coactivity states across the Up and Down phases. As these states decreased with learning, two-, three- and four-muscle states increased. The increase in coactivity paralleled the steady decrease in movement times for these participants across the first 9–11 recorded trials. Indeed, the relationship between state activity and movement time was remarkably close. For example, KJ showed a rapid decrease in movement time across recorded trials 1–3 relative to the more gradual decrease across recorded trials 4–9. This shift was mirrored by changes in state activity. The proportion of AD/BI activity during the second half of the Up phase decreased dramatically across trials 1–3. This state was replaced by PD/AD/BI during trials 4–9. Finally, this three-muscle state was replaced by All 4 coactivity across the remaining practice trials.

Further support for the *increasing* coactivity hypothesis came from the rapid state changes during the slow tri-

als. When we changed the task instructions, all participants showed a dramatic increase in movement time. Associated with this increase was a reversion to patterns of coactivity common early in learning. Given the close parallels between muscle state and movement time changes across the practice and slow trials, we conducted multiple regression analyses with Up and Down movement times as the criterion variables and the proportion of time each state occurred as the predictor variables. Results of these analyses confirmed the close ties between coactivity states and movement times.

It is important to note that the patterns of coactivity in the final slow trials were not exactly the same as those seen earlier in the practice session. This could reflect two factors. Participants generally moved slower during the slow trials relative to the early practice trials. Thus, differences between the two trial types could reflect speed-related constraints on muscle coactivity. Indeed, individual muscle states – states in which only one muscle was active – were much more frequent during the slow trials. An alternative explanation is that differences were due to non-speed-related factors. For instance, during the first 100 trials, participants might have learned that some patterns of coactivity maximized “efficiency” or accuracy.

One critical question is what function the coactivity-speed relationship might serve. Flanders and Soechting (1990) have demonstrated that many muscles of the arm produce force in multiple directions and around multiple joints. Given this broad “tuning,” the activity of individual muscles often produces torque in unwanted directions. This would be especially likely as more torque is needed during fast movements. Muscle coactivity could serve to counteract such increases in unwanted rotational forces. Similarly, Schneider and colleagues (1989) have suggested that muscle coactivity could stiffen the shoulder and elbow joints, thereby counteracting increases in motion-dependent torques generated during fast movements. Both of these accounts are likely explanations of the increased muscle coactivity found in the present report.

Although muscle coactivity can serve several functions, it is important to question whether this was the most appropriate variable to measure in this task. For instance, there was an increase in All 4 coactivity during the second half of the Up phase that replaced PD/AD/BI activity. This was caused by a change in the activity of the triceps. Thus, an analysis of individual muscle activity might have revealed the same speed-related learning change, but in a more parsimonious way. Indeed, Flanders and Herrmann (1992) have reported that the activity of individual muscles changes as speed increases, primarily due to an increase in the phasic drive to individual muscles. Unfortunately, methodological differences between their study and the present report prevent strong comparisons across studies. In particular, we did not attempt to separate the phasic and tonic components of the EMG waveforms.

Several other coactivity changes would have been more difficult to detect in a single-muscle analysis. For

example, the reversion to the AD/BI state during the slow trials would have been difficult to detect because it involved the subtraction of two muscles – PD and TRI – from the All 4 state. Ultimately, the measures one uses should be driven by the hypothesis in question. Given that our main goal was to test competing hypotheses about muscle coactivity, the state analysis was appropriate. Nevertheless, it is an important question whether our description of state changes emerged from changes in the control of individual muscles or changes in the control of muscle states or “synergies.”

### Bernstein’s learning hypothesis

Although data from this study support the increasing coactivity hypothesis, it is premature to completely reject the alternative. The task studied herein explicitly emphasized changes in movement speed over learning. It is certainly possible that muscle coactivity would *decrease* in tasks that emphasize changes in movement accuracy. We contend that this important possibility can be tractably investigated in future studies using the state analysis. Such a study would not only contribute to the understanding of how muscle coactivity changes over learning in multijoint tasks. It would also shed light on the relationship between Bernstein’s learning hypothesis and multimuscle activity.

Bernstein’s ideas are often translated into hypotheses about muscle coactivity. Nevertheless, there is disagreement about what Bernstein’s ideas imply at this level of analysis. For instance, it is not clear how to translate Bernstein’s proposal that constraints on degrees of freedom become more “economical” over learning. One possibility, emphasized above, is that muscle coactivity decreases over learning, thereby economizing force production. This is consistent with Bernstein’s proposal that the CNS strives to prevent the waste of “superfluous force in extinguishing reactive phenomena” (1967, p. 109). We did not find support for this hypothesis in the present study. A second interpretation of Bernstein’s ideas is that the CNS “economizes” by only using active muscle forces “in the capacity of complementary forces” (Bernstein 1967, p. 109). Schneider and colleagues (1989) proposed that the increase in muscle torque they observed as participants approached the upper target is consistent with this second interpretation. Thus, two studies of learning using the *same* multijoint task have produced opposite conclusions regarding Bernstein’s learning hypothesis.

Given these divergent interpretations of Bernstein’s ideas at the level of muscle activation, it is critical for future studies to examine precisely what patterns of muscle activity change over learning and how such changes relate to specific task constraints such as speed and accuracy. Once these relationships are known, a more general evaluation of Bernstein’s learning hypothesis can be made.

### Evaluation of the state analysis

This paper is a first step toward understanding a relatively understudied issue in motor control – how multimuscle activity changes over learning. One central contribution herein is the new state analysis. In this final section, we evaluate this new method.

Several strengths of the state analysis were revealed in the present report. First, the state analysis provided an operational definition of muscle coactivity. This allowed us to test two competing hypotheses about how muscle coactivity would change over learning. Second, the state analysis provided a rich description of which muscles worked together when in this task. Using this description, we were able to identify several coactivity states that were significantly associated with changes in movement time, and when these state changes occurred during the complex movement. This moved our analysis beyond the use of exemplar EMG waveforms to a detailed quantitative analysis of learning changes. Finally, the state analysis proved to be a tractable way to study changes in multimuscle activity over learning. Many states did not meet the inclusion criteria. This kept the number of predictor variables in the regression analyses small enough to detect significant relationships between movement time and state activity.

An important question is how the state analysis compared to the analyses performed by Schneider and colleagues (1989). Like Schneider et al., we found an increase in PD activity over practice as participants approached the upper target and reversed directions. We also found some increase in BI activity around the reversal. Nevertheless, there were several differences. We did not find a significant decrease in deltoid burst durations, nor did we find an increase in alternation between BI and TRI or AD and PD.

There are several factors that might help explain the differences between these studies. First, Schneider and colleagues did not analyze EMG activity in great detail. Their primary goal was to examine changes in arm kinetics over practice. Thus, differences between these studies may be due, in part, to the more detailed nature of the state analysis. However, this does not explain why we failed to find significant changes in deltoid burst durations. It is likely that this failure to replicate was due to the different thresholds used in each study to identify EMG bursts. Schneider and colleagues selected bursts visually, while we used a threshold criterion computed from baseline trials. Given that visual methods tend to exclude low-level tonic activity, it is possible that their method primarily captured the phasic components of the EMG signal, while ours included both phasic and tonic components.

More generally, it is an open question how sensitive the state analysis is to the threshold criteria used. Inspection of Fig. 2 suggests that raising the threshold would not necessarily eliminate the major sequence of states we identified, because underlying this sequence are large PD, AD, BI, and TRI bursts. Instead, a higher threshold would introduce states in-between the global

sequence. This is indeed what we found when we plotted the data in Fig. 4 using states identified with two higher threshold criteria.<sup>3</sup> Thus, the results reported herein appear to be robust to some changes in threshold. It is certainly possible, however, that the state analysis would be less robust with other threshold values or in other applications.

In conclusion, while there are limitations of the state analysis which may place constraints on its effectiveness in future studies, the strengths of this method outweighed these limitations in the current report. This has been the case in two other studies as well: we have used the state analysis to examine how infants' muscle coactivity changes as they learn to reach (Spencer and Thelen 1999) and walk (Angulo-Kinzler et al. 1999). It is our hope that this method will foster a growing interest in multijoint learning, moving researchers beyond exemplar-based EMG approaches to a richer understanding of motor learning.

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<sup>3</sup> The thresholds used were 10% and 20% of the EMG signal range for each muscle where the range was bounded by the maximum amplitude (with extreme spiking activity removed) and the “noise” threshold computed from the baseline trials.