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Changes in muscle and joint coordination in learning to direct forces

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Abstract

While it has been suggested that bi-articular muscles have a specialized role in directing external reaction forces, it is unclear how humans learn to coordinate mono- and bi-articular muscles to perform force-directing tasks. Participants were asked to direct pedal forces in a specified target direction during one-legged cycling. We expected that with practice, performance improvement would be associated with specific changes in joint torque patterns and mono- and bi-articular muscular coordination. Nine male participants practiced pedaling an ergometer with only their left leg, and were instructed to always direct their applied pedal force perpendicular to the crank arm (target direction) and to maintain a constant pedaling speed. After a single practice session, the mean error between the applied and target pedal force directions decreased significantly. This improved performance was accompanied by a significant decrease in the amount of ankle angular motion and a smaller increase in knee and hip angular motion. This coincided with a re-organization of lower extremity joint torques, with a decrease in ankle plantarflexor torque and an increase in knee and hip flexor torques. Changes were seen in both mono- and bi-articular muscle activity patterns. The mono-articular muscles exhibited greater alterations, and appeared to contribute to both mechanical work and force-directing. With practice, a loosening of the coupling between bi-articular thigh muscle activation and joint torque co-regulation was observed. The results demonstrated that participants were able to learn a complex and dynamic force-directing task by changing the direction of their applied pedal forces through re-organization of joint torque patterns and mono- and bi-articular muscle coordination.

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1. Introduction

Many everyday tasks require contact between a limb and the environment. In such cases, both the magnitude and direction of external contact forces must be controlled through the coordination of net joint torques, while simultaneously producing required joint angular displacements. While many joint torque combinations can result in a particular contact force magnitude, a unique combination of joint torques is necessary for a particular force magnitude and direction (van Ingen Schenau, Boots, de Groot, Snackers, & van Woensel, 1992). In dynamic movement tasks, the need for a specified combination of angular segmental motions further constrains the coordination solutions available to the neuromuscular system.

Van Ingen Schenau (1989) hypothesized that bi-articular muscles may be of special importance in force-directing because of their ability to simultaneously regulate or "tune" adjacent joint torques. In contrast, mono-articular muscles were viewed as work generators that would be active primarily during muscle shortening. This hypothesis was supported by the relationships between lower extremity joint torques and mono- and bi-articular muscle activity during cycling at a high workload (van Ingen Schenau et al., 1992; van Ingen Schenau et al., 1995). Further research studied participants pushing in specified directions against a stationary or moving force platform (Doorenbosch & van Ingen Schenau, 1995; Doorenbosch, Welter, & van Ingen Schenau, 1997; Jacobs & van Ingen Schenau, 1992). Although supporting the involvement of bi-articular muscles during external force-directing, these studies did not establish distinct roles for mono- and bi-articular muscles as initially hypothesized. An alternate hypothesis was proposed, that mono- and bi-articular muscles contributed to gross and fine regulation of net joint torques, respectively (Doorenbosch et al., 1997). However, it has also been argued that it is inappropriate to specify unique roles for mono- and bi-articular muscles due to the redundant nature and coupled dynamics of the musculoskeletal system (Kuo, 2001). From this viewpoint the function of an individual muscle would depend on its ability to contribute synergistically to the successful completion of a specified task, regardless of the number of joints it crosses (Kuo, 1994; Kuo, 2001; Nozaki, Nakazawa, & Akai, 2005).

Many force-directing studies have used constrained isometric or isovelocity movements, or dynamic movements in which a pre-established motor pattern already existed. An alternate approach is to study changes during the *learning* of a task that involves external force directing. It has been shown that bi-articular thigh muscles play an important role in regulating joint torques as participants learn to direct ground reaction forces during isometric leg extensions (van Deursen, Cavanagh, van Ingen Schenau, Becker, & Ulbrecht, 1998). However, this study did not focus on the learning process, and the task did not promote much change in joint torques as learning progressed. Further, this isometric task lacked movement requirements that could constrain and complicate the control of force magnitude and direction (van Ingen Schenau et al., 1992).

Cycling is a complex movement that has been studied extensively (Gregor, Broker, & Ryan, 1991). While ordinary cycling is familiar to most participants, the task is much more challenging if limited to the use of only one leg. In one-legged cycling, gravitational forces assist crank torque production in the first, downward, half of the crank cycle, but impede in the second, upward, half. With two legs, the torque contribution of the front leg in its downstroke helps overcome gravitational torque of the other leg in its upstroke. Without the front leg's assistance, flexor muscles must be used to pull the leg back, upward, and around the latter half of the crank cycle. Thus, in one-legged cycling the direction of pedal force should be much more varied than in two-legged cycling, where the pedal force is directed predominantly downward in the first half of the crank cycle, with smaller shear force components (Davis & Hull, 1981; Kautz & Hull, 1993).

We used the novel task of one-legged cycling to examine changes in coordination during the learning of a force-directing task. Participants with no prior one-legged cycling experience were instructed to maintain a constant pedaling speed while directing their applied pedal force in a target direction, always perpendicular to the crank arm. Participants were expected to have the most difficulty in the second half of the crank cycle where they must pull upwards and resist gravitational forces, without assistance from the contralateral front limb. Alterations in task performance with learning were assessed, along with associated changes in joint kinematics, joint kinetics, and mono- and bi-articular muscle coordination.

2. Methods

2.1. Participants

Nine healthy male subjects (age: 25 ± 4 yrs; mass: 83 ± 13 kg; height: 1.77 ± 0.07 m) with no previous one-legged cycling experience participated in the study. Prior to the experiment subjects read and signed an informed consent form approved by the University of Massachusetts Amherst institutional review board.

2.2. Instrumentation

Participants cycled on a standard road bicycle mounted on a computerized ergometer (Velodyne, Schwinn Bicycle Company, Chicago, IL). The front wheel of the bicycle was removed and the wheel fork rigidly fixed to the ergometer. The rear wheel sat on an electronically braked roller, with the resistance automatically adjusted so the workload remained constant, regardless of changes in rolling resistance, rider/bicycle mass, component wear, and pedaling cadence.

Pedal forces were measured using an instrumented clip-in pedal with two piezoelectric transducers (Broker & Gregor, 1990) mounted on the left crank arm (length = 0.17 m). Crank arm and pedal angular positions were quantified with digital optical encoders (resolution = 0.35°, US Digital, Vancouver, WA) that measured changes from a calibrated reference position (crank arm vertical, pedal horizontal). Pedal force and encoder data were sampled at 100 Hz with a computer using a 16-bit analog-to-digital converter (PCI-6034E, National Instruments, Austin TX).

Surface electromyographic (EMG) data were collected from three mono-articular muscles (tibialis anterior [TA], soleus [SO], and vastus lateralis [VL]), and three bi-articular muscles (medial gastrocnemius [GA], rectus femoris [RF], and semitendinosus [HAM]) of the left leg using bipolar pre-amplified (35×) Ag/AgCl circular electrodes (8 mm diameter, 20 mm interelectrode distance, input impedance >25 MΩ at DC; Therapeutics Unlimited, Iowa City, IA). EMG channel gains were adjusted for each muscle and participant to obtain optimal range and resolution. Electrodes were aligned parallel to the fibers on the center of the muscle belly (Cram, Kasman, & Holtz, 1998), with a reference electrode on the lateral malleolus. EMG data were sampled at 1000 Hz with a 16-bit analog-to-digital converter (CIO-DAS1402/16, Measurement Computing, Norton MA) synchronized with the kinetics/kinematics data collection computer.

2.3. Anthropometrics

Anthropometric measures included each participant's left thigh (greater trochanter–lateral femoral condyle), leg (lateral femoral condyle–lateral malleolus), and trochanteric (floor to the center of the greater trochanter while standing) lengths. The bicycle seat height was adjusted such that the distance from the pedal at bottom-dead-center to the greater trochanter was equal to 90% of the trochanteric length (Redfield & Hull, 1986). Participants placed their hands on the handlebars, and the angle of their trunk (greater trochanter to the acromion process, with respect to the vertical) was measured for computation of hip angle. The foot and pedal were considered as a single rigid body, with foot length and angle defined by a line joining the lateral malleolus to the center of the pedal axis.

2.4. Task instructions and real-time feedback

Participants were instructed to maintain a constant pedaling speed while always directing their applied pedal force vector in the target direction perpendicular to the crank arm. Real-time visual feedback from a custom software program (Visual Basic 6.0, Microsoft Corp.) was displayed on a computer monitor in front of the bicycle (Fig. 1). The 360° crank cycle was divided into 16 equal 22.5° arc sectors. During pedaling, the instantaneous crank arm position and the direction of the average target and applied force vectors for each sector were displayed (Fig. 1; filled and open arrows, respectively). The average error

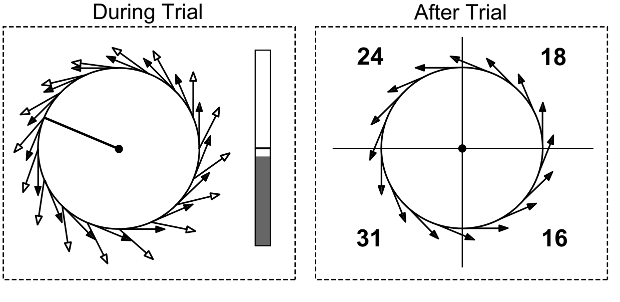

Fig. 1. Screen captures of real-time feedback given to participants. Left: Feedback given during trials. Filled and open arrows represent the target and applied force directions at selected points in the crank cycle, respectively. Each applied force arrow is the average over a 22.5° sector. For the actual feedback, the open arrows were color-coded depending on the magnitude of the error (see text for details). The vertical bar displays the crank angular velocity. Right: Summary feedback given at the end of each trial. Each number (also color-coded) represents the root-mean-squared error in degrees for the quadrant (0 = perfect score).

between the target and applied force directions was calculated. Although colored black in Fig. 1, the participants saw applied pedal force arrows color-coded for error magnitude: error $<10° =$ green; $10° \leqslant$ error $\leqslant 30° =$ orange; error $> 30° =$ red. Applied force arrows were updated immediately after the crank arm passed each sector to give sequential updating of all 16 arrows during each complete crank revolution. Crank angular velocity was displayed as a vertical bar (Fig. 1); the participants saw a green bar when the desired crank velocity was attained, but the bar turned red if the velocity varied more than 10% from the target. At the end of each 45 s trial (see next section), participants were given a summary (Fig. 1) of the root-mean-squared error (RMSE) between the applied and target force directions for each of the four crank cycle quadrants (Quadrant I: 0–90°, II: 90–180°, III: 180–270°, IV: 270–360°). This allowed easy identification of poor performance in different regions of the crank cycle.

2.5. *Experimental conditions and procedures*

A pilot study was conducted to determine the optimal pedaling speed and workload, trial and rest duration, and the number of trials for the greatest improvements in performance. Participants could perform the force-directing task better at a slow pedaling speed; at faster speeds the crank would tend to freewheel, causing a large acceleration when the participant "caught up" to the spinning rear wheel. The workload was also an issue; if too high the hip flexor muscles fatigued, but if too low pedal forces were small and the resolution of the pedal force vector angle was poor. An optimal workload of 28 W was chosen, which required an average crank torque of 9 Nm to maintain a constant target crank angular velocity of $\sim$180°/s ($\sim$3.14 rad/s). Participants performed 18 trials, each 45 s in duration with 1 min of rest between trials. This duty cycle allowed subjects sufficient time to improve their performance in the task without fatiguing.

A timeline of the experimental session is shown in Fig. 2. Participants warmed up by cycling with two legs at the 28 W workload for four minutes. Each participant was then shown a diagram and given standardized verbal instructions regarding the target pedal force direction and on maintaining a constant pedaling speed. Participants were told to focus on the force direction, and that they would be given verbal feedback if their speed was too slow or too fast. After an initial baseline trial without feedback, participants began a series of 16 trials in which they received visual feedback (Fig. 1), accompanied

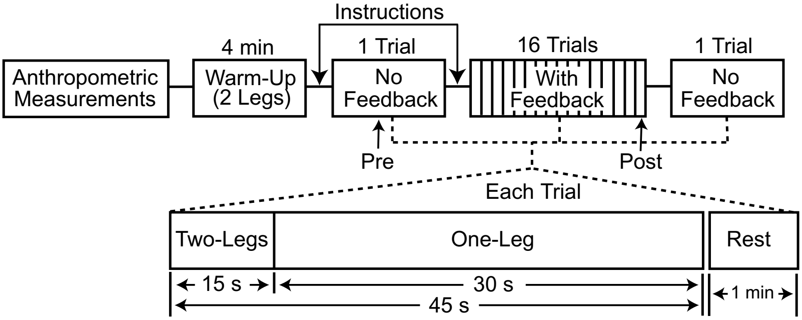

Fig. 2. Timeline of the experimental session.

by standardized instructions for interpreting the feedback. Afterwards, a final trial without feedback completed the set.

At the beginning of each trial, the crank arm and pedal were placed in the calibrated reference position without the participant's foot to zero the force pedal amplifiers. The participant's foot was then clipped into the pedal and data collection was initiated as the participant began a warm-up, pedaling with both legs to reach and maintain the desired pedaling rate. After 15 s, the participants removed their right foot from the pedal and placed it on a support, continuing to pedal for an additional 30 s with only the left leg (Fig. 2). The 15 s warm-up and the first second of single-leg pedaling were not included in the analysis.

2.6. Data reduction

Data post-processing was done in MATLAB (Version 7, MathWorks, Inc., Natick, MA). The raw kinematic, kinetic, and EMG (detrended and rectified) data were smoothed with a low-pass zero-lag fourth-order Butterworth digital filter. Based on frequency power-spectral analysis and residual analysis (Winter, 1990), the filter cut-off frequencies were set at 4 Hz for pedal forces and pedal angle, and 1 Hz for crank angle. A filter cut-off frequency of 6 Hz was used to produce EMG linear envelopes (Winter, 1990). The filtered pedal forces, crank angles, pedal angles, and EMG linear envelopes were interpolated at 1° increments of crank angle relative to top-dead-center (0°) using a cubic spline algorithm (Li & Caldwell, 1998). The interpolated EMG linear envelopes were scaled to the maximum EMG value occurring for each muscle and participant during the practice session.

The pedal forces were transformed from the pedal coordinate system to the global coordinate system (Caldwell, Li, McCole, & Hagberg, 1998). The dot product between the applied and target force vectors was used to determine the magnitude of the force–direction error, while their cross product determined the sign of the error (positive = applied force directed "outward" from the circle scribed by the pedal path). The RMSE between the applied and target force directions was calculated for the entire 360° and for individual 90° quadrants.

Joint positions and angles were computed by modeling the bicycle and rider as a sagittal plane five-bar linkage with two independent mechanical degrees-of-freedom (specified by the crank and pedal angles) and a fixed hip joint (Hull & Jorge, 1985). At full extension the knee and hip angles equal 180°, and decrease as the joints flex. The ankle angle between the foot and leg segments equals 90° when the segments are at right angles, and increases with plantarflexion. Segment masses, center of mass positions, and radii of gyration were estimated from De Leva (1996). Segment and joint velocities and accelerations were computed by numerical differentiation. Newton–Euler equations of motion were then solved for the reaction forces and torques at the ankle, knee, and hip joints (Bresler & Frankel, 1950; Elftman, 1939).

For each participant, consecutive crank cycles were averaged within each trial. Maximum values and the mean absolute change (pre vs. post difference) throughout the entire crank cycle were computed for the joint angles, joint torques, and pedal forces. The area under the curve was also calculated for the joint torques and pedal forces. Maximum value and area computations were performed separately for different phases (joints: dorsiflexion/plantarflexion, flexion/extension; pedal forces: anterior/posterior, upwards/downwards).

The maximum and minimum values, range, and within-cycle mean and standard deviation were computed for the crank torque, velocity, and acceleration. The scaled EMG linear envelopes were integrated across each crank cycle, and the integrated EMG (IEMG) values for each cycle were averaged together.

2.7. Statistical analysis

A paired *t*-test was performed to compare mean pre-practice (no feedback, Trial 1) RMSE scores with the last trial with feedback (Trial 17) to test for improvement in task performance. These trials were chosen because they gave the maximum pre-post differences in the RMSE scores, and trials 17 and 18 (no feedback) were not significantly different ($p = .1069$). To investigate differences in RMSE for individual quadrants, a 2×4 repeated measures analysis of variance (ANOVA) was performed using trial (pre vs. post) and quadrant (I–IV) as main factors. Tukey's honestly significant difference was used for post-hoc analysis.

One-sample *t*-tests were used to determine whether the mean absolute pre-post changes in joint angles, pedal forces, and joint torques were significantly different from zero. Paired *t*-tests were used to compare the areas, maximum and minimum values, ranges, and within-cycle mean and standard deviations for participant/bicycle kinematics and kinetics and IEMG from pre- to post-practice. A significance level of $p < .05$ was used for all tests.

3. Results

3.1. Force-directing error

One participant was excluded from the analysis because he started practice with a very low RMSE (similar to the others' post-practice scores), and his post-practice RMSE was 17.5% higher than pre-practice (Table 1, Subject 0). Therefore, his data did not provide information on coordination changes with improved force-directing. For the other eight subjects, RMSE decreased non-linearly as practice progressed (Fig. 3A), with significant reductions in overall RMSE from pre- to post-practice (Table 1).

The 2×4 factorial ANOVA on RMSE scores revealed significant main effects for trial ($F = 32.49$, $p < .001$) and quadrant ($F = 6.12$, $p < .01$), as well as their interaction ($F = 7.43$, $p < .01$). Post-hoc analysis indicated that in the pre-practice baseline trial, the

Table 1
RMSE scores for entire crank cycle

Trial/variable	Subject number									Mean ± SD
	0[b]	1	2	3	4	5	6	7	8	
Pre	20.0	32.4	43.9	51.5	53.7	48.0	65.4	52.4	39.7	45.2 ± 13.3
Post	23.5	21.1	15.0	26.2	19.4	24.3	26.7	12.5	35.8	22.7 ± 6.9[*]
Difference[a]	+3.5	−11.3	−28.9	−25.3	−34.3	−23.7	−38.7	−39.9	−3.9	−22.5 ± 15.4
% Change	+17.5	−34.9	−65.8	−49.1	−63.9	−49.4	−59.0	−76.1	−9.7	−43.4 ± 30.0

[a] Difference is computed post–pre.
[b] Subject 0 was excluded from the analysis (see text for details).
[*] Post significantly different than pre ($p < .001$).

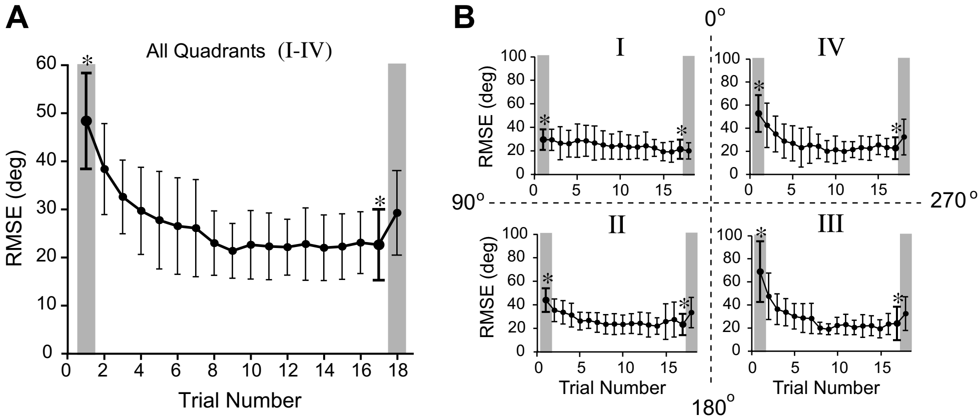

Fig. 3. (A): Root-mean-squared error (RMSE) scores as a function of trial number. (B): RMSE scores partitioned into individual crank cycle Quadrants (I–IV). Each data point is the average of all cycles within a trial averaged across subjects. Statistical tests on the baseline (pre) and last visual feedback trial (post) revealed a significant improvement where noted (*). Error bars are ±1 standard deviation. The shaded regions indicate a no feedback condition.

error scores in Quadrant III (180°– 270°) were significantly higher than Quadrants I (0°–90°) and II (90°–180°), and the error in Quadrant IV (270°–360°) was significantly higher than Quadrant I (Table 2). The RMSE scores decreased significantly in all quadrants with practice (i.e., pre- vs. post-practice, Table 2 and Fig. 3B). The improvement in the direction of the applied force vectors is evident when viewing the signed force-directing error scores in polar coordinates as a function of crank angle (Fig. 4A), and by examining the target and average applied force vectors (Fig. 4B).

3.2. Kinematics

In the baseline trial, subjects demonstrated large fluctuations in crank angular velocity, caused by high positive crank angular accelerations in the first half of the crank cycle and high negative accelerations in the second half (Fig. 5A). Post-practice, subjects demonstrated a more consistent crank angular velocity, although they tended to pedal slightly faster (~3°/s) than the 180°/s target speed. There were significant decreases in the range and standard deviation of the mean for crank angular velocity and acceleration from pre- to post-practice (Table 3).

Table 2
RMSE scores for individual crank cycle quadrants (mean ± between-subjects SD)

Trial	Quadrant number**			
	I	II	III	IV
Pre	29.2 ± 8.6	43.5 ± 9.9	67.2 ± 25.8	52.1 ± 15.8
Post	21.2 ± 8.0*	23.1 ± 8.9*	23.1 ± 14.2*	22.2 ± 9.9*

* Post significantly lower than pre for Quadrants I–IV ($p < .05$).
** In the pre-practice trial, Quadrant III error was significantly higher than Quadrants I and II; Quadrant IV error was significantly higher than Quadrant I ($p < .001$). No significant differences between quadrants were found in the post-practice trial.

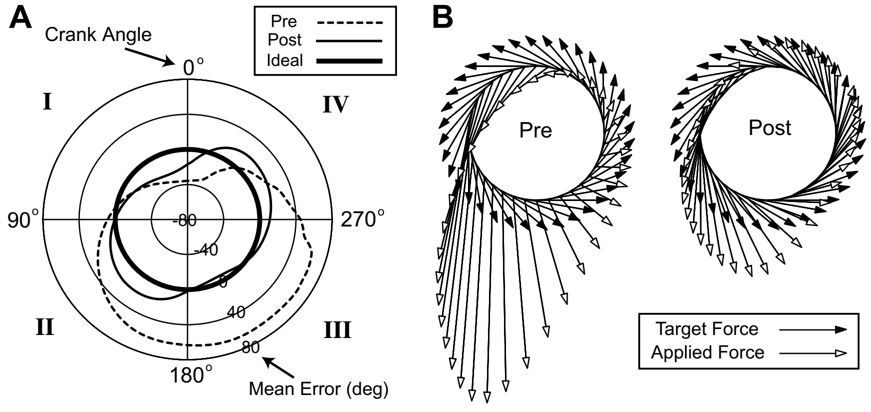

Fig. 4. (A): Polar plot of the mean force-directing error as a function of crank angle pre- and post-practice. A positive magnitude indicates that the applied force was directed outward with respect to the target force direction. (B): Schematics depicting the target and average applied force vectors pre- and post-practice. Vectors are shown in 10° increments.

The mean absolute change (pre vs. post) was significant for the ankle, knee, and hip joint angles (Table 3). There was a large decrease in the amount of ankle angular motion, while small increases were evident in knee and hip angular motion (Fig. 5B). However, with practice there were no significant differences in maximum joint angles for the plantarflexion, dorsiflexion, flexion, and extension phases of movement.

3.3. Kinetics

The mean absolute change in anterior–posterior and vertical pedal forces illustrates the significant alteration in pedal kinetics from pre- to post-practice (Table 4). Participants learned to push down with less force in the first half of the crank cycle and to pull up with more force in the second half, as reflected in the significant changes in vertical force areas and maximum downward force values (Table 4, and Fig. 6A). Participants also learned to pull with significantly more posterior force through the bottom of the crank cycle after practice. These learning effects are accentuated by comparison with hypothetical "ideal" anterior–posterior and vertical applied force curves that would match the target force direction and produce a constant crank torque of 9 Nm (the post-practice mean). With practice, the applied pedal force patterns became more similar to these ideal force profiles (Fig. 6A, thick solid lines).

Although the mean crank torque did not change from pre- to post-practice, the within-cycle standard deviation and the peak-to-peak range decreased significantly (Table 4). These alterations were accompanied by significant changes in all three net joint torques from pre- to post-practice. After practice, the ankle torque vs. crank angle curve was shifted downwards (Fig. 6B), and the plantarflexor torque area decreased significantly (Table 4). Knee flexor torque increased over a large portion of the crank cycle (from ~20° to 350°), such that knee flexor torque maximum and its area increased significantly. Hip flexor torque also showed an increase (from ~225° to 140°), although changes in the hip flexor and extensor areas and maximum values were not significant.

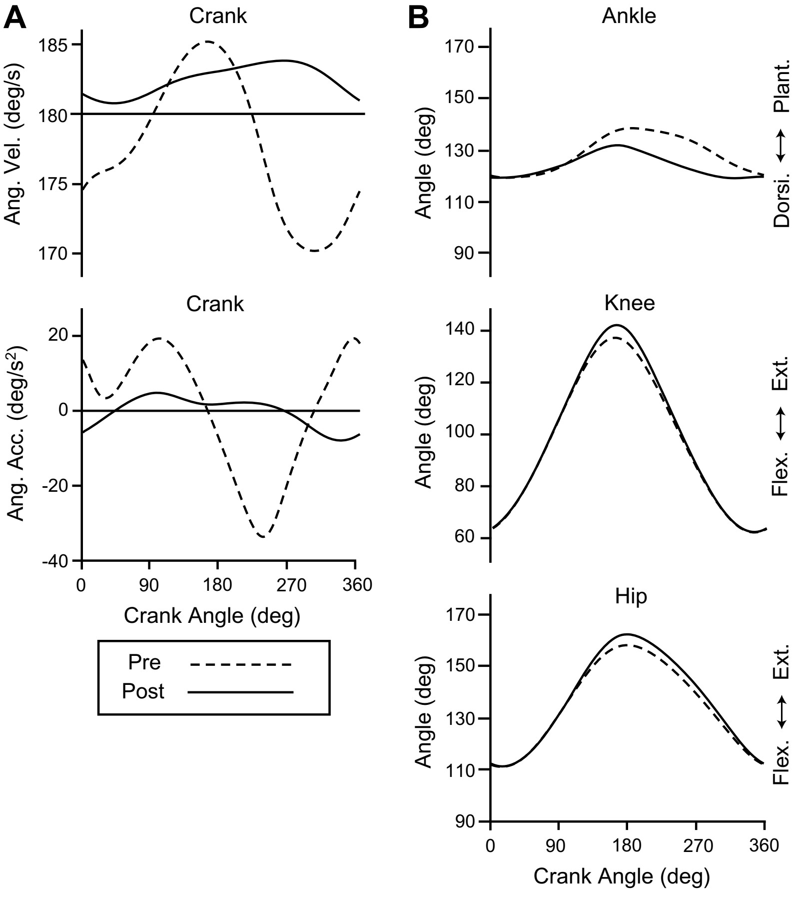

Fig. 5. (A): Mean crank angular velocity and acceleration as a function of crank angle pre- and post-practice (the target velocity, 180°/s, is indicated). (B): Mean ankle, knee, and hip joint angular displacements as a function of crank angle (see text for a description of angular conventions).

3.4. Electromyographic data

The mean EMG linear envelopes plotted against crank angle indicate that practice induced changes in activity patterns (Fig. 7). After the practice trials, TA activity increased throughout the entire crank cycle, with significantly higher IEMG overall and in Quadrants III and IV (Table 5). Overall SO IEMG decreased significantly from pre- to post-practice, with most of the decrease occurring in Quadrants I and II (~0°–110°). The GA activity increased in the top half of the crank cycle (~270°–360° and 0°–90°), while RF and HAM muscles showed smaller changes. The GA IEMG was statistically larger in Quadrant I, and the RF IEMG decreased in Quadrant II (Table 5).

The relationship between applied pedal force direction, net joint torques, and muscular activity at the midpoints of each crank cycle quadrant is shown for one participant in Fig. 8. Pre-practice, at a crank angle of 45° all three joint torques were extensor, with high SO, VL, and RF activity resulting in a large downward applied pedal force. After practice, the SO and VL displayed less activity, while the TA, GA, and RF became more active. As a result,

Table 3
Statistics for crank and joint kinematics (mean ± between-subjects SD)

Variable		Trial	
		Pre	Post
Crank angular velocity (deg/s)			
Max		186 ± 15.9	184 ± 8.47
Min		165 ± 24.7	180 ± 9.33
Range		20.8 ± 14.1	4.38 ± 1.40*
Mean[a]		178 ± 18.3	182.4 ± 8.63
SD of Mean[a]		6.38 ± 4.09	1.49 ± 0.52*
Crank angular acceleration (deg/s^2)			
Max CCW		47.4 ± 31.2	8.17 ± 2.34*
Max CW		−46.6 ± 34.0	−8.50 ± 2.34*
Range		94.1 ± 63.7	16.7 ± 4.45*
Mean[a]		−0.07 ± 0.89	−0.26 ± 0.36
SD of Mean[a]		25.0 ± 16.0	5.20 ± 1.48*
Ankle angle			
Max (deg)	Plantarflexion	142 ± 9.13	132 ± 14.4
	Dorsiflexion	117 ± 14.9	118 ± 16.3
Mean absolute change (deg)[b]			12.7 ± 6.25*
Knee angle			
Max (deg)	Extension	137 ± 4.99	142 ± 5.76
	Flexion	62.2 ± 4.64	62.4 ± 4.45
Mean absolute change (deg)[b]			2.60 ± 1.62*
Hip angle			
Max (deg)	Extension	158 ± 5.55	163 ± 5.69
	Flexion	111 ± 5.83	112 ± 6.38
Mean absolute change (deg)[b]			4.36 ± 2.42*

Note: CCW (counter-clockwise; direction of pedal progression); CW (clockwise).
[a] Mean and SD are within-cycle.
[b] Change is computed pre to post across entire crank cycle.
* $p < .05$.

the ankle torque became slightly dorsiflexor and a large flexor torque was seen at the hip. These changes reduced the pedal force magnitude and provided an almost perfect match to the target force direction. In the bottom half of the crank cycle at 135° and 225°, there was a substantial increase in muscle activity from pre- to post-practice, particularly in TA, GA, and HAM. These changes led to a large increase in knee flexor torque that helped to re-direct the pedal force to closely match the target force direction. At 315°, although there was only a small change in the knee joint torque from extensor to flexor pre- vs. post-practice, the GA muscle activity increased considerably. In this particular example, the changes seen at 315° overcompensated and directed the pedal force above the target force direction.

4. Discussion

4.1. Main findings

The aim of this study was to investigate changes in muscle and joint coordination after participants learned to perform a complex force-directing task. Participants demonstrated

Table 4
Statistics for pedal, crank, and joint kinetics (mean ± between-subjects SD)

Variable		Trial	
		Pre	Post
Anterior–posterior pedal force			
Area (Ns)	Posterior	32.1 ± 17.3	54.0 ± 15.2
	Anterior	−47.4 ± 26.8	−39.6 ± 11.5
Max (N)	Posterior	30.7 ± 11.2	47.4 ± 10.5*
	Anterior	−41.5 ± 20.0	−41.2 ± 8.86
Mean absolute change (deg)[b]			19.8 ± 6.54*
Vertical pedal force			
Area (Ns)	Up	18.0 ± 26.1	54.7 ± 19.8*
	Down	−242 ± 63.7	−108 ± 23.5*
Max (N)	Up	20.6 ± 22.5	46.5 ± 14.8
	Down	−168 ± 38.4	−87.9 ± 14.8*
Mean absolute change (deg)[b]			53.0 ± 23.4*
Crank torque (Nm)			
Max CCW		24.9 ± 6.17	14.7 ± 1.87*
Max CW		−0.1. ± 1.78	4.79 ± 1.35*
Range		25.0 ± 6.49	9.88 ± 2.87*
Mean[a]		9.16 ± 1.49	8.96 ± 0.59
SD of Mean[a]		8.61 ± 2.68	3.20 ± 0.93*
Ankle torque			
Area (Nms)	Plantarflexor	26.3 ± 9.19	16.0 ± 3.52*
	Dorsiflexor	−3.73 ± 2.58	−6.38 ± 2.13
Max (Nm)	Plantarflexor	20.5 ± 6.77	13.2 ± 2.91
	Dorsiflexor	−5.65 ± 2.77	−7.64 ± 1.71
Mean absolute change (deg)[b]			5.51 ± 2.31*
Knee torque			
Area (Nms)	Extensor	20.5 ± 14.0	14.0 ± 5.14
	Flexor	−31.7 ± 14.6	−50.6 ± 9.90*
Max (Nm)	Extensor	25.0 ± 11.7	21.5 ± 4.78
	Flexor	−21.6 ± 7.89	−32.6 ± 7.17*
Mean absolute change (deg)[b]			11.6 ± 5.05*
Hip torque			
Area (Nms)	Extensor	31.6 ± 21.8	26.2 ± 14.2
	Flexor	−55.3 ± 24.6	−63.84 ± 17.8
Max (Nm)	Extensor	32.4 ± 16.4	28.1 ± 11.3
	Flexor	−44.6 ± 11.7	−49.8 ± 10.2
Mean absolute change (deg)[b]			15.1 ± 5.34*

Note: CCW (counter-clockwise; direction of pedal progression); CW (clockwise).
[a] Mean and SD are within-cycle.
[b] Change is computed pre to post across entire crank cycle.
* $p < .05$.

significant improvements in force-directing ability after a single practice session. A clear strategy emerged; participants restructured their muscle activity patterns resulting in specific joint torque and pedal force profile modifications. The largest activity changes were seen in the mono-articular muscles; smaller changes were observed in the bi-articular muscles.

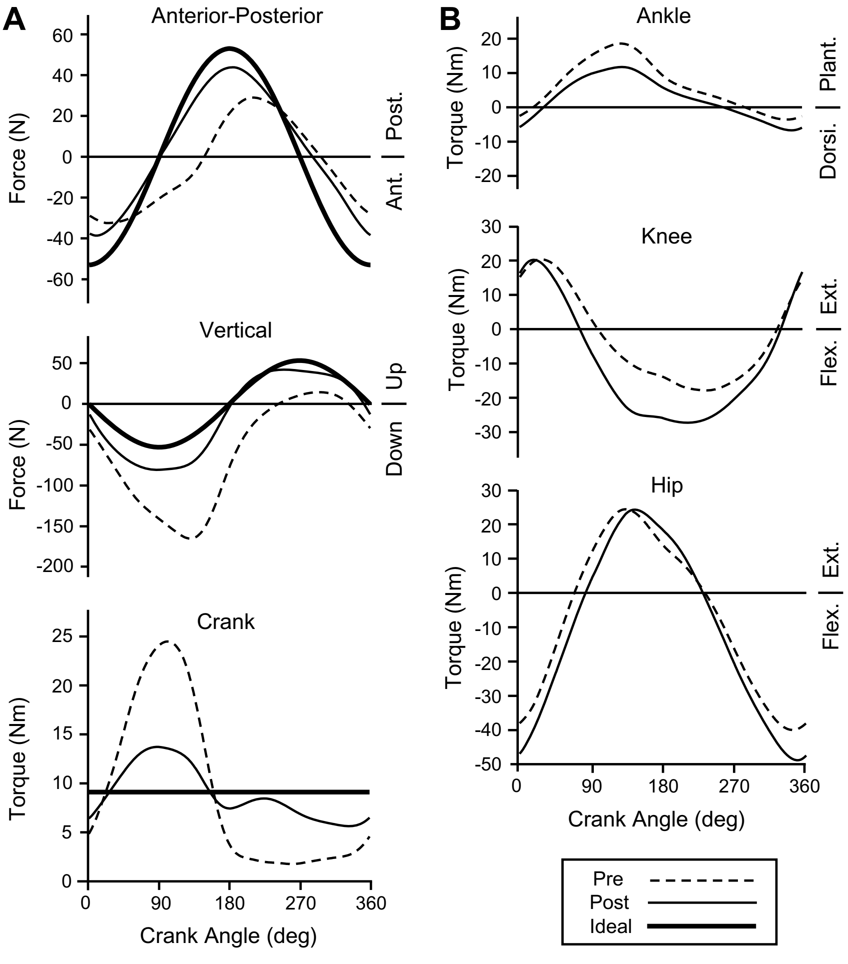

Fig. 6. (A): Mean anterior–posterior and vertical applied pedal forces and crank torque as a function of crank angle pre- and post-practice. In the graphs of force vs. crank angle, the thick solid lines represent the anterior–posterior and vertical forces needed to achieve a constant crank torque of 9 Nm, which represents the average post-practice crank torque. (B): Mean ankle, knee, and hip joint torques as a function of crank angle.

4.2. Task difficulty

Several factors made this task challenging, including the variety of task demands and constraints faced by the participants. Lower extremity motion was constrained by the circular path of the pedal, with joints extending more or less simultaneously in the first half of the crank cycle, and then flexing together during the second half. The direction of these joint motions may be in conflict with the directions of joint torques needed to generate the ever-changing target pedal force direction (van Ingen Schenau et al., 1992). Further, pedal forces must be applied smoothly to avoid hesitation and crank "freewheeling" (resistance dropping to zero) with an abrupt subsequent re-engagement, which would produce large fluctuations in crank torque and force direction. These task challenges were magni-

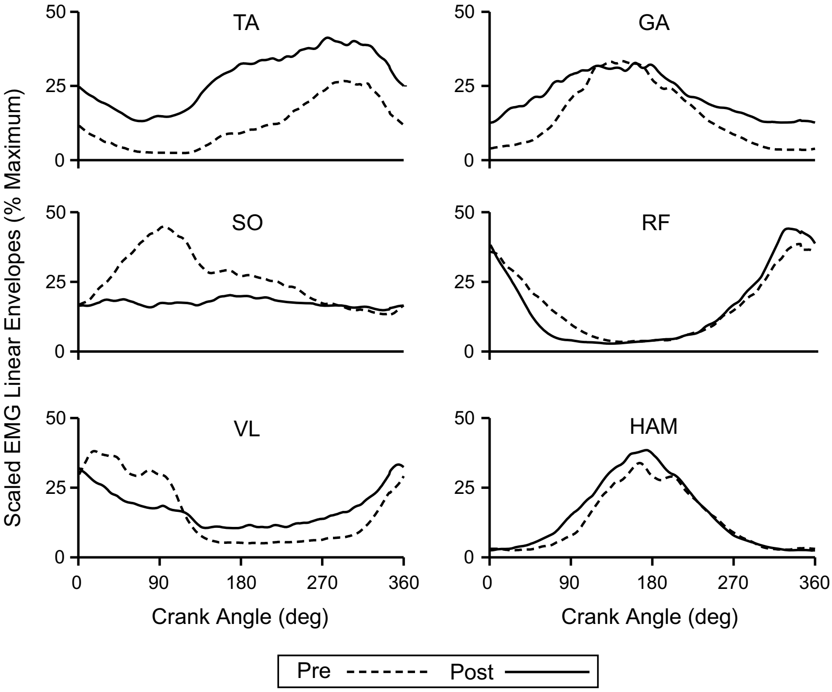

Fig. 7. Mean scaled EMG linear envelopes as functions of crank angle, pre- and post-practice, for the tibialis anterior (TA), soleus (SO), vastus lateralis (VL), medial gastrocnemius (GA), rectus femoris (RF), and semitendinosus (HAM).

Table 5
Integrated EMG (mean ± between-subjects SD)

Muscle	Trial	All quadrants	Individual quadrants			
			I	II	III	IV
TA	Pre	42.6 ± 18.3	6.5 ± 4.9	3.5 ± 1.9	11.3 ± 7.3	21.4 ± 11.6
	Post	99.9 ± 53.1*	17.5 ± 12.2	17.5 ± 17.9	30.4 ± 16.0*	34.5 ± 12.7*
SO	Pre	93.0 ± 35.5	23.1 ± 9.3	33.0 ± 12.8	22.7 ± 16.1	14.2 ± 9.9
	Post	62.6 ± 28.1*	15.6 ± 7.7*	15.8 ± 7.0*	16.9 ± 9.3	14.4 ± 8.1
VL	Pre	58.3 ± 23.6	29.2 ± 15.1	15.1 ± 7.3	4.8 ± 1.9	9.2 ± 3.9
	Post	62.4 ± 52.7	22.7 ± 13.5	13.0 ± 13.0	10.1 ± 14.9	16.5 ± 16.9
GA	Pre	54.8 ± 19.4	5.7 ± 2.5	25.0 ± 8.2	19.0 ± 9.6	5.1 ± 4.3
	Post	78.6 ± 33.5	16.2 ± 12.6*	27.2 ± 13.5	22.3 ± 10.4	12.9 ± 14.9
RF	Pre	57.4 ± 20.6	24.2 ± 12.7	5.5 ± 2.1	5.2 ± 3.4	22.5 ± 7.7
	Post	54.9 ± 13.8	20.5 ± 3.4	3.0 ± 0.9*	5.4 ± 3.6	26.0 ± 9.4
HAM	Pre	46.8 ± 19.8	2.9 ± 1.8	17.1 ± 10.6	22.0 ± 8.7	4.9 ± 3.3
	Post	55.2 ± 22.1	4.0 ± 3.1	22.4 ± 10.6	24.2 ± 11.1	4.6 ± 2.0

Note: TA: tibialis anterior, SO: soleus, VL: vastus lateralis, GA: medial gastrocnemius, RF: rectus femoris, HAM: semitendinosus. Units are: (EMG / Max. EMG) * deg.

* Post significantly different than pre ($p < .05$, within-subjects analysis).

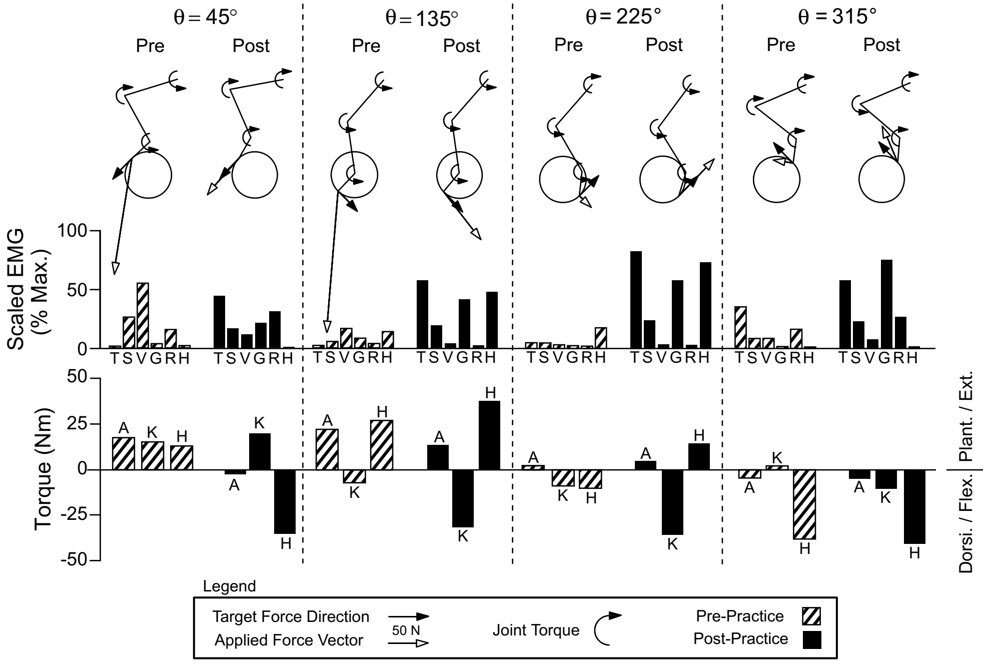

Fig. 8. Stick figure schematics, muscle activity (EMG), and joint torque bar graphs for Participant 2 during a representative crank cycle in the baseline (pre) and last practice trial with feedback (post). EMG bar graphs: tibialis anterior (T), soleus (S), vastus lateralis (V), medial gastrocnemius (G), rectus femoris (R), and semitendinosus (H); joint torque bar graphs: A = ankle, K = knee, H = hip. θ = crank angle.

fied by the continually changing contribution of gravity that aided movement in the first half of the crank cycle but resisted movement in the second half. Participants had to develop a strategy to coordinate their muscles to perform the pedal force-directing accurately, while attending to the numerous demands and constraints of the task.

4.3. Coordination strategy

Although our participants were naïve to the one-legged task, all had at least some experience with recreational two-legged cycling. This experience gave them a pre-existing strategy that they could draw upon in their initial attempts at the targeted force direction task. Indeed, the pedal force and joint torque profiles measured in the pre-practice baseline trial were similar in shape to those of two-legged cycling (Caldwell, Hagberg, McCole, & Li, 1999; Davis & Hull, 1981; Kautz & Hull, 1993). The pre-practice muscle activity profiles were also similar to those reported for two-legged cycling (van Ingen Schenau et al., 1995). However, in recreational cycling the exact direction of the pedal force is not normally emphasized, and most people focus on pushing downward on the forward pedal. This two-legged strategy would therefore be ineffective in the current one-legged task in which participants must continuously target their pedal force vector to be perpendicular to the crank arm. The high error scores in the pre-practice baseline trial are consistent with such an ineffective strategy.

Due to the absence of contralateral contributions, we expected that participants would have the most difficulty in the latter half of the crank cycle. The force–direction error scores confirmed this difficulty. However, the high error in this period may have been associated with events occurring earlier in the first half of the crank cycle. In the pre-practice baseline trial, participants produced large extensor joint torques in the first half, causing a large downward pedal force and crank torque. The resulting crank acceleration gave subjects less time to direct forces accurately at the bottom of the crank cycle and in the third quadrant. This may have been due to a pre-established strategy from recreational two-legged cycling, where the large pedal force and crank torque would aid contralateral efforts to pull up in the latter half of the crank cycle. After practice, participants significantly reduced the crank torque in the first half, resulting in more uniform crank torque throughout the task and therefore a more constant crank angular velocity.

The significant improvement in force-directing error was similar to that of participants asked to modify the shear component of pedal force using visual feedback (Broker, Gregor, & Schmidt, 1993). In the present study the error scores leveled off after nine 30 s trials, while the participants in Broker et al. continued to improve through fifteen 30 s trials. This difference may be due to the type of feedback given to participants. Broker et al. asked participants to match a template plot of shear pedal force versus crank angle recorded from an expert cyclist, which may have been more difficult to follow compared to our simple color-coded display of the task performance versus requirements. Broker et al. also used two-legged cycling at a much higher workload, and participants were only concerned with changing a single component of the applied pedal force vector. In our study, participant performance decreased with feedback removal, although not significantly. It is unknown whether a retention trial performed on a later day would have resulted in larger changes in performance, or whether further practice would have caused additional improvement. Nonetheless, the limited practice period fulfilled our purpose of eliciting a significant improvement in pedal force-directing performance.

Many of the changes that accompanied improvement in force-directing were focused at the ankle and knee joints. For example, participants demonstrated the largest kinematic change at the ankle, with less plantarflexion motion after practice. The most significant changes in joint kinetics with practice were increased knee flexor torque and a switch to less plantarflexor and more dorsiflexor torque at the ankle. The muscular activity data support this observation, with the largest modifications seen in the TA, SO, GA and VL muscles. Strategically, participants chose to "stiffen" the ankle joint in the bottom and latter part of the crank cycle, with increased dorsiflexor torque contributions through heightened TA activity (and thus greater co-contraction). The stiffening of the ankle joint is consistent with Bernstein's (1967) idea that in the early stages of learning a new task, individuals try to "freeze" or reduce the number of mechanical degrees-of-freedom. Plantarflexion was further suppressed by de-activating SO throughout the crank cycle. Necessary plantarflexor torque in the downstroke was supplied instead by increased GA activity, which was advantageous because it also enhanced knee flexor torque in the second and third quadrants. A small increase in HAM activity also helped provide additional knee flexor torque in the second quadrant. The activity changes in VL (less in the first quadrant; higher afterwards) may be related to the reduction in crank torque in the first part of the crank cycle. Overall, the kinematic, kinetic and muscular alterations with practice represent modifications from an original "two-legged cycling" strategy to one aimed at fulfilling the specific requirements of the one-legged force-directing task.

4.4. Contributions of mono- and bi-articular muscles

Previous studies have suggested specialized roles for mono- and bi-articular muscles during multi-segment movements such as cycling (van Ingen Schenau et al., 1992, 1995), and have sought evidence through controlled laboratory force–direction tasks (Doorenbosch & van Ingen Schenau, 1995; Doorenbosch et al., 1997; Jacobs & van Ingen Schenau, 1992; Wells & Evans, 1987). The present study used a more complex and difficult force-directing task, in which participants learned to re-organize their muscular coordination and joint torque patterns to direct their pedal force vector towards a pre-defined target. We found changes in both mono- and bi-articular muscles, with the three mono-articular muscles (VL, SO, TA) displaying the largest changes in activity from pre- to post-practice (Fig. 7). Among the bi-articulars, only the GA showed substantial changes, with smaller alterations for RF and HAM. It is unknown whether additional practice would elicit further changes in mono- and bi-articular muscle coordination.

The large post-practice activity reduction in mono-articular SO and VL in the first half of the crank cycle may have been associated with the decrease in crank torque and mechanical work which helped meet the task requirement of constant crank angular velocity. Similarly, greater TA activity in the second half of the crank cycle would help increase crank torque and mechanical work to the same end. These muscular functions would support the contention that a primary function of mono-articular muscles is to generate energy and perform mechanical work (van Ingen Schenau et al., 1995). However, TA and VL activity also increased during periods where they were acting as antagonists and therefore absorbing energy (~45°–270° for TA, ~150°–340° for VL). In particular, the mono-articular TA muscle played an important role in re-directing the external force vector during the third quadrant, as the large post-practice activity changes were linked to both kinematic and kinetic alterations at the ankle. After practice, the participants learned to activate the mono-articular TA and bi-articular GA together through much of the second half of the crank cycle in an attempt to direct the pedal force upwards.

In past studies, evidence for the importance of bi-articular muscles in force-directing has focused on the correlations between adjacent joint torques and the activity of the muscles that cross both joints. Several studies have found strong linear relationships between the difference in the activity of the RF and HAM muscles and the difference in knee and hip joint moments (Doorenbosch & van Ingen Schenau, 1995; Doorenbosch et al., 1997; Jacobs & van Ingen Schenau, 1992; Prilutsky & Gregor, 1997). These tight linear relations provided evidence that the RF and HAM activities were being co-regulated to control the combination of hip and knee moments that would generate the correct external force direction. In the present study we found a similar strong linear relationship in the pre-practice baseline condition (Fig. 9). However, if the RF and HAM activity were strongly related to pedal force direction control and the tuning of hip and knee torques, it would be expected that this relationship should be maintained (or even strengthened) after practice. In contrast, the relationship was more scattered in the post-practice condition, such that both muscles were active over a wider range of joint moment combinations. As mentioned earlier, in this particular task the changes in pedal force direction were focused mainly at the knee and ankle joints, so perhaps it is not surprising that the RF–HAM activity difference was not as closely linked to the hip–knee torque difference as task performance improved. This more diffuse linkage as force-directing improved indicates that bi-articular muscles can develop a more complex coupling within a force-directing task, and may sug-

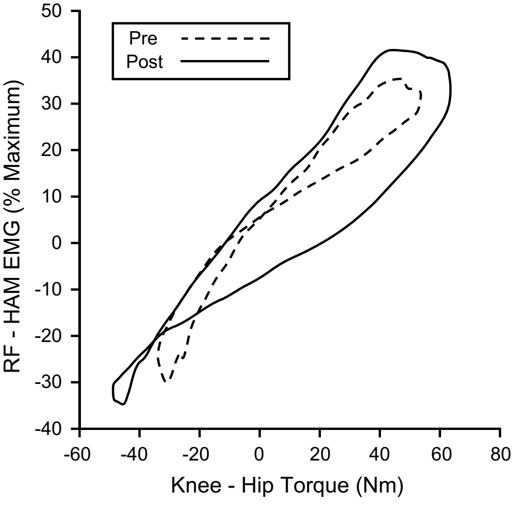

Fig. 9. Plot of the mean difference between rectus femoris (RF) and semitendinosus (HAM) muscle activity (scaled EMG) versus the mean difference between the knee and hip joint torques pre- and post-practice across the crank cycle.

gest that the neuromuscular system became more flexible with practice. In contrast to the ankle joint stiffening that may indicate simplified control and a decrease in the degrees-of-freedom of the task, the looser coupling of the bi-articular thigh muscles may mark the beginning of a proximal-to-distal progression of the release of degrees-of-freedom, as previously shown during the learning of throwing and writing tasks (McDonald, van Emmerik, & Newell, 1989; Newell & van Emmerik, 1989).

The one-legged cycling task incorporated many elements of multi-segment movements commonly found in daily living. External forces had to be controlled through regulation of joint torques; however, the number of solutions was limited by the constraints imposed by required joint excursions and the need for constant crank velocity. In such tasks all muscles, mono- and bi-articular, must work together in a synergistic manner. In previous studies using relatively simple isometric or isovelocity force-directing tasks, differences in mono- and bi-articular muscle responses may have resulted from the constraints of the tasks. For example, static force-directing against a force plate can be accomplished with only hip and knee torques, so the nervous system may use the RF–HAM co-activation strategy to simplify the task. More “complicated” tasks may require the central nervous system to use different strategies to meet task goals.

These results support the viewpoint of Kuo (2001), who considered muscle coordination using a mathematical approach based on the coupled dynamics of the multi-segmented human body. He argued that all individual muscles have unique actions that can contribute to the motion and dynamics of multiple segments whether they are directly connected to those segments or not. Therefore, all muscles can contribute in some way to joint torques, angular accelerations, and contact forces. The manner and degree to which any particular muscle contributes to a given outcome such as external force direction will depend on the redundant nature of the musculoskeletal system, the synergism that exists among contributing muscles, and the constraints present for the task at hand. From this perspective there is nothing inherently "special" in the functioning of bi-articular muscles, and it is futile to classify muscles based on the number of joints crossed. The nature of the task being performed will dictate possible roles for each muscle, regardless of the number of joints spanned by each.

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