INTRODUCTION

Adult cats that receive a complete spinal cord transection can regain the ability to step (Barbeau and Rossignol 1987; Lovely et al. 1986) and to stand (Pratt et al. 1994). It has been shown that the ability to regain full weight-bearing stepping is to a large extent dependent on the animals being trained to perform that task over a period of weeks following spinalization (de Leon et al. 1998; Lovely et al. 1986). Further, evidence has been presented that the stepping ability was not attributable to the effects of training on the skeletal musculature (Roy and Acosta 1986; Roy et al. 1991, 1998). The present paper addresses the question of whether the recovery of standing following spinalization depends on the repetitive practice of that specific task. Kozak and Westerman (1967) reported improvements in weight bearing following spinalization in kittens that were trained to stand by electrically stimulating the sciatic nerve to elicit hindlimb extension, although no data were presented on the lengths of time that standing occurred without collapse. Pratt et al. (1994) reported that one cat that was unable to stand immediately after spinalization could perform full weight-bearing episodes lasting 15 min 4 wk postspinal. Although this cat was trained daily (30–45 min) for several weeks beginning 4 days after spinalization, the degree to which the recovery of the ability to stand was attributable to training versus spontaneous recovery following surgery is unclear because recovery without training was not tested.

Some recovery of the ability to stand can occur without training. For example, standing episodes in spinal animals have been observed (Giuliani and Smith 1985; Kellogg et al. 1946) as have certain extension reflexes, i.e., positive supporting responses (Goldberger 1988; Robinson and Goldberger 1986), in the absence of any type of training. Thus the extent to which improvements in standing ability following spinalization can be attributed to the effect of practicing that specific task versus spontaneous recovery has not been determined.

In the present study, two approaches were used to determine whether practicing a standing task daily affects the ability of adult spinal cats to stand. First, behavioral and physiological characteristics of standing in nontrained spinal cats and in spinal cats that received daily weight-bearing training of both hindlimbs (bilateral hindlimb standing) were compared. The second approach was to compare the performance and physiological characteristics of standing in the hindlimbs of the same cat when only one hindlimb was trained to stand (unilateral hindlimb standing). The present results demonstrate that both bilateral and unilateral stand training improved standing ability following spinalization significantly more than can be attributed to spontaneous recovery from spinalization. Furthermore, the data indicate that the recovery of this postural task in the hindlimbs, like locomotor recovery (de Leon et al. 1998; Edgerton et al. 1997a,b; Hodgson et al. 1994), can be largely an experience-dependent process mediated by neural networks in the spinal cord and, therefore, provides another example of spinal learning. Some preliminary results have been published (Edgerton et al. 1997a,b).

METHODS

Experimental design

Electromyographic (EMG) electrodes were implanted in selected hindlimb muscles of 10 adult female cats. EMG and kinematic data were collected from the hindlimbs while each cat stood quietly. After sufficient data were collected, the spinal cords of the cats were completely transected (T12–T13).

To determine the effect of bilateral hindlimb stand training on the recovery of standing, two spinal cats were trained daily to perform bilateral full weight-bearing standing beginning 1 wk after...
spinalization. The standing ability of the two trained animals was compared with standing in six spinal cats that were not trained during the 12 wk after spinalization. Performance of standing was tested 1, 6, and 12 wk after spinalization. EMG and kinematic data were collected during the tests of standing on the 12th wk postspinalization.

To determine the effect of unilateral stand training on the recovery of standing, two other spinal cats were trained daily to stand beginning 1 wk after spinalization on one hindlimb while the contralateral hindlimb was unweighted. To compare the standing ability in the trained and nontrained hindlimbs, tests of unilateral standing of both limbs and of bilateral standing were performed 12 wk after spinalization. EMG, kinematic, and ground reaction force data were collected during all standing tests.

Surgical procedures

During all surgical procedures, pentobarbital sodium (35 mg/kg ip) was administered to each cat after pretreatment with atropine (ip) and acepromazine (im). Supplemental doses of anesthesia were administered as needed during surgery to maintain a low level of arousal (Roy et al. 1992).

Before spinalization, intramuscular recording electrodes were chronically implanted in selected hindlimb muscles in the right hindlimb [deep region of the distal compartment of the semitendinosus (St), lateral deep portion of the vastus lateralis (VL), distal portion of the iliopsoas (IP), midbelly of the gluteus medius (GM), midbelly of the soleus (Sol), midbelly deep portion of the tibialis anterior (TA), medial deep portion of the medial gastrocnemius (MG), and lateral deep portion of the lateral gastrocnemius (LG)] as previously described (de Leon et al. 1994; Pierotti et al. 1989). After each muscle was back-stimulated to ensure proper electrode placement, each wire was secured in the muscle with a suture at its entry and exit from the muscle.

The spinal cords were transected at the T12–T13 junction as described in detail previously (Roy et al. 1992). Briefly, a skin incision was made on the back to expose the vertebral processes between T10 and T1. A partial laminectomy was performed to expose the spinal cord at the T12–T13 junction. Fine scissors and forceps were used to cut the dura and to perform the transection beginning on the dorsal surface of the cord between T12 and T13. After the transection, no spinal cord matter was visible between the two cut ends of the cord. The ends of the cord retracted leaving a clear space between the two cut ends. This procedure allowed for the preservation of the large ventral artery of the spinal cord. Gel foam was inserted in the space, and the muscle and skin above the lesion site were closed with sutures.

Animal care procedures

Postspinalization management of the spinal cats has been detailed elsewhere (Roy et al. 1992). Cats were housed in spacious cages, two to four cats per cage, with the cage floors covered with shredded newspaper. The bladders and colons of the cats were expressed manually twice daily for the duration of the experiment. Dry kibble and water were given ad libitum, and wet food was given once daily. All procedures were performed in accordance with the American Physiological Society Animal Care Guidelines and were approved by the Animal Use Committee at the University of California, Los Angeles.

Hindlimb training and testing procedures

During all training and testing procedures, a cloth harness was fitted over the shoulders, between the forelimbs, and around the upper trunk, and the forelimbs of the cats rested on a platform raised ~2.5 cm above the training surface. Food rewards (Gerbers Baby Food) were used to encourage the animals to maintain a steady posture while in the harness.

After spinalization, training was performed for 30 min/day, 5 days/wk. To train full weight-bearing bilateral hindlimb standing, the hindpaws were placed on the plantar surfaces, and the skin around the knee or ankle was patted lightly or pinched to elicit extensor reflexes. These stimuli were not used to maintain standing but were delivered when necessary to reinitiate standing when the hindlimbs collapsed to a sitting, non-weight-bearing position. The trainers held the tail only to provide lateral support during standing. To monitor improvements in standing ability across training sessions, the duration of each bout of standing during training, i.e., lengths of time that full weight-bearing extension was maintained in the hindlimbs, was recorded.

To train unilateral standing, weight bearing was allowed in only one hindlimb (trained limb) while the other limb (nontrained limb) was held above the training surface. To maintain lateral stability during unilateral standing, it was necessary to shift the weight of the hindquarters onto the trained limb. Typically, the trainers held the paw of the nontrained limb and moved it posteriorly and dorsally to the near edge of the tail, resulting in the hindquarters leaning toward the weight-bearing limb. Lateral support was provided by holding the nontrained limb and the tail of the animal. Cutaneous stimuli, as noted for bilateral standing, were used to initially facilitate but not to maintain standing in the weight-bearing limb. When the hindlimb collapsed to a sitting, non-weight-bearing position, the trained and nontrained limbs were repositioned before weight-bearing was reinitiated.

To evaluate standing ability after spinalization, weight bearing in one or both hindlimbs was initiated using the same stimuli that were used during training. After a weight-bearing posture was attained, the initiating stimuli were removed, and the hindlimbs were allowed to stand until they collapsed to a sitting, non-weight-bearing position. The tail, and in the case of unilateral standing, the paw, were held to aid lateral stability of the hindquarters. When providing assistance during tests of bilateral standing, the trainers sought to maintain an equal distribution of weight between the two hindlimbs. Several bouts of standing were initiated to ensure a consistent performance. To minimize any training effects during testing of unilateral standing, the duration of the unilateral stand tests performed 12 wk after spinalization was limited to 240 s.

Data recording and analysis

EMG and kinematic data during standing were recorded from all animals (with the exception of 1 nontrained spinal cat, from which only kinematic data were recorded after spinalization), and the recording procedures have been previously described in detail (de Leon et al. 1994). Briefly, raw EMG signals were amplified and recorded on an FM tape recorder (TEAC Model XR-510, TEAC, Montebello, CA) while a camera and video cassette recorder (Panasonic System Camera, WV D5100; Panasonic AG1280P Panasonic, Cypress, CA) were used to record the video sequences from which EMG activity was recorded and analyzed.
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Statistics

Computer-based resampling (‘‘bootstrap’’) (Efron and Tibshirani 1993) software (Resampling Stats 4.0.2, Arlington, VA) was used to analyze differences in group means (trained vs. nontrained) as described previously (de Leon et al. 1998). Group means for standing duration were calculated by averaging the duration of the first three standing episodes that were observed in each animal during a testing session. This ensured that the values for standing duration were not influenced by any training effect that could have occurred during testing.

To analyze changes in standing ability over time, the longest standing episodes measured during tests performed 1, 6, and 12 wk after spinalization were used to generate scatter plots of maximum standing duration versus time. Slope values for the trained and nontrained groups were calculated from the scatter plots, and a resampling approach was used to determine whether the slope values for the two groups were significantly different from zero ($P < 0.01$).

RESULTS

Performance of bilateral hindlimb standing

Spinal cats that received bilateral stand training were able to stand for longer periods of time than nontrained cats 12 wk after spinalization. Figure 1 shows an episode of standing from a representative stand-trained and nontrained cat. At the beginning of each standing episode, full weight-bearing hindlimb extension was initiated in the stand-trained and nontrained cats. After the initiating stimulus was removed and the tail was held only for lateral stability, the stand-trained cats continued to maintain full weight-bearing extension while the hindlimbs of the nontrained cats gradually collapsed to a non-weight-bearing position. For example, an elevated hip position was maintained for 720 ± 1,120 s during the longest episodes of standing in stand-trained cats (Fig. 2). In contrast, the hip position in five of the nontrained cats gradually lowered within 10–250 s after the initiation of weight bearing. One nontrained cat failed to exhibit any period of weight bearing (Fig. 2, ♦).

The overall average standing duration of the stand-trained cats (585 ± 162 s, mean ± SE, $n = 2$ cats, $n = 6$ episodes) was significantly longer than in the nontrained cats (44 ± 16 s, $n = 6$ cats, $n = 18$ episodes) based on tests performed on the 12th wk after spinalization ($P < 0.01$). Of the total number of standing episodes measured in the stand-trained cats after 12 wk of training, greater than one-half of the episodes lasted ≈60 s (Fig. 3). In contrast, the nontrained cats rarely (10% of the episodes) stood for >60 s (Fig. 3).

The ability of the stand-trained cats improved dramatically between 4 and 12 wk of training. For example, the longest episodes in the two stand-trained cats after 4 wk was <100 s, but at 12 wk, the maximum standing duration increased to 750 and 1,120 s (Fig. 4A). In contrast, the mean standing duration of the nontrained cats changed little between 6 and 12 wk (Fig. 4B). On the basis of the tests of standing (1, 6, and 12 wk after spinalization), the increase in maximum standing duration over time was significant for the stand-trained cats, i.e., nonzero slope ($P < 0.01$), whereas the maximum duration for the nontrained cats did not change significantly after spinalization.

Hindlimb kinematics and EMG activity during bilateral hindlimb standing

During full weight-bearing hindlimb standing in stand-trained and nontrained cats, the acute angles at the hip, knee, and ankle joints were maintained at >60° (Fig. 5). When the hindlimbs of the nontrained cats collapsed at the end of a standing episode, the angles at the knee and/or ankle decreased to <60°. In the stand-trained cats, the longest episodes of standing were typically disrupted when one of the hindlimbs initiated a step rather than from a hindlimb collapse (see Fig. 6, 12 wk postspinal, Stand-trained). Thus a sufficient amount of extension was maintained at the ankle and knee joints of the stand-trained cats (>60°) throughout a standing episode, although fluctuations in the joint angles were observed (Fig. 5). Hip angle changed little during the standing episodes in the stand-trained and nontrained cats (Fig. 5), indicating that the training effect was occurring primarily in the control of the more distal joints.

Relative to the mean joint angles before spinalization, ankle angles tended to be lower while hip angles were greater in the spinal cats (Fig. 5). Knee angles after spinalization were within the range of knee angles measured during standing before spinalization (Fig. 5).

EMG activity levels sufficient to accommodate standing were maintained for longer durations in the trained than nontrained cats 12 wk after spinalization (Figs. 6 and 7). When weight bearing was initiated in the nontrained cats, Sol (ankle extensor) EMG activity was observed but was not maintained for >240 s (Figs. 6 and 7). In contrast, the Sol remained active in the stand-trained cats for periods up to 1,120 s (Figs. 6 and 7). The levels of VL (knee extensor) and MG (ankle extensor) EMG activity were relatively low throughout the standing episodes in both the stand-trained and nontrained cats (Figs. 6 and 7).

The levels of EMG activity in the Sol, VL, and MG during full weight-bearing after spinalization was within the normal (prespinal) range of EMG activity (Fig. 7). Activity in the GM (hip extensor) was not observed consistently before or
after spinalization (Fig. 6), as has been reported during standing in intact cats (Rasmussen et al. 1978). Of the four extensor muscles studied, the Sol consistently exhibited the highest EMG amplitudes. The muscles having a flexor function, i.e., St, TA, and IP, were inactive during standing before and after spinalization (Fig. 6).

Performance of unilateral and bilateral standing in cats trained to stand on one hindlimb

To determine the effect of unilateral stand training on the recovery of standing, two cats were trained to stand only on the right hindlimb while weight bearing on the left hindlimb was prevented. Based on performances that were observed during the weekly training sessions, the duration of standing on the trained leg increased progressively during the 12 wk of training with maximum durations lasting up to \( \sim 15 \) min. To preclude any possible training effects during testing on the nontrained limb, only one unilateral standing test was administered at the end of the 12-wk training period, and the maximum test duration was predetermined not to exceed 240 s. A similar level of performance was observed in the nontrained and trained legs during this 4-min test (Fig. 8). However, evidence of a greater effect in the trained leg was evident in tests of bilateral standing at 12 wk. For example, the forces exerted by the hindlimbs on two independent force plates placed underneath the hindpaws were greater on the trained than the nontrained hindlimb (Fig. 9). The forces exerted by the trained limb of the two stand-trained spinal cats were 2.5

![Fig. 1. Stick figure representations of a hindlimb from 1 stand-trained and 1 nontrained cat during bilateral hindlimb standing before and 12 wk after spinalization. The postspinal stick figures represent the hindlimb during 1 standing episode beginning with the initiation of weight bearing (downward arrow) to the end of weight bearing (upward arrow). Both hindlimbs collapsed at the end of the standing episode in the nontrained cat while a step in the contralateral limb (not shown) disrupted bilateral weight bearing in the stand-trained cat. The position of the hindlimb every 60 s is shown (for clarity, the stick figures are horizontally displaced). Horizontal and vertical calibration, 5 cm. Angles between the joints shown in Prespinal, Stand-trained were measured (see Fig. 5).](http://jn.physiology.org/)

![Fig. 2. Vertical displacement of the hip during one episode of standing in 6 nontrained (top) and 2 stand-trained spinal cats (bottom). Data are from the longest episodes of standing measured in each cat 12 wk after spinalization. The distance between the hip and toe markers at a particular time point during the standing episode is shown from the initiation of weight bearing (time 0) to the end of weight bearing. Each symbol represents 1 spinal cat.](http://jn.physiology.org/)

![Fig. 3. Cumulative frequency of the durations of bilateral hindlimb standing episodes in 2 stand-trained (■) and 6 nontrained (○) spinal cats. The durations of all of the episodes of standing measured during tests performed 12 wk after spinalization are shown. To obtain an approximately equal number of observations between the stand-trained and nontrained cats, data that were obtained during the last training session on the 12th wk postspinal are also included for each stand-trained cat. Vertical line indicates a standing duration of 60 s.](http://jn.physiology.org/)
times and 5 times greater than by the nontrained limb (Fig. 10). Before spinalization, the distribution of weight on the two hindlimbs was similar (Figs. 9 and 10).

A decrease in the forces exerted by the hindlimbs during bilateral standing was observed after spinalization (Fig. 9) as has been reported previously (Pratt et al. 1994). This effect appeared to be due primarily to a forward displacement of the center of gravity and more weight bearing on the forelimbs due to a redistribution of body mass after spinalization.

Differences in the relative amounts of EMG activity in the Sol and VL during bilateral standing also were apparent in the trained and nontrained legs (Fig. 9). After spinalization, Sol activity was approximately two to six times greater on the trained than on the nontrained side, whereas two- to threefold differences were measured for VL activity (Fig. 10). Thus, although the unilaterally trained cat stood bilaterally, it was clear that a larger proportion of the weight of the hindquarters was borne by the trained leg during bilateral tests.

DISCUSSION

The present findings suggest that the recovery of weight bearing in the hindlimbs of spinal cats can be enhanced by stand training. Bilateral stand training improved the length of time that full weight-bearing extension could be maintained in the hindlimbs while unilateral stand training selectively, but not exclusively, improved the weight-bearing capacity of the weight-supporting limb. Several studies have demonstrated that weight bearing (Giuliani and Smith 1985; Kellog et al. 1946; Kozak and Westerman 1967; Pratt al. 1994) and positive supporting responses (Robinson and Goldberger 1986) in the hindlimbs can recover after spinalization. The present findings demonstrate that the duration of continuous hindlimb weight bearing and the motor pool recruitment patterns during standing after spinalization were largely attributable to the repetitive execution of that motor task over a period of weeks.

Postural stability and weight bearing during standing in spinal cats

Performance of long episodes (15–20 min) of unilateral or bilateral standing was observed in the present study when lateral, but not vertical, support of the hindquarters was provided intermittently by the trainers. Deficits in balance during quiet and randomly perturbed standing tests have been reported after spinalization in the cat, and these deficits persisted for at least 1 yr after spinalization and postural training (Pratt et al. 1994). In the absence of trainer assistance, these authors reported that the hindlimbs could maintain weight bearing for up to 45 s, but eventually, lateral movements of the hindquarters caused a loss of balance and a collapse of the hindlimbs. This instability in lateral posture could not have accounted for the short standing durations observed in the nontrained cats in the present study, because lateral support was provided by the trainers during all assessments of weight-bearing capacity.

In cats that were trained to stand on one leg, both the trained
FIG. 6. Electromyographic (EMG) activity during standing in 2 cats before and 12 wk after spinalization. One cat (STD1) received weekly training after spinalization, whereas the other cat (NT1) was not trained. Raw EMG recorded from selected hindlimb muscles (St, semitendinosus; VL, vastus lateralis; GM, gluteus medius; IP, iliopsoas; Sol, soleus; MG, medial gastrocnemius; TA, tibialis anterior; LG, lateral gastrocnemius) is shown from the initiation of weight bearing (downward arrow) to the end of weight bearing (upward arrow). In the stand-trained cat, a step was initiated (see EMG bursts) thus disrupting the standing episode. Numbers on the horizontal scale indicate the duration at particular points in the record. Horizontal calibration, 1 s and vertical calibration, 1.0 mV for all muscles except for the Sol (2.0 mV).

and the nontrained hindlimbs exhibited full weight-bearing extension during tests of unilateral standing. To maintain postural stability during unilateral standing, the nonweight-bearing limb was held in a flexed position. Asymmetrically positioning the hindlimbs in this manner often inadvertently and concomitantly elicited EMG activity in the nonweight-bearing limb (see Fig. 8). The extent that the weight-bearing ability of the nontrained leg was facilitated by the contralateral excitation of extensors during unilateral training cannot be determined in the present experiments. It seems quite clear, however, that bilateral excitation even while weight support was physically precluded on the nontrained leg was sufficient to induce some training effect on the nontrained limb. However, it was equally evident that a greater weight-bearing training effect occurred in the trained limb during the bilateral standing tests (Figs. 9 and 10).

Does training enhance standing performance by improving neuromuscular properties that are associated with endurance?

One possibility was that training modified hindlimb extensor muscle properties thereby extending the length of time that the hindlimbs could support the weight of the hindquar ters. However, it seems highly unlikely that the improved ability to stand can be attributed to adaptations in the hindlimb musculature for several reasons. For example, the limbs of all nontrained and trained spinal cats exhibited full weight-bearing extension capability, demonstrating that an inadequate force-generating capacity of extensor muscles was not responsible for the decreased weight-bearing capability that occurred in the absence of training. Recent findings from studies of Sol force and fatigue properties following spinalization in adult cats also suggest that muscle force adaptations cannot account for the observed differences in standing performance (Roy et al. 1998). The maximum force potential of the Sol was similar in nontrained and stand-trained cats. In addition, a high resistance to fatigue was maintained in the soleus muscles in both nontrained and stand-trained spinal cats.

Several observations in the present study also argue against fatigue as a determining factor in standing performance. The duration of each episode of standing varied within a given training or testing session, and the durations did not decrease progressively within a session as would be characteristic of a “fatiguing” phenomenon, whether of a neural or muscular origin. Furthermore, weight bearing in the hindlimbs was reinstalled immediately after the hindlimbs collapsed, thus allowing
Spinal cord of the cat learns to execute standing by practicing that specific task

The present experiments are consistent with the conclusion that the spinal cord of the cat learned to execute successful weight-bearing standing in the absence of any supraspinal control of posture. These results are consistent with several other observations from our laboratory. In 21 trained and nontrained spinal cats that were tested up to 3 yr after spinalization (Edgerton et al. 1997a), standing performances that were equal to the weight-bearing ability of the stand-trained cats in the present study or in the study of Pratt et al. (1994) were never observed in the absence of stand training. For example, hindlimb step training for 30 min/day following spinalization failed to enhance the duration of standing (Edgerton et al. 1997b). Furthermore, we have previously demonstrated that the recovery of standing ability in spinal cats was actually hindered when the tail was stimulated mechanically to facilitate standing during bilateral stand training (Edgerton et al. 1997a). The cats trained to stand with tail stimulation could stand only in the presence of tail stimulation even after months of training. Together these findings support the conclusion that practicing to perform the standing task using specific sensory and motor pathways largely defines the ability of spinal cats to stand.

The present experiments cannot identify the mechanisms responsible for the acquisition of more prolonged periods of standing in the trained spinal cats. The acquisition of simple flexion and extension responses in the hindlimbs of spinal animals has been shown to be mediated by associative (Durkovic and Damianopoulos 1986; Joynes et al. 1997; Patterson et al. 1973; Sherman et al. 1982) and nonassociative (Kozak and Westerman 1967; Thompson and Spencer 1966) mechanisms. However, the mechanisms that have been used to explain these short-term and reflexive forms of spinal learning are not likely to be sufficient to account for the learning of a postural task by spinal networks. It seems that learning complex motor tasks over long periods of time by the spinal cord will require inducing long-term changes in insufficient time for a significant level of recovery of force-generating capacity by the muscles recruited during standing. Together, these findings suggest that the differences in standing duration between the trained and nontrained spinal cats reflect neural adaptations to the repetitive practice of the standing task, rather than to an enhanced force or resistance to fatigue of the hindlimb musculature.

FIG. 7. EMG amplitudes in Sol, VL, and MG during standing in 2 stand-trained (lines with open symbols) and 5 nontrained (lines with filled symbols) cats 12 wk after spinalization. Mean EMG is shown from the initiation of weight bearing (time 0) and every 60 s thereafter until the hindlimbs collapsed or a step disrupted standing. Muscle abbreviations are the same as in Fig. 6.

FIG. 8. EMG activity and ground reaction force (F, in g) during full weight-bearing standing on 1 leg in 1 spinal cat that received unilateral hindlimb stand training. Note, the right hindlimb was trained to perform unilateral standing after spinalization. Raw EMG recorded from selected muscles from the trained (right) and nontrained (left) hindlimbs is shown during full weight-bearing standing on either limb. Downward arrow denotes the beginning of weight bearing. Muscle abbreviations are the same as in Fig. 6. Horizontal calibration, 1 s and vertical calibration, 1.0 mV for all muscles except for the Sol (2.0 mV).
spinal pathways that control the movements of the hindlimb. Some of these adaptations must include the appropriate modulation of the synaptic efficacies of extensor and flexor pathways and of the levels of excitatory and inhibitory inputs to these pathways from ipsilateral and contralateral projections.

Perspective

In conclusion, it appears that standing, like stepping, represents a motor task that can be learned in spinal cats trained to execute that specific task. These findings have important implications for rehabilitation following spinal injury because they suggest that the specific patterns of use of selected neural pathways within the CNS will determine to a large extent the level and kind of functional motor recovery that can be expected. These studies raise the obvious question of which neural pathways and neurotransmitter systems within the spinal cord are modified during the acquisition of these hindlimb motor tasks following spinalization and training.

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REFERENCES


EDGERTON, V. R., ROY, R. R., DE LEON, R., TILLAKARATNE N., and HODG-


