Published in final edited form as:

Restor Neurol Neurosci. 2013 ; 31(1): 53–62. doi:10.3233/RNN-120247.

Effects of motor skill learning on reciprocal inhibition

Mary Kay Floeter^a, Laura E. Danielian^a, and Yong Kyun Kim^{b,*}

^aHuman Spinal Physiology Unit, National Institute of Neurological Disorders and Stroke, National Institutes of Health, Bethesda, MD, USA

^bDepartment of Physical Medicine and Rehabilitation, Kwandong University College of Medicine, Myongji Hospital, Koyang, South Korea

Abstract

Purpose—Learning a skilled movement is associated with more efficient use of subcortical motor circuits which can coordinate features of the movements such as the timing and patterns of activation of different muscles. Learning a motor skill could strengthen spinal interneuron circuits that facilitate the movement. We hypothesized that learning a simple, alternating movement would produce changes in spinal circuits that mediate reciprocal inhibition between antagonist muscles.

Methods—Sixteen healthy adult subjects were trained to perform a wrist flexion and extension task to control the movement of a cursor between targets appearing on a computer display. The goal of the task was to hit the targets. Subjects practiced for 15 minutes daily until reaching the acquisition criterion. Surface EMG recordings from wrist flexor and extensor muscles showed reduced co-contraction during acquisition of the task.

Results—Compared to the initial session, in the final session short-latency reciprocal inhibition was enhanced during the late-extension phase in the final session. This phase-dependent increase in short-latency reciprocal inhibition is likely to facilitate switching activation between wrist antagonistic muscles.

Conclusions—Learning a motor skill can produce alterations in spinal reflex circuits that facilitate the desired movement.

Keywords

Motor skill learning; reciprocal inhibition; electromyography; dual task; spinal plasticity

1. Introduction

The process of learning a goal-directed motor skill involves several stages. In the naïve state, the movement is performed poorly; with practice, the accuracy of the movement

© 2013 – IOS Press and the authors. All rights reserved

*Corresponding author: Yong Kyun Kim, MD, PhD, Department of Physical Medicine and Rehabilitation, Kwandong University Myongji Hospital, 697-24 Hwajung-dong, Dukyang-ku, Koyang, Kyunggi, South Korea, 412-270. Tel.: +82 31 810 5407; Fax: +82 31 969 0500; yongkyunk@gmail.com.

Conflict of interest

No commercial party having a direct financial interest in the results of the research supporting this article has or will confer a benefit on the authors or on any organization with which the authors are associated.

progressively improves, with an initial rapid rate of acquisition followed by a slower rate of improvement. Acquisition of a motor skill can be defined by success in achieving the intended goal, for example hitting a target with a particular level of accuracy. As the performance improves, changes occur concurrently in the smoothness of the movement and the pattern of muscle activity (Thoroughman and Shadmehr, 1999). However, the initial state of acquisition of the motor skill may be labile, susceptible to interference by introduction of competing motor tasks (Brashers-Krug et al., 1996) or to disruption by stimulation of the motor cortex (Muellbacher et al., 2002). A more stable post-acquisition state appears to require the passage of time for consolidation (Brashers-Krug et al., 1996; Krakauer and Shadmehr, 2006). Later, with extended practice and repetition, the motor skills may become so well-learned that they can be carried out relatively automatically, with reduced effort and little attention to the details of the performance of the movement (Lang and Bastian, 2002; Wu et al., 2004). Achievement of a post-acquisition state of automaticity, when the motor skill is well-learned, can be demonstrated by showing that the level of performance is maintained during simultaneous performance of a second task (Lang and Bastian, 2002; Poldrack et al., 2005).

The finding that motor skills become resistant to disruption by motor cortex stimulation as they become well-learned suggests that the site where the motor memory is encoded shifts during the process of motor learning. Functional imaging studies have also shown changes in the patterns and intensity of activity in various brain regions when motor sequence tasks became well-learned to the point of automaticity (Wu et al., 2004). The specific regions of the nervous system that undergo changes to encode motor skills is likely to be somewhat distinct for each task, reflecting its non-motor and motor elements (Lang and Bastian, 2002; Pascual-Leone et al., 1994; Wu et al., 2004). However for several simple motor tasks, it has been proposed that the site of encoding shifts from the primary motor cortex to cortical-subcortical networks in later stages of learning (Jensen et al., 2005; Pascual-Leone et al., 1994). Once a motor skill has been well-learned to the state of automaticity, cortical-subcortical networks appear to operate with stronger connectivity and greater efficiency (Wu et al., 2004). To date, most studies have examined changes occurring in supraspinal networks with motor skill learning. However, voluntary movements, particularly those involving repetitive movements, also use spinal circuits to generate patterns of coordinated muscle contraction, and spinal proprioceptive reflexes to refine the movement patterns (McCrea and Rybak, 2008; Nielsen, 2004). Several studies have shown that spinal stretch reflexes can be trained directly using operant conditioning (Wolpaw, 1987), but few studies have examined changes in spinal reflex pathways that occur indirectly during the course of learning a motor skill (Wolpaw, 2007).

To examine whether learning a motor skill produces changes in spinal circuits, we designed a task in which subjects learned to play a game that required wrist flexion-extension movements. The underlying movement that led to the best performance consisted of a rhythmic alternating contraction of antagonist muscles. We hypothesized that learning to play this game would indirectly lead to changes in circuits that promote alternating contraction between antagonists and reduce co-contraction. Reciprocal inhibition between antagonist muscles is mediated through spinal and cortical circuits, and is activated by cortical commands (Ethier et al., 2007) and by sensory feedback (Hultborn et al., 1976). At

the spinal level, reciprocal inhibition through reflex circuits occurs at short latencies, activated by primary Ia afferents acting at pre-and post-synaptic sites (Berardelli et al., 1987; Day et al., 1984; Hultborn et al., 1976). Short-latency reciprocal inhibition of wrist extensor muscles has previously been studied during tonic contraction by assessing the attenuation of the EMG signal elicited by stimulation of wrist flexor afferents in the median nerve (Crone et al., 2004). During repetitive movements, such as arm cycling, stretch reflexes and cutaneous reflexes have been shown to be modulated in a phase-dependent and task-dependent manner (Carroll et al., 2006; Carson, 2006; Stinear and Byblow, 2004b; Zehr et al., 2003). Short-latency reciprocal inhibition has not been previously examined during rhythmic arm movements, but in animals, the activity of the Ia inhibitory interneuron pathway exhibits strong phase-dependence during locomotion and scratching, increasing as the antagonist is in the latter portion of its activity phase (Degtyarenko et al., 1998; Pratt and Jordan, 1987).

In this study, our goals were 1) to determine whether the task exhibited a time course consistent with motor skill acquisition and attainment of automaticity, a state in which the motor skill has been well-learned, 2) to test whether flexor and extensor muscle activity patterns showed changes in co-contraction with learning the skill, and 3) to assess changes in short-latency reciprocal inhibition during the movement performance before and after the skill was well-learned, with conditions to assess task-and phase-dependence.

2. Materials and methods

2.1. Subjects

Sixteen healthy volunteers (3 men and 13 women, aged 22–45 years) participated in the study. The protocol was approved by the Institutional Review Board and all subjects gave written, informed consent in accord with the Declaration of Helsinki. All subjects were right-handed (laterality index was 0.8 to 1.0) as measured by the Edinburgh Inventory (Oldfield, 1971). They were free of wrist and neck pain and with no known history of medical problems.

2.2. Experimental setup

The subjects were seated in a chair with their right forearm supported by a horizontal platform and strapped in a neutral (semi-prone) position (Fig. 1). The right hand was secured between 2 vertical plates of a single-axis manipulandum that limited wrist movement to flexion and extension in the horizontal plane. The wrist joint was aligned with the axis of rotation of the manipulandum which controlled a cursor displayed on a computer screen. The manipulandum was coupled to a brushless servomotor (PMA23D, Pacific Scientific, IL) that supplied a constant resistive torque of 0.5 N-m, ensuring a steady and smooth wrist movement. The wrist was initially positioned at a neutral angle that produced no contraction in wrist flexors and extensors, designated as 0 degrees of wrist displacement.

2.2.1. Experiment 1: Performance of the motor task—Subjects were instructed to move the manipulandum back and forth to cause the cursor to hit circular targets that would appear alternately on the right and left sides of a computer screen at 5-s interval which is the

amount of time for hitting each pair of targets. There were two pairs of small and large targets were interdigitated: large targets at 10 degrees wrist flexion and extension and small targets at 5 degrees wrist flexion and extension. The diameters of the targets were 20% of the target location angle (i.e., the 10 degree targets were 2 degrees in diameter, centered at ± 10 degrees off midline). The criteria for a successful target “hit” was based on the timing of an ideal sinusoidal movement of the manipulandum in which the cursors reached the target centers at an exact rate of 0.2 Hz. A successful hit was defined as reaching the target without overshooting and staying within 10% of the target angle with the frequency of 0.2 Hz. Subjects received visual feedback of their success in each trial by a color change of the target. No instructions were given regarding the movement trajectory to perform or the electromyographic (EMG) pattern to produce, and subjects did not receive feedback about either of these measures.

Each training session consisted of 360 target trials. The 15-min sessions were broken up into 3 segments of 5 minutes with a brief rest period between the segments to avoid fatigue. Training sessions occurred every weekday until the task was learned. Acquisition of the skill was defined as improvement of the success rate by at least 20% from the initial session in two successive sessions. After acquisition of the skill, training continued for at least 2 more sessions until the skill was learned to the state of automaticity. Achievement of automaticity was defined by the ability to perform an acoustic discrimination task without decline in success at hitting targets (Lang and Bastian, 2002; Poldrack et al., 2005). The 5-min acoustic discrimination task was tested at the end of the post-acquisition training sessions. Subjects were asked to count the number of high-toned beeps from a random presentation of high and low-toned beeps while simultaneously carrying on the movement task. For experiment 1 only, to characterize whether this paradigm resulted in long-term retention of the motor skill, eight subjects were tested one week later, without any intervening practice.

2.2.2. Experiment 2: Co-contraction—Surface EMG recordings were evaluated from the initial session, the session at which the acquisition criterion was achieved and the final session when the task could be performed automatically. Although several forearm muscles participate in wrist movement, the flexor carpi radialis (FCR) and extensor carpi radialis (ECR) were chosen for recording because these two muscles have been shown to be active and function as strict antagonists during wrist flexion-extension movements in the horizontal plane (Bawa et al., 2000). EMG was recorded from paired 10-mm stainless steel disk electrodes with the active electrodes placed on each muscle belly and the reference electrode 3 cm distally. Recordings were made using a Counterpoint EMG machine (Dantec, Allendale, NJ) with a filter bandwidth of 10 Hz to 5 kHz. Waveforms were digitized to a personal computer at a sampling rate of 11 kHz with rectification and smoothing for off-line analysis using Spike 2 software program (CED 1401 interface, Cambridge, UK).

The wrist movement cycle was divided into two flexion and extension phases whose timing was defined by the ideal sinusoidal movement (Fig. 2, upper and middle traces). The rectified EMG area from each muscle during each phase was expressed as a percentage of its EMG area during the full cycle to normalize for recording differences between sessions. Co-contraction was defined as EMG activity occurring during the phases of the cycle produced by antagonist muscle contraction. Thus, the area of the ECR EMG during the flexion phases

was expressed as a percentage of the ECR EMG area in both flexion and extension phases as a measure of co-contraction.

2.2.3. Experiment 3: Reciprocal inhibition during motor task training—Short-latency reciprocal inhibition of wrist extensor muscles was assessed using a stimulus-triggered averaging method. Bipolar stimulation of the median nerve at the elbow level, in which cathode was proximal, produces a depression of rectified EMG of wrist ECR muscle (Capaday et al., 1990; Crone et al., 2004). This inhibition is likely to be mediated mostly by Ia inhibitory inter-neurons projecting from wrist flexors to wrist extensors. In this method, electrical stimulation of the median nerve, which innervates the FCR muscle, was used to activate the primary afferents of the wrist flexor muscles. The median nerve was stimulated at the elbow with a 1-ms duration pulse using an intensity of 1.1 times the motor threshold, an intensity that has previously been shown to activate Ia afferents and spinal pathways for reciprocal inhibition at rest (Day et al., 1984; Fuhr and Hallett, 1993). It is low enough to avoid saturation of the reciprocal inhibitory pathway (Petersen et al., 1999). Time-locked depression of the ECR EMG by median nerve stimulation was assessed in a 22-ms time window beginning approximately 25 ms after the stimulus (Fig. 3). The early period of ECR EMG excitation is cross-talk from the FCR compound muscle action potential (CMAP) elicited by the median nerve stimulation, which was done at 1.1 times the motor threshold. A duration of this window encompassed the entire period of EMG depression for all subjects. The latency of the inhibition was determined individually for each subject by visual inspection of the averaged waveform which best demonstrated EMG suppression. The area of ECR EMG in the 22-ms time window in cycles with median nerve stimulation was subtracted from the area of ECR EMG in cycles without stimulation at the corresponding time points to quantify reciprocal inhibition. Reciprocal inhibition was measured at two phase time-points, at mid-extension and late-extension (Fig. 2, lower trace), and separately during a tonic contraction at matched wrist joint angles and torques as described in experiment 4. The extension movements toward the larger targets were assessed because the duration of this phase was sufficiently long to allow assessment of more than one phase time-point. The timing of median nerve stimulation was set in pilot studies to observe the onset of EMG activity as wrist moved in flexion and extension. Mid-extension occurred 0.5 seconds after the onset of the extension phase, and late-extension occurred 0.8 seconds before the end of the extensor phase, as calculated from the idealized sinusoidal wave. The median nerve was stimulated every 4th cycle, alternating between mid- and late-extension timings. The interleaved cycles without stimulation were used as the baseline EMG. Forty-eight epochs were averaged for each condition: mid-extension with and without stimulation, and late-extension cycles with and without stimulation. Epochs consisted of 300-ms beginning 40 ms prior to the stimulus. Waveforms were digitized for off-line analysis using custom software (Labview 6.1; National Instruments, Austin, TX) at a sampling rate of 10 kHz.

2.2.4. Experiment 4: Reciprocal inhibition during tonic contraction—To control for changes in reciprocal inhibition attributable to the magnitude of contraction, joint angle, or muscle length, reciprocal inhibition was evaluated during tonic contraction prior to beginning the session with the motor skill task. The wrist was positioned at either 0 degrees

(midline) or 10 degrees of extension in the manipulandum, corresponding to the positions at the mid-extension and late-extension time point of the movement task. The torque motor was switched to a fixed-position mode, and subjects were asked to maintain a steady torque of 0.5 N-m to match the resistance level during task training. Fifty epochs of median nerve stimulation were collected at each position during this tonic contraction. Reciprocal inhibition was assessed as described above, using the same time windows for each subject and using the ECR EMG preceding the stimulus artifact as a baseline.

2.3. Statistical analysis

A repeated measures ANOVA was used to assess the effects of training on the motor performance and co-contraction using Fisher's PLSD to detect significant *post-hoc* contrasts. A 2-factor (session X phase) repeated measures ANOVA was used to assess reciprocal inhibition between the first and last training sessions and the two time points during the extension phase. For ANOVAs, p values of $p < 0.05$ were considered significant. All descriptive statistics are reported as mean $\pm$ SD.

3. Results

3.1. Experiment 1: Performance of the motor task

Nine healthy adult subjects participated in the first experiment to determine the time course of acquisition, achievement of automaticity, and long term retention of the motor task. Acquisition of the skill was defined as improvement of the success rate for hitting targets by at least 20% from the initial session in two successive sessions. Subjects continued training after acquisition for at least 2 more sessions until the skill was learned to the criterion for the state of automaticity. Achievement of automaticity was defined by the ability to perform an acoustic discrimination task without decline in success at hitting targets (Lang and Bastian, 2002; Poldrack et al., 2005). Only eight of the nine subjects were able to learn the task to the criterion for acquisition. One subject was unable to learn the task after twelve training sessions and will not be further included in the analysis. For the remaining subjects, the initial success rates varied among individual subjects (35.6%–75.0%). However, with successive sessions, performance rapidly improved (Fig. 4). Acquisition of the motor skill typically was achieved within one week. Seven of the subjects reached the criterion for acquisition by the third training session. The eighth subject required seven training sessions. Variability of performance declined with additional practice. When tested after one week without intervening practice, all subjects maintained their level of performance without a significant decline in success rate. Seven of the subjects achieved automaticity, as demonstrated by their ability to maintain the level of performance in the motor task while performing an auditory discrimination task. Automaticity was achieved in 7.9 ± 2.0 training sessions. In all subjects, the wrist motion trajectory changed as the skill was learned, to more closely approximate the trajectory of the ideal sinusoidal movement that would theoretically produce a perfect score. The time course of the improvement in trajectory paralleled the time course of improved performance in obtaining successful target hits.

3.2. Experiment 2: Co-contraction

In thirteen subjects, surface EMG from the FCR and ECR muscles was analyzed during the initial training session and the sessions in which criteria for acquisition and automaticity were achieved to assess co-contraction. Co-contraction was defined as the EMG activity in each muscle during the phase of movement produced by the antagonist muscle. For the FCR muscle, the amount of EMG activity occurring during wrist extension did not change significantly across the three sessions. However, ECR EMG activity during flexion declined over the three sessions (repeated measures ANOVA, $p < 0.05$; Fig. 5), with a significant difference from the first to the last session, when the criterion for automaticity was achieved (Fisher's test $p < 0.025$).

3.3. Experiment 3: Reciprocal inhibition during motor task training

Short-latency reciprocal inhibition of ECR EMG during performance of the movement was elicited with median nerve stimulation, as described in experimental procedures section, interleaving trials in which the stimulus was timed for mid-extension and for late-extension. The latency of inhibition differed slightly in the seven subjects who participated in this experiment, as expected from variations in electrode position and arm length, but there was no change in latency over the training sessions (25.5 ± 2.7 ms in the first training session and 25.1 ± 4.1 ms in the final training session). The strength of reciprocal inhibition increased from the initial session to the final session (Fig. 6). There was a significant main effect of training session ($F = 10.16$, $p < 0.05$) and an interaction with the phase ($F = 4.01$, $p < 0.05$). The greatest increase in reciprocal inhibition occurred in late-extension (Fig. 6A), suggesting that training may differentially interact with underlying circuits that produce phase-dependent modulation of reciprocal inhibition. Because reciprocal inhibition was only tested in the first and last session, we could not determine whether these changes occurred at the time of skill acquisition or with automaticity. There was no correlation between the magnitude of change in reciprocal inhibition and rate of motor learning in individual subjects.

3.4. Experiment 4: Reciprocal inhibition during tonic contraction

To control for changes produced by the level of muscle contraction or joint angles at the time points in the cycle that were tested during the movement task, reciprocal inhibition was measured at matched levels of torque and joint angle just before the first and final training sessions of Experiment 3 (Fig. 6). Overall there was a trend for weaker reciprocal inhibition during the performance of the movement task than during tonic contraction. There was also a trend for less reciprocal inhibition at the wrist position corresponding to the late-extension position in the first training session compared to the last session, although the difference did not reach significance ($F = 4.379$, $p = 0.07$). There was considerable variability between individual subjects, as Fig. 6 illustrates, and further studies would be needed to assess this issue.

4. Discussion

In this study, we found that the movement task was learned with a characteristic time-course for motor skill learning, having an initial rapid rate of acquisition over several daily sessions

and long-term retention for at least one week without practice after the task was learned. The explicit instruction to subjects was only to achieve a goal – moving a cursor on a computer screen to hit targets as they appeared. The criteria for a successful hit were not explicitly provided, only trial-by-trial feedback on success. In these respects, the task was analogous to the real-life manner of learning many motor skills, in which the objective is to achieve a goal, not to perform a specific pattern of muscle contraction or produce an EMG signal. The changes that were observed in muscle co-contraction occurred as an indirect accompaniment of the goal-directed learning. We focused on short-latency reciprocal inhibition in this study because it is one mechanism that could underlie reduced co-contraction during movement, but recognize that it is unlikely to be the only change that occurs with learning this task. Other studies of motor skills learned with a similar time course have demonstrated changes in the excitability of the motor cortex representations of the muscles used (Jensen et al., 2005; Muellbacher et al., 2002) and changes in presynaptic inhibition of muscle afferents (Perez et al., 2005). To our knowledge previous studies have not assessed the status of spinal circuits for reciprocal inhibition when motor skills are acquired and well-learned.

Training caused a greater change in reciprocal inhibition at the end of the extension than in mid-extension. This timing, as the movement approached the transition from extension to flexion, would be appropriate to facilitate a braking activity of the extensor muscles and switch to the alternate phase of movement. This observation is compatible with a phase-dependent mechanism for modulation of reciprocal inhibition, which has been described for locomotor rhythms (Capaday et al., 1990; Degtyarenko et al., 1998; Petersen et al., 1999; Pratt and Jordan, 1987; Pyndt and Nielsen, 2003). Phase dependent modulation of reciprocal inhibition would be consistent with previous studies showing phase dependent modulation of sensory reflexes during cyclic arm movement (Carroll et al., 2006; Zehr et al., 2003). The trend for weaker reciprocal inhibition during movement than tonic contraction is consistent with a state-or task-dependent modulation of spinal reflex circuits (Burke, 1999). However, there are a number of factors that could contribute to task-dependent modulation. Initiating voluntary contraction modulates reciprocal inhibition by changing the excitability of Ia inhibitory interneurons (Nielsen et al., 1995). Corticospinal excitability has been shown to decline during rhythmic arm cycling compared to tonic contraction (Carroll et al., 2006), indicating that the descending commands that modulation reciprocal inhibition during tonic contraction are probably attenuated during continued active movement. Passive movement of the arm alone has been shown to reduce the gain of stretch reflexes (Brooke et al., 2000), and the reduced afferent input would also lead to less activation of reciprocal inhibition. However, because the same task was used throughout in this study, task-related modulation is not sufficient to explain changes in reciprocal inhibition observed with training.

The method we used for assessing reciprocal inhibition was adapted from a method described for assessing reciprocal inhibition of the ankle dorsiflexors (Capaday et al., 1990; Crone et al., 2004; Petersen et al., 1999). The time window chosen for assessing inhibition primarily evaluates effects in short-latency circuits with a timing appropriate for disynaptic and presynaptic Ia inhibition, but contributions from other circuits cannot be excluded. It is possible that long-loop or transcortical reflexes may come into play near the end of the time window assessed. It is known that a significant portion of the cortical control of the wrist is relayed through cervical propriospinal interneurons (Gracies et al., 1991; Pierrot-

Deseilligny, 1996) which also show modulation during unilateral arm movements (Stinear and Byblow, 2004a). Cervical propriospinal interneurons also receive Ia input, but because they project in a rather diffuse pattern to arm motor neuron pools they seem less likely to be contributing to the inhibition measured. The applicability of enhanced reciprocal inhibition to reduced co-contraction also needs further careful assessment. Reduced co-contraction can arise in different ways, including a more selective activation of corticospinal projections as well as reflex pathways. A decline in co-contraction with practice can be observed when learning discrete targeted movements of the arm (Gribble et al., 2003; Osu et al., 2002; Thoroughman and Shadmehr, 1999). Further studies would be needed to assess whether changes in co-contraction in non-rhythmic tasks are associated with changes in short-latency reciprocal inhibition similar to those reported here.

The finding that rhythmic, alternating movement training can strengthen reciprocal inhibition and decrease co-contraction during active movement may provide support for exercise training using an arm or bicycle ergometer in a clinical setting to decrease spasticity or other conditions with abnormal muscle co-contraction. Our finding that spinal circuits for short-latency reciprocal inhibition underwent modification as this simple task was learned highlights the importance of assessing multiple levels of the motor system to better understand how motor skills are encoded.

This phase-dependent increase in short-latency reciprocal inhibition is likely to facilitate switching activation between wrist antagonistic muscles. Learning a motor skill can produce alterations in spinal reflex circuits that facilitate the desired movement.

Acknowledgments

Grants

This research was supported by the Intramural Research Program of the NIH, National Institute of Neurological Disorders and Stroke.

We thank the Research Services Branch, NIH for fabrication and technical support of instrumentation.

References

- Bawa P, Chalmers GR, Jones KE, Sogaard K, Walsh ML. Control of the wrist joint in humans. *Eur J Appl Physiol.* 2000; 83:116–127. [PubMed: 11104052]
- Berardelli A, Day BL, Marsden CD, Rothwell JC. Evidence favouring presynaptic inhibition between antagonist muscle afferents in the human forearm. *J Physiol.* 1987; 391:71–83. [PubMed: 3443961]
- Brashers-Krug T, Shadmehr R, Bizzi E. Consolidation in human motor memory. *Nature.* 1996; 382:252–255. [PubMed: 8717039]
- Brooke JD, Peritore G, Staines WR, McIlroy WE, Nelson A. Upper limb H reflexes and somatosensory evoked potentials modulated by movement. *J Electromyogr Kinesiol.* 2000; 10:211–215. [PubMed: 10818342]
- Burke RE. The use of state-dependent modulation of spinal reflexes as a tool to investigate the organization of spinal interneurons. *Exp Brain Res.* 1999; 128:263–277. [PubMed: 10501799]
- Capaday C, Cody FW, Stein RB. Reciprocal inhibition of soleus motor output in humans during walking and voluntary tonic activity. *J Neurophysiol.* 1990; 64:607–616. [PubMed: 2213135]
- Carroll TJ, Baldwin ER, Collins DF, Zehr EP. Corticospinal excitability is lower during rhythmic arm movement than during tonic contraction. *J Neurophysiol.* 2006; 95:914–921. [PubMed: 16251263]

- Carson RG. Changes in muscle coordination with training. *J Appl Physiol.* 2006; 101:1506–1513. [PubMed: 16888047]
- Crone C, Petersen NT, Nielsen JE, Hansen NL, Nielsen JB. Reciprocal inhibition and corticospinal transmission in the arm and leg in patients with autosomal dominant pure spastic paraparesis (ADPSP). *Brain.* 2004; 127:2693–2702. [PubMed: 15509621]
- Day BL, Marsden CD, Obeso JA, Rothwell JC. Reciprocal inhibition between the muscles of the human forearm. *J Physiol.* 1984; 349:519–534. [PubMed: 6737302]
- Degtyarenko AM, Simon ES, Norden-Krichmar T, Burke RE. Modulation of oligosynaptic cutaneous and muscle afferent reflex pathways during fictive locomotion and scratching in the cat. *J Neurophysiol.* 1998; 79:447–463. [PubMed: 9425213]
- Ethier C, Brizzi L, Giguere D, Capaday C. Corticospinal control of antagonistic muscles in the cat. *Eur J Neurosci.* 2007; 26:1632–1641. [PubMed: 17880397]
- Fuhr P, Hallett M. Reciprocal inhibition of the H-reflex in the forearm: Methodological aspects. *Electroencephalogr Clin Neurophysiol.* 1993; 89:319–327. [PubMed: 7691571]
- Gracies JM, Meunier S, Pierrot-Deseilligny E, Simonetta M. Pattern of propriospinal-like excitation to different species of human upper limb motoneurons. *J Physiol.* 1991; 434:151–167. [PubMed: 2023116]
- Gribble PL, Mullin LI, Cothros N, Mattar A. Role of cocontraction in arm movement accuracy. *J Neurophysiol.* 2003; 89:2396–2405. [PubMed: 12611935]
- Hultborn H, Illert M, Santini M. Convergence on interneurons mediating the reciprocal Ia inhibition of motoneurons. I. Disynaptic Ia inhibition of Ia inhibitory interneurons. *Acta Physiol Scand.* 1976; 96:193–201. [PubMed: 1258669]
- Jensen JL, Marstrand PC, Nielsen JB. Motor skill training and strength training are associated with different plastic changes in the central nervous system. *J Appl Physiol.* 2005; 99:1558–1568. [PubMed: 15890749]
- Krakauer JW, Shadmehr R. Consolidation of motor memory. *Trends Neurosci.* 2006; 29:58–64. [PubMed: 16290273]
- Lang CE, Bastian AJ. Cerebellar damage impairs automaticity of a recently practiced movement. *J Neurophysiol.* 2002; 87:1336–1347. [PubMed: 11877508]
- McCrea DA, Rybak IA. Organization of mammalian locomotor rhythm and pattern generation. *Brain Res Rev.* 2008; 57:134–146. [PubMed: 17936363]
- Muellbacher W, Ziemann U, Wissel J, Dang N, Kofler M, Facchini S, Boroojerdi B, Poewe W, Hallett M. Early consolidation in human primary motor cortex. *Nature.* 2002; 415:640–644. [PubMed: 11807497]
- Nielsen J, Crone C, Sinkjaer T, Toft E, Hultborn H. Central control of reciprocal inhibition during fictive dorsiflexion in man. *Exp Brain Res.* 1995; 104:99–106. [PubMed: 7621944]
- Nielsen JB. Sensorimotor integration at spinal level as a basis for muscle coordination during voluntary movement in humans. *J Appl Physiol.* 2004; 96:1961–1967. [PubMed: 15075316]
- Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia.* 1971; 9:97–113. [PubMed: 5146491]
- Osu R, Franklin DW, Kato H, Gomi H, Domen K, Yoshioka T, Kawato M. Short- and long-term changes in joint co-contraction associated with motor learning as revealed from surface EMG. *J Neurophysiol.* 2002; 88:991–1004. [PubMed: 12163548]
- Pascual-Leone A, Grafman J, Hallett M. Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science.* 1994; 263:1287–1289. [PubMed: 8122113]
- Perez MA, Lugholt BK, Nielsen JB. Presynaptic control of group Ia afferents in relation to acquisition of a visuo-motor skill in healthy humans. *J Physiol.* 2005; 568:343–354. [PubMed: 16051628]
- Petersen N, Morita H, Nielsen J. Modulation of reciprocal inhibition between ankle extensors and flexors during walking in man. *J Physiol.* 1999; 520(Pt 2):605–619. [PubMed: 10523426]
- Pierrot-Deseilligny E. Transmission of the cortical command for human voluntary movement through cervical propriospinal premotoneurons. *Prog Neurobiol.* 1996; 48:489–517. [PubMed: 8804118]

- Poldrack RA, Sabb FW, Foerde K, Tom SM, Asarnow RF, Bookheimer SY, Knowlton BJ. The neural correlates of motor skill automaticity. *J Neurosci*. 2005; 25:5356–5364. [PubMed: 15930384]
- Pratt CA, Jordan LM. Ia inhibitory interneurons and Renshaw cells as contributors to the spinal mechanisms of fictive locomotion. *J Neurophysiol*. 1987; 57:56–71. [PubMed: 3559681]
- Pyndt HS, Nielsen JB. Modulation of transmission in the corticospinal and group Ia afferent pathways to soleus motoneurons during bicycling. *J Neurophysiol*. 2003; 89:304–314. [PubMed: 12522181]
- Stinear JW, Byblow WD. Modulation of human cervical premotoneurons during bilateral voluntary contraction of upper-limb muscles. *Muscle Nerve*. 2004a; 29:506–514. [PubMed: 15052615]
- Stinear JW, Byblow WD. Rhythmic bilateral movement training modulates corticomotor excitability and enhances upper limb motricity poststroke: A pilot study. *J Clin Neurophysiol*. 2004b; 21:124–131. [PubMed: 15284604]
- Thoroughman KA, Shadmehr R. Electromyographic correlates of learning an internal model of reaching movements. *J Neurosci*. 1999; 19:8573–8588. [PubMed: 10493757]
- Wolpaw JR. Operant conditioning of primate spinal reflexes: The H-reflex. *J Neurophysiol*. 1987; 57:443–459. [PubMed: 3559687]
- Wolpaw JR. Spinal cord plasticity in acquisition and maintenance of motor skills. *Acta Physiol (Oxf)*. 2007; 189:155–169. [PubMed: 17250566]
- Wu T, Kansaku K, Hallett M. How self-initiated memorized movements become automatic: A functional MRI study. *J Neurophysiol*. 2004; 91:1690–1698. [PubMed: 14645385]
- Zehr EP, Collins DF, Frigon A, Hoogenboom N. Neural control of rhythmic human arm movement: Phase dependence and task modulation of hoffmann reflexes in forearm muscles. *J Neurophysiol*. 2003; 89:12–21. [PubMed: 12522155]

Fig. 1.

Experimental set-up. The subject sat facing a computer display on which a cursor's movement was controlled by wrist movements. As the subject moved his wrist between targets on alternating sides of the display, the wrist position and surface EMG of flexor and extensor muscles were recorded to a separate computer viewed by the experimenter.

Fig. 2.

Individual subject recording. An example of raw data recorded during a portion of the wrist movement task from a single subject during experiment 3, testing of reciprocal inhibition. Seven complete cycles are illustrated, with each cycle consisting of two extension and two flexion phases. Upper trace: wrist displacement. Middle trace: timing of extension phase onset for a sinusoidal trajectory that would produce ideal performance. Lower trace: surface EMG recording from the Extensor carpi radialis muscle. Arrowheads indicate timing of median nerve stimulation at mid-and late. Effects of motor skill learning on reciprocal inhibition Kim et al. extension. Tick mark shows cycle used for baseline measurement. In this figure, the surface EMG recording from the FCR muscle is not shown.

Fig. 3.

Averaged waveforms for measurement of reciprocal inhibition. Rectified averaged ECR EMG with and without median-nerve stimulation during mid-extension in an individual subject. The black waveform shows the averaged ECR EMG from 48 traces from the baseline cycles (without stimulation). The superimposed gray waveform shows the averaged ECR EMG from 48 interleaved cycles in which median nerve stimulation was given. Vertical cursors indicate the 22-ms analysis window used for measuring short-latency reciprocal inhibition. The asterisk shows the area assessed, the difference between the baseline and stimulated traces.

Fig. 4.

Time course of motor skill learning. Performance of the motor task over successive days of training in 8 subjects. The success rate in hitting targets rapidly improved over several days. Performance level was maintained when tested after one week later without intervening practice.

Fig. 5.

Co-contraction with motor skill learning. Co-contraction, defined by percent of ECR EMG activity occurring during flexion expressed as a percent of ECR EMG in full cycle, declined from with skill learning. Measures shown are from surface EMG recordings from the initial training session, the session in which the criterion for acquisition was achieved, and the final session when automaticity was attained 13 subjects. Asterisk indicates $p < 0.025$ by *post-hoc* Fisher's test. Activity of FCR EMG in extension did not change (not shown).

Fig. 6.

Reciprocal inhibition. Measures of short-latency reciprocal inhibition of the ECR EMG area by median nerve stimulation were made during the movement task at A) Late-extension and B) Mid-extension and during tonic contraction at corresponding matched joint angles and torque. Individual subjects (symbols) and group means (lines) are shown. Reciprocal inhibition increased from the initial to the final training sessions of the movement task ($p < 0.05$, right side of both panels) with a greater change in late extension (A) than mid-extension (B). Inhibition was quantified as the area of depression of ECR EMG from stimulation minus non-stimulated cycles for the movement task and from stimulation minus pre-stimulus baseline epochs for tonic contraction.