Weight Support and Balance During Perturbed Stance in the Chronic Spinal Cat

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Macpherson, Jane M. and Joyce Fung. Weight support and balance during perturbed stance in the chronic spinal cat. *J. Neurophysiol.* 82: 3066–3081, 1999. The intact cat maintains balance during unexpected disturbances of stance through automatic postural responses that are stereotyped and rapid. The extent to which the chronic spinal cat can maintain balance during stance is unclear, and there have been no quantitative studies that examined this question directly. This study examined whether the isolated lumbosacral cord of the chronic spinal cat can generate automatic postural responses in the hindlimbs during translation of the support surface. Responses to 16 directions of linear translation in the horizontal plane were quantified before and after spinalization at the T6 level in terms of forces exerted by each paw against the support, motion of the body segments (kinematics), and electromyographic (EMG) activity. After spinalization, the cats were trained on a daily basis to stand on the force platform, and all four cats were able to support their full body weight. The cats usually required assistance for balance in the horizontal plane, which was provided by an experimenter exerting gentle lateral force at the level of the hips. Three of the four animals could maintain independent stance for a brief period (10 s) after the experimenter stabilized them. The fourth cat maintained weight support but always required assistance with balance. Perturbations were delivered during the periods of independent stance in three cats and during assisted stance in the fourth. A response to translation in the spinal cats was observed only in those muscles that were tonically active to maintain stance and never in the flexors. Moreover, latencies were increased and amplitudes of activation were diminished compared with control. Nevertheless, flexors and extensors were recruited easily during behaviors such as paw shake and stepping. It is concluded that centers above the lumbosacral cord are required for the full elaboration of automatic postural responses. Although the spinal cat can achieve good weight support, it cannot maintain balance during stance except for brief periods and within narrow limits. This limited stability is probably achieved through spinal reflex mechanisms and the stiffness characteristics of the tonically active extensors.

INTRODUCTION

Perturbations of stance in the intact cat evoke automatic postural responses that are stereotyped across animals and that restore equilibrium (Macpherson 1988a,b). Postural responses are characterized by a spatial and temporal pattern of muscle activation and inhibition that is specific to the direction and velocity (or acceleration) of the disturbance. Perturbations of the support surface on which the animal stands elicit electromyographic (EMG) activity in the range of 40–80 ms after the onset of surface acceleration. Little is known about where in the nervous system these postural responses are organized. The purpose of this study was to determine whether lumbosacral spinal circuits in isolation from higher centers could generate the postural equilibrium response to translations of the support surface. The response to moderately slow translation (16 cm/s) does not depend on vestibular or visual inputs (Inglis and Macpherson 1995), and therefore somatosensory signals are the most likely trigger for this postural response. If postural responses that are observed in the hindlimbs are organized at the lumbosacral spinal level, then it should be possible to evoke such responses in an animal that has been trained to stand after complete transection of the thoracic spinal cord (chronic spinal cat).

The lumbosacral spinal cord of the cat contains the neural circuitry not only for segmental reflex behavior such as flexion withdrawal and crossed extension but also for rhythmic, alternating movements, including paw shake and stepping and coordination of the two hindlimbs for both in-phase and out-of-phase gaits (Rossignol 1996). Cats that have been spinalized can be trained to stand and step with full weight support (Barbeau and Rossignol 1987; Carter and Smith 1986; Forssberg and Grillner 1973; Grillner 1975; Shurrager and Dykman 1951; Smith et al. 1982). During spinal locomotion, the forelimbs typically remain stationary on a platform while the hindlimbs step on a moving treadmill belt. Most studies report that adult spinal cats have poor balance control and that stability must be provided by the experimenter, usually through gentle holding of the animal’s tail or abdomen. In contrast, cats spinalized shortly after birth appear to recover better locomotor performance even without training (Grillner 1973; Robinson and Goldberger 1986; Shurrager and Dykman 1951) and are reported to have some residual balance control. The extent to which the spinal cat can maintain balance independently is unclear, and there have been no quantitative studies that examined this question directly. Either the automatic postural response is present in the adult spinal cat but of insufficient amplitude to maintain stability or it is absent. The experiments in this report were designed to address this issue. Part of this work has been reported previously (Fung et al. 1993; Macpherson et al. 1995, 1997; Pratt et al. 1994).
trained over several months to stand quietly on a force platform and then implanted with chronically indwelling EMG electrodes as detailed in Fung and Macpherson (1999).

After recovery from the implantation surgery, control data were collected. The cat then was spinalized at the level of the sixth thoracic vertebra (for details, see Fung and Macpherson, 1999), and data collection resumed as soon as the animal was able to support all its own weight. Data collection continued for several months until the animal’s stance behavior reached a plateau (cats Ni and Go) or began to deteriorate due to increasing tone and spasms (Ru and Re).

Experimental protocol

Postural stability was assessed by quantifying the response to linear translation of the support surface in each of 16 different directions, evenly spaced in the horizontal plane. The translation was a ramp-and-hold displacement with mean peak velocity of 16 cm/s. The amplitude was constant for any one direction but was scaled from a maximum of 4 cm for translations along the longitudinal (y) axis to 2.5 cm for the lateral (x) axis. The recording period was 1 s, with 160 ms of background activity before the perturbation. A perturbation was initiated while the cat was working at the quiet stance task. The animal was given no cue about the timing of the perturbation and was not rewarded for any particular response although it was encouraged not to lift the paws from the force plates. Trials were sequenced in blocks by direction but the order of directions was randomized from day to day. Under these conditions, the predictability of direction has no perceptible effect on the timing, magnitude, or spatial pattern of the rapid postural response (Macpherson 1994). Only one recording session was carried out each day. Five trials were collected for each direction of translation and, for control animals, 16 directions were usually sampled, giving a total of 80 trials per session. For the spinalized cat, a full data set of 80 trials normally required two or more recording sessions.

The recorded data included the three linear forces from each of the four force plates (12 force channels), 8 channels of EMG, and platform position, all digitized at 500 samples/s using a PDP11 computer (Digital Equipment). EMGs were band-pass filtered (200 Hz and 2 kHz), full-wave rectified, and low-pass filtered (35 Hz) before sampling. Raw EMGs (band-pass filtered) were monitored on an oscilloscope. Kinematic data were recorded at 100 samples/s using a PC based Optotrak system (Northern Digital) with infrared emitting markers fixed over bony landmarks of the fore- and hindlimbs on the left side: metacarpo-phalangeal (MCP), wrist, elbow, and shoulder (glenohumeral) joints, scapula tip at the top of the spine, metatarsophalangeal (MTP), ankle, knee, and hip joints, iliac crest of the pelvis. The markers were affixed with Stomahesive paste (Convatec) by the same experimenter on a daily basis, using palpation of bony landmarks. For sites over which the skin is particularly loose (e.g., knee, shoulder, scapula), the markers were placed while the cat was standing in position on the platform. A reference marker was placed on the left posterior force plate.

After spinalization, the cat was placed on the four force plates and received food reward during data collection as in the control case. However, the weight distribution requirement was applied only to the forelimbs and not the hind. Two experimenters acted as “spotters” for the animal, one in front and one behind. One experimenter provided intermittent perineal stimulation when required for the animal to maintain weight support of the hindquarters. The position of the lumbar trunk was adjusted gently by applying a small lateral force to one side or the other of the animal’s hindquarters. With this technique the animal could be made to balance independently for brief periods in some trials. When stability was achieved, the experimenter withdrew her hands and the computer operator initiated the translation. If the animal lost its balance at any time, falling was prevented by the spotters. Each trial was scored by the two spotters according to whether stability was provided at the beginning of the trial or not (supported, unsupported). The unsupported trials were scored according to whether balance was maintained during the entire trial or not (balanced, unbalanced) and the direction of fall when balance was not maintained (left, right, collapse in flexion).

Data analysis

The various data types were all imported into one file for each trial and subsequent analysis was performed using Matlab (Mathworks). The kinematic data were low-pass filtered at 8 Hz using a fourth-order Butterworth filter with zero phase shift. The choice of cutoff frequency was based on a residual analysis of representative kinematic data. Joint and segment angles were computed for the sagittal and frontal planes. Net joint torques were computed for fore- and hindlimbs using inverse dynamics from the kinematic and ground reaction force data, body weight, and segment lengths, and a segment model of the cat (Hoy and Zernicke 1985). Each cat was weighed weekly, and the value recorded closest in time to the date of data collection was used for the inverse dynamics calculations for that session.

Each of the data traces was treated in the following manner. The mean and SD of the background period was determined. Then a running average and SD were calculated at 10-ms intervals for bins of 40-ms width from the onset of platform acceleration to the end of the trial. The chosen parameters resulted in good smoothing of the traces without a significant reduction in signal amplitude; using the midpoint of each bin as the time marker resulted in little or no phase shift (Fig. 1). This treatment also reduced the number of data points, making the analysis of multiple trials more tractable. Subsequent analysis was performed on single trials of the binned data. Means and SDs of the original time series are used for illustrative purposes (e.g., Figs. 2 and 3).

Changes in EMG binned data were deemed to be significant when the bin value exceeded the mean background by 2.0 × SD of the mean (excitation) or fell below the mean minus 1.5 × SD (inhibition) for a period of at least three consecutive bins (i.e., 30-ms duration). The response amplitude was quantified in terms of the area under the curve for a fixed duration of 80 ms. The criteria for significant change were similar to those used previously on the standard time series data (Macpherson 1988b). Preliminary tests comparing raw and binned data for control trials showed that the latencies of EMG onset were similar (given that the binned data has a time accuracy of 10 ms compared with 2 ms for the raw data). Only those EMG latencies that were <100 ms were considered for further analysis in the control data. The postspinal data criterion was relaxed to include latencies ≤300 ms because most responses were considerably delayed compared with control values. The time and amplitude of the peak change in forces, torques, and joint and segment angles were noted, and all variables were plotted as a function of the direction of translation.

RESULTS

After spinalization all four cats in this study could stand with full weight support after training as described in detail in the accompanying report (Fung and Macpherson 1999), but they showed considerable variability in the time course of their recovery and in the capacity to stand unsupported. All cats except Go were able to stand at their preferred distance as determined before spinalization. Stance distance was calculated from the y-axis distance between MCP and MTP joints, and the mean pre- and postspinalization values in centimeters for each cat are as follows: Ni, 29.4 and 30.2; Ru, 30.7 and 28.7; Re, 29.0 and 29.1; and Go, 29.3 and 21.3.

Table 1 shows the total number of translation trials recorded after spinalization and the proportion in which the cat was unsupported at the beginning of the trial. Unsupported trials ranged from 8% in Go to 72% in Ru. Only the unsupported trials were used for analyzing the response to
EMG responses

In the control condition, all muscles studied showed robust responses to translation with characteristic timing and amplitude tuning in relation to the direction of perturbation. After spinalization, only some of the extensor muscles were modulated in relation to the translation and the onsets and peaks of the EMG activity were delayed compared with the control data. No flexor muscles were ever recruited in response to platform translation. The following lists the number of samples of each muscle that responded following onset of platform translation in all spinalized animals and number of samples that were tested: ilipsoas, 0/2; semitendinosus, 0/2; posterior biceps femoris, 0/1; medial sartorius, 0/1; tibialis anterior, 0/2; anterior semimembranosus, 0/2; posterior semimembranosus, 0/3; vastus lateralis, 0/1; vastus medialis, 1/1; glutus medius, 3/4; anterior biceps femoris, 3/4; rectus femoris, 4/4; anterior sartorius, 3/4; adductor femoris, 1/1; and lateral gastrocnemius, 2/2. None of the eight implanted flexors showed any response, whereas 17 of the 26 implanted extensors showed some pattern of activation. These 17 extensors were distributed across subjects as follows: Ni, 4; Ru, 4; Re, 4; and Go, 5.

Figure 2 shows examples of averaged time series data of flexor EMGs before (control) and after spinalization (post). For each muscle, the response is shown for the direction of translation which evoked the maximum EMG activation in the control condition. Note that the postspinal data have been plotted with a high gain and that no response is evident. Figure 3 illustrates the types of responses observed in the extensor muscles after spinalization. EMG amplitudes were typically lower than control (note scale for control vs. postspinal). The bursting patterns were variable and tended to build slowly and to maintain an increased level relative to background throughout the trial (e.g., Fig. 3 vastus medialis) in contrast to control EMGs, which showed a rapid rise and then a return to baseline after the translation (Figs. 2 and 3). After spinalization, the extensors sometimes exhibited an early burst after translation onset that was short in duration and that was smaller in amplitude relative to background than in control trials. Some of these bursts (Fig. 3, †) are, presumably, stretch-evoked reflexes.

In contrast to the poor or absent response to translation, both flexors and extensors of all four spinal cats were recruited robustly during various typical spinal behaviors. Figure 4 shows examples from each cat, including paw shake (Fig. 4, A, C, and D), airstepping (Fig. 4, A and D), and flexion withdrawal (Fig. 4B). Paw shake was elicited while the cat stood on the platform by dipping one hindpaw in water or by gently pulling strands of fur on the toes. For airstepping, the hind-
limbs were elevated above the platform surface using the tail while the animal maintained weight support with the forelimbs. Flexion withdrawal and crossed extension were elicited during stance on the platform by pinching the toes of one hindlimb. The paw shake responses exhibited the EMG patterns described by Giuliani and Smith (1985, 1987) with hip and ankle extensors and knee flexors forming one synergy, hip and ankle flexors and knee extensors the other, in alternating activation (Fig. 4, C and D).

The EMG response to translation was quantified on a trial-by-trial basis from the binned data as described in METHODS. For all muscles that showed significant increases in activity evoked by translation, the mean onset latencies were delayed compared with control and more variable (Table 2). In the intact condition, EMG onsets were somewhat variable across muscles, ranging from 50–80 ms in Ru, Re, and Go and 50–70 ms in Ni. After spinalization, EMGs showed longer mean latencies ranging across muscles from 100 to 160 ms in Ru, 130 to 200 ms in Ni, 90 to 290 ms in Re, and 80 to 160 ms in Go (Table 2). In some trials across all four cats, onsets could be as early as 20–30 ms when short-latency reflex bursts were present. Nevertheless all postspinal mean latencies were significantly longer than control except for gluteus medius in cat Re (Table 2), which was influenced heavily by the early, short-duration reflex burst in the EMG (see Fig. 3). The standard deviations of the mean onsets also were increased postspinally. Note that the postspinal responses for cat Go were well within the range of the postspinal responses of the other three cats even though Go received assistance for balance and the other three cats did not.

EMGs were compared across trials in which the cat remained balanced at the end of translation, and those in which it did not. In two cats, data across all stance distances were pooled (Ni: 19–31 cm and Re: 18–33 cm, respectively), to obtain sufficient trials with EMG responses in both balanced and unbalanced categories. For the third cat (Ru), only trials at the preferred distance were compared. Table 3 shows that there was no systematic difference in overall latency of excitation between balanced and unbalanced trials. Only 1 of the 12 muscles showed a delay in latency during unbalanced trials, with borderline significance ($P = 0.05$). Figure 5 shows the mean ± 1 SD of the postspinal onset latencies as a function of the direction of translation for cats Ru (Fig. 5A) and Ni (Fig. 5B). Increases in activity are shown with a positive, upward going rectangle, whereas decreases in activity are shown with a negative, downward going rectangle. For both excitations and inhibitions, there was no trend in the onsets between balanced and unbalanced trials.
as illustrated in Fig. 6

yielded no difference in EMG amplitude or pattern of response
teus medius in
detected and quantified (e.g., anterior biceps femoris and glu-
tion, allowing the inhibition during unloading to be more easily
Go
others it was expanded (e.g., lateral gastrocnemius in

shows that in some cases, the postspinal tuning curve was
excitatory response was smaller in the spinal cat. Figure 6
postspinal conditions (Fig. 6A) although the amplitude of the
tuning curve) was generally similar between control and
perturbation as a function of direction of translation (EMG
ms across all cats. Nevertheless the pattern of response to the
range of 90 –110 ms. Postspinally, the peak mean EMGs were
the extensor muscles during trials when the limb was loaded
than returning toward the center of the platform, as in the
tcondition, the CoPx for the hindlimb, but not the forelimb,
tended to remain displaced for the duration of the trial rather
than returning toward the center of the platform, as in the
control condition. This observation corresponds with the pro-
duction in both control and postspinal conditions. Across the
180 ms after the onset of platform accel-
eration in both control and postspinal conditions. Across the
intact cats, the peak vertical force scaled with body weight.
Therefore in comparing the control and postspinal data within
each cat the peak force was normalized to weight to account for
the loss in body weight (≤20%) that followed spinalization.
Figure 7A shows an example of the normalized peak force
before and after spinalization plotted against direction of trans-
lation. For all cats, the hindlimbs showed a reduction in peak
force for those directions in which the limb was loaded. In
contrast, the forelimbs showed an increase in peak force when
they were loaded. The decreases in force, or unloading, were
similar before and after spinalization for all limbs.

The peak rate of change in vertical force also was examined
and is shown in Fig. 7B. In intact cats, this variable is compa-
urable across cats regardless of body weight. In the postspinal
case, the hindlimbs showed a reduction in the peak rate of
change that was most profound for lateral translations (near 90
and 270°). The forelimbs were less affected, with a small
increase in rate of force change, particularly for the lateral
translations in which the limbs were loaded (270° for the left
forelimb and 90° for the right).

The center of pressure (CoP), which is the resultant of the
vertical forces, was calculated for the two axes, lateral (x) and
longitudinal (y). The mean change in CoP over time is plotted
in Fig. 8 for all directions of translation, superimposed. In
addition, the x component of CoP has been calculated sepa-
rately for fore- and hindlimb components. The excursion of
CoPx was reduced in all cats after spinalization (Fig. 8A, left).
This reduction could be attributed primarily to the hindlimbs
(Fig. 8A, CoPx-hind) and reflects the reduction in peak vertical
force illustrated in Fig. 7A. For all cats in the postspinal
condition, the CoPx for the hindlimb, but not the forelimb,
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than returning toward the center of the platform, as in the
control condition. This observation corresponds with the pro-
longed changes in vertical force after platform translation in
the spinal cat (not illustrated) and the sustained activation of
the extensor muscles during trials when the limb was loaded
(Fig. 3).

The change in CoPy (Fig. 8A) did not differ between the
control and postspinal trials except for greater variability at the
end of the postspinal trials. Figure 8B shows the trajectories in
the horizontal plane of the CoP for all 16 directions of trans-
lution superimposed before and after spinalization. The
postspinal plots are displaced forward, reflecting the more
anterior position of the CoP during quiet stance as described in
the accompanying paper (Fung and Macpherson 1999). Note
the elegant loops in the control plot that reflect the coordination
in vertical forces among the four limbs and the disorganized
appearance of the CoP trajectories in the postspinal plots. Note
also that there is no systematic difference in the postspinal CoP
time series data between those trials in which the cat remained
balanced and those in which it did not (Fig. 8B).

The peak change in horizontal force evoked by translation is
shown for each limb in Fig. 9 as a vector projecting from a
common origin for each of the 16 directions of translation,
superimposed. The control data show the bimodal distribution
and unbalanced trials. Some balanced trials had shorter laten-
cies and some longer.

Not only was the onset of EMG activity increased after
spinalization, but so too was the peak of excitation (Table 4).
In the control trials, the excitation peaks all fell within the
range of 90–110 ms. Postspinally, the peak mean EMGs were
not only delayed but also dispersed, ranging from 120 to 310
ms across all cats. Nevertheless the pattern of response to the
perturbation as a function of direction of translation (EMG
tuning curve) was generally similar between control and
postspinal conditions (Fig. 6A) although the amplitude of the
excitatory response was smaller in the spinal cat. Figure 6A
shows that in some cases, the postspinal tuning curve was
phase-shifted relative to control (e.g., vastus medialis in Ni), in
others it was expanded (e.g., lateral gastrocnemius in Go).
Sometimes, a muscle had higher tonic activity after spinaliza-
tion, allowing the inhibition during unloading to be more easily
detected and quantified (e.g., anterior biceps femoris and glu-
teus medius in Ru).

Comparison of balanced and unbalanced postspinal trials
yielded no difference in EMG amplitude or pattern of response
as illustrated in Fig. 6B.

FIG. 4. Postspinal EMG activity during automatic hindlimb behaviors, re-
corded from each cat, Ni (A), Ru (B), Re (C), and Go (D). Traces are from
single representative trials. In some traces the amplifier was saturated e.g.,
posterior biceps in A. - - -, peaks of bursts in lateral gastrocnemius.

Forces at the ground

The peak change in vertical force evoked by translation
typically occurred ~180 ms after the onset of platform accel-
eration in both control and postspinal conditions. Across the
intact cats, the peak vertical force scaled with body weight.
Therefore in comparing the control and postspinal data within
each cat the peak force was normalized to weight to account for
the loss in body weight (≤20%) that followed spinalization.
Figure 7A shows an example of the normalized peak force
before and after spinalization plotted against direction of trans-
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The peak rate of change in vertical force also was examined
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The peak change in horizontal force evoked by translation is
shown for each limb in Fig. 9 as a vector projecting from a
common origin for each of the 16 directions of translation,
superimposed. The control data show the bimodal distribution
of vectors that was previously described (Macpherson 1988a) and characterizes the response to translation when cats stand at their preferred stance distance. The pattern of horizontal force vectors was severely disrupted postspinally in all three cats that stood unsupported. Figure 9 shows an overall reduction in vectors that was previously described (Macpherson 1988a) for all joints but the ankle. The relative phasing of the joint torque plots remained similar before and after spinalization: hip, ankle, and MTP joint torque plots remained in phase as a function of direction of translation; the phase shift of the knee torque relative to the other joints that is observed in the control data also remained postspinally. The forelimb sagittal plane torque recorded postspinally (Fig. 10) was only slightly larger than the control. Figure 10C shows that for the hindlimb torques of cat Ru, there was no difference between the balanced and the unbalanced trials in the postspinal condition.

The plots of joint torque (Fig. 10), vertical force (Fig. 7), and EMG amplitude (Fig. 6A) versus direction of translation generally showed a slight phase shift between control and postspinal data that was counterclockwise for the left fore- and hindlimb and clockwise for the right. These phase shifts can be attributed to the anterior displacement of the mean center of pressure (and therefore center of mass) in the postspinal condition as follows. During translation, the limbs are carried with the platform and the trunk remains behind due to inertia. The direction for which a limb undergoes maximal increase in vertical force, torque, and extensor EMG is that direction in

### TABLE 2. Mean latency of excitatory EMG responses after onset of platform translation in each subject

<table>
<thead>
<tr>
<th></th>
<th>Ru</th>
<th>Ni</th>
<th>Re</th>
<th>Go</th>
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<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Postspinal</td>
<td>Control</td>
<td>Postspinal</td>
</tr>
<tr>
<td>Anterior biceps femoris</td>
<td>60 ± 10 160 ± 80</td>
<td>70 ± 20 200 ± 60</td>
<td>80 ± 10 NR</td>
<td>80 ± 10 140 ± 40</td>
</tr>
<tr>
<td>n</td>
<td>70</td>
<td>79</td>
<td>43</td>
<td>31</td>
</tr>
<tr>
<td>Gluteus medius</td>
<td>80 ± 10 140 ± 80</td>
<td>50 ± 20 160 ± 60</td>
<td>80 ± 10 90 ± 70*</td>
<td>50 ± 20 NR</td>
</tr>
<tr>
<td>n</td>
<td>22</td>
<td>82</td>
<td>55</td>
<td>23</td>
</tr>
<tr>
<td>Rectus femoris</td>
<td>50 ± 10 100 ± 60</td>
<td>60 ± 10 200 ± 80</td>
<td>50 ± 10 140 ± 60</td>
<td>60 ± 10 150 ± 70</td>
</tr>
<tr>
<td>n</td>
<td>84</td>
<td>100</td>
<td>61</td>
<td>6</td>
</tr>
<tr>
<td>Anterior sartorius</td>
<td>60 ± 10 130 ± 80</td>
<td>60 ± 10 60 ± 10</td>
<td>60 ± 20 290 ± 170</td>
<td>70 ± 20 160 ± 80</td>
</tr>
<tr>
<td>n</td>
<td>86</td>
<td>116</td>
<td>61</td>
<td>NR</td>
</tr>
<tr>
<td>Vastus medialis</td>
<td>—   —</td>
<td>70 ± 20 130 ± 70</td>
<td>—   —</td>
<td>—   —</td>
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<tr>
<td>n</td>
<td>—   —</td>
<td>36</td>
<td>42</td>
<td>—   —</td>
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<tr>
<td>Adductor femoris</td>
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<td>n</td>
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<tr>
<td>Lateral gastrocnemius</td>
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<tr>
<td>n</td>
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Values are means ± SD in milliseconds. n, number of trials contributing to mean value; NR, no response; —, electromyographs (EMGs) not recorded in this subject. * Significant difference in latency between balanced and unbalanced trials (P > 0.05).

### TABLE 3. Mean latency of postspinal excitatory EMG responses comparing balanced and unbalanced trials

<table>
<thead>
<tr>
<th></th>
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<th>Ni</th>
<th>Re</th>
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<tbody>
<tr>
<td></td>
<td>Balanced</td>
<td>Unbalanced</td>
<td>Balanced</td>
</tr>
<tr>
<td>Anterior biceps femoris</td>
<td>170 ± 80 160 ± 70</td>
<td>170 ± 70 200 ± 70</td>
<td>NR</td>
</tr>
<tr>
<td>n</td>
<td>29</td>
<td>54</td>
<td>30</td>
</tr>
<tr>
<td>Gluteus medius</td>
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<td>140 ± 70 130 ± 50</td>
<td>90 ± 70 90 ± 70</td>
</tr>
<tr>
<td>n</td>
<td>39</td>
<td>48</td>
<td>6</td>
</tr>
<tr>
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<td>90 ± 60 100 ± 60</td>
<td>100 ± 90 190 ± 80</td>
<td>120 ± 60 110 ± 70</td>
</tr>
<tr>
<td>n</td>
<td>36</td>
<td>72</td>
<td>4</td>
</tr>
<tr>
<td>Anterior sartorius</td>
<td>130 ± 80 130 ± 80</td>
<td>NR</td>
<td>NR</td>
</tr>
<tr>
<td>n</td>
<td>39</td>
<td>71</td>
<td>—</td>
</tr>
<tr>
<td>Vastus medialis</td>
<td>—   —</td>
<td>150 ± 90 150 ± 80</td>
<td>—</td>
</tr>
<tr>
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<tr>
<td>Lateral gastrocnemius</td>
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</tr>
<tr>
<td>n</td>
<td>—   —</td>
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</tbody>
</table>

Values are means ± SD in milliseconds. Responses for Ru were at preferred distances and at all distances for Ni and Re. n, number of trials contributing to mean value; NR, no response; —, EMG not recorded in this subject. * Significant difference in latency between balanced and unbalanced trials (P = 0.05).
which the limb is moved closest to the body center of mass and undergoes maximal loading. In the intact cat, 225° is the direction of translation that usually brings the left hindpaw closest to the body center of mass. However, when the center of mass is located more anteriorly, as in the postspinal condition, the translation that will maximally load the limb will be rotated counter-clockwise (more anterior) compared with control. Similarly, the direction of maximal loading for the right hindlimb will be rotated clockwise (mirror-image of the left side).

Kinematics

Figure 11 shows example stick figures of fore- and hindlimb position plotted at a series of time points during the response to various translations. Sagittal plane plots are shown for forward (180°) and backward (0°) translations and frontal plane plots for left (90°) and right (270°). When the support surface was translated, the paws were carried with the platform and the trunk remained behind due to inertia. In the intact cat, the trunk typically is restored to its initial position with respect to the paws. Part of this recovery is passive, due to the deceleration and stopping of the platform, which comes to rest at 230–315 ms after onset, depending on the amplitude of translation (largest amplitude translation for the longitudinal axis, smallest for the lateral). As evident in Fig. 11, the stick figure profiles were similar for control and postspinal conditions, especially for the sagittal plane. In the frontal plane, part of the apparent change in initial limb configuration was due to the loss of muscle mass over the hip and pelvis. In addition, there were changes in the motion of the segments, proximal in particular.

The quantitative changes in joint and segment angles are illustrated in Figs. 12 and 13.

Figure 12, A and B, shows that the angular position of the fore- and hindlimb axes changed in a monotonic manner during the translation as the limbs moved out from under the trunk and then the trunk moved back over the paws. The hindlimb axis (Fig. 12 A) is defined as the straight line joining the MTP joint and the hip joint and the angle is measured with respect to earth horizontal (see Fig. 12 A figurines). Similarly, the forelimb axis (Fig. 12 B) is the line joining the MCP joint and the shoulder (glenohumeral) joint.

TABLE 4.  

<table>
<thead>
<tr>
<th></th>
<th>Ru</th>
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<th>Go</th>
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<tr>
<td></td>
<td>Control</td>
<td>Postspinal</td>
<td>Control</td>
<td>Postspinal</td>
</tr>
<tr>
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<td>100</td>
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<td>110</td>
<td>260</td>
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<tr>
<td>Gluteus medius</td>
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<td>160</td>
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<td>Adductor femoris</td>
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<td>Lateral gastrocnemius</td>
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</table>

Values are in milliseconds. NR, no response; —, EMG not recorded in this subject.
difference in the static pelvis angle during quiet stance. In the control case, the iliac crest was more elevated than in the postspinal case (difference of 15° in this example), as indicated by the mean and SD of background angles. Figure 12C also shows the mean time series of change in hip height with height measured as the vertical distance of the hip above the support surface. Sagittal translations in the control case were characterized by a small drop in hip height for both anterior and posterior directions. Postspinalization, the scapula showed an increase in angular excursion. In contrast, the shoulder joint showed a more limited excursion and underwent flexion (retraction of humerus) for both forward and backward translations. This finding was consistent across cats. The quiet stance angles for scapula and shoulder were similar for control and postspinal data. Shoulder height, which is the vertical distance of the shoulder joint above the surface, also was affected by spinalization. During both anterior and posterior control translations the change in shoulder height showed a slight decrease, as for the hip height. In all cats after spinalization, there was a greater

spinalization (Fig. 12D). In the control case, the angle changes during sagittal translations were similar for scapula and shoulder joint. Postspinalization, the scapula showed an increase in angular excursion. In contrast, the shoulder joint showed a more limited excursion and underwent flexion (retraction of humerus) for both forward and backward translations. This finding was consistent across cats. The quiet stance angles for scapula and shoulder were similar for control and postspinal data. Shoulder height, which is the vertical distance of the shoulder joint above the surface, also was affected by spinalization. During both anterior and posterior control translations the change in shoulder height showed a slight decrease, as for the hip height. In all cats after spinalization, there was a greater

difference in the static pelvis angle during quiet stance. In the control case, the iliac crest was more elevated than in the postspinal case (difference of 15° in this example), as indicated by the mean and SD of background angles. Figure 12C also shows the mean time series of change in hip height with height measured as the vertical distance of the hip above the support surface. Sagittal translations in the control case were characterized by a small drop in hip height for both anterior and posterior directions. Postspinally, two cats (Ru and Re) maintained a hip height similar to the control case for anterior translations in which both hindlimbs were loaded; the other two cats showed a more pronounced drop in hip height, probably due to the fact that the trace reflects the mean of both balanced and unbalanced trials.

The sagittal plane forelimb motion also was affected by

\[ \text{FIG. 6. Mean amplitude and SD of evoked response of selected extensor} \]
\[ \text{muscles as a function of direction of translation. A: comparison of amplitudes} \]
\[ \text{before and after spinalization. Postspinal data are from trials in which the} \]
\[ \text{cat was standing independently before the perturbation for all cats except Go.} \]
\[ \text{B: comparison of normalized EMG amplitudes after spinalization for trials} \]
\[ \text{in which the cat remained standing at the end of translation (balanced) and for} \]
\[ \text{trials in which it did not (unbalanced). At each direction of translation, there} \]
\[ \text{is little difference between EMG amplitudes for balanced (black) and for unbal-} \]
\[ \text{anced (gray) trials. Data for A and B are normalized within each muscle to the} \]
\[ \text{maximum mean evoked response during the control period.} \]

\[ \text{FIG. 7. Vertical force exerted by each limb before (control) and after} \]
\[ \text{spinalization (postspinal) for cat Re. A: curves show mean and SD of peak} \]
\[ \text{force evoked in each limb by 16 directions of translation. Peak force was} \]
\[ \text{normalized to body weight to correct for the animal’s loss of weight after} \]
\[ \text{spinalization. Horizontal lines indicate proportion of body weight that was} \]
\[ \text{supported by each limb during quiet stance before translation. Note the} \]
\[ \text{increase in support under forelimbs and decrease under hindlimbs postspinal-} \]
\[ \text{ization (gray lines). B: mean and SD of peak rate of change in force for each} \]
\[ \text{direction of translation. Postspinal means for A and B were computed from} \]
\[ \text{trials in which the animal stood independently before translation. LF and RF,} \]
\[ \text{left and right forelimbs; LH and RH, left and right hindlimbs.} \]
As with the sagittal plane, the main changes in frontal plane kinematics were at the proximal segments of fore- and hindlimbs. During lateral translations in control trials, the main angle change in the hindlimb was at the pelvis and not the hip joint (Fig. 12E), as previously described (Macpherson and Fung 1998). In other words, during lateral translations the body rolled about the long axis of the trunk as the paws were carried to one side or the other. After spinalization, body roll was diminished (smaller change in pelvis angle) and instead, the limb axes rotated by abduction and adduction at the hip joint in all four cats. The onset of hip joint angle change was delayed and coincided with the peak of the change in pelvis angle (Fig. 12E, postspinal—compare hip and pelvis angle plots, 1).

Therefore shortly after the onset of translation, the body began to roll (pelvis rotation), but this roll was reversed when the limb began to abduct or adduct at the hip joint (for left and right translations, respectively). This difference between control and spinalized conditions is clearly seen in the stick figures of Fig. 11B (270°). In the frontal plane control trials (Fig. 12E), hip height underwent a large change; this is consistent with the roll motion of the pelvis. Postspinally the change in hip height was reduced, again consistent with the reduction in roll compared with control. Hip height was well maintained in all cats, even when the left hindlimb was loaded during rightward translations.

The forelimb proximal segments also demonstrated changes in frontal plane angles (Fig. 12F). In the control case, the scapula contributed the major change in limb axis angle in the early part of the translation, again suggesting that the body rolled about its long axis. When the change in scapula angle peaked, the limb axis motion continued through rotation at the shoulder joint for three cats (Re, Ru, and Go). For example, when the platform moved to the left, the scapular angle decreased, indicating that the body rolled to the right (clockwise on the figurine of Fig. 12F) as the limbs were carried to the left. As the scapular angle peaked, the shoulder joint began to

![Image](image_url)
abduct (increase in angle), allowing the limb to continue mov-
ing as the body rolled back toward upright. In contrast, cat Ni
showed no change in shoulder joint angle, suggesting that the
entire change in limb axis occurred through scapular rotation
and therefore body roll. Postspinally, the scapula angular
change was similar to control across cats. Changes in shoulder
joint angle began near the time of the peak change in scapula
angle as in the control. However, postspinally the shoulder
joint moved in the opposite direction to the control condition.
For example, during a leftward translation the scapular angle
decreased as the body rolled to the right. At the peak of the
scapular angle change, the shoulder joint began to adduct
(decrease in angle) rather than abduct as in the control case.
This change in shoulder joint angle was observed for all four
cats and suggests that the animals were using a strategy of
limiting the motion of the forelimbs relative to the trunk.
Shoulder height decreased during translations for both direc-
tions in the frontal plane pre- and postspinally (Fig. 12A). The
decrease for rightward directions is consistent with a counter-
clockwise roll motion of the trunk. The decrease for leftward
translations suggests that not only did the scapula rotate clock-
wise with the trunk, but it also moved vertically downward
relative to the trunk as the limb was unloaded. The scapula has
no bony attachments to the vertebral column, allowing the limb
to be suspended from its muscular attachments when it is not
supporting weight. During stance, however, the thoracic trunk
is suspended by the muscles from the scapula as in a sling.
Because of this arrangement of muscular attachments, we do
not know how much of the frontal plane roll of the scapula was
transmitted to the thoracic trunk as body roll. In contrast,
rotation of the pelvis likely reflects the rotation of the entire
lumbar trunk because there is limited capacity for torsion be-
tween the lumbar vertebral joints (Macpherson and Ye
1998).

Figure 13 illustrates the horizontal plane displacement of the
paws with respect to the trunk during translation, from which
inferences can be made about the relative stiffness of the limbs
before and after spinalization. Postspinally, the left hindlimb
moved further and faster during rightward translations, in
which the limb was loaded and moved inward relative to the
trunk (Fig. 13A). This suggests that, in the spinal animal, the
hindlimb was more compliant in the frontal plane for adduction
motion. In contrast, the left forelimb moved less and achieved
a lower peak velocity of motion for both left and right trans-
lations postspinally, suggesting that the forelimb was stiffer for
both abduction and adduction. In the sagittal plane (Fig. 13B),
the hindlimb of the spinal cat moved further and faster in both
anterior and posterior directions, suggesting that the limb was
more compliant in flexion and extension. In contrast, the fore-
limb moved less and with lower peak velocity, suggesting that
this limb was stiffer for both flexion and extension. Figure 13C
shows the horizontal plane trajectory of the position of the
paws relative to the hip and shoulder joints for hindlimb and
forelimb, respectively. Note the increased displacement for the
hindlimb, postspinally and the increased width of the loops,
particularly for those directions in which the limb was loaded
suggesting that the postural response of the spinal cat does not which the cat remained balanced and those in which it did not, did occur after translation were not different for those trials in unexpected disturbances of stance. In particular, responses that lack of an appropriately timed automatic postural response to citations of the spinal cat for stability appear to be related to the capacity to maintain balance despite daily stance training and Balance mechanisms are impaired in spinal cats

DISCUSSION

Balance mechanisms are impaired in spinal cats

The adult chronic spinal cat was severely impaired in its capacity to maintain balance despite daily stance training and recording. Stability was limited to short periods (on the order of seconds) and a narrow range of stance distances. The limitations of the spinal cat for stability appear to be related to the lack of an appropriately timed automatic postural response to unexpected disturbances of stance. In particular, responses that did occur after translation were not different for those trials in which the cat remained balanced and those in which it did not, suggesting that the postural response of the spinal cat does not contribute to balance but, rather, to weight support. In contrast, all cats achieved excellent weight support with the hindlimbs under both static and dynamic conditions, suggesting that the response evoked by translation was adequate to resist the downward acceleration due to gravity. The limited stability that was observed in the spinal animal was likely due to the inherent stiffness, both passive and active, of the tonically active extensors, as well as spinal reflexes. The two functions of weight support and balance may be controlled by different mechanisms and by different regions of the CNS.

EMG evidence

The conclusion that automatic postural responses are absent in the spinal cat comes primarily from the EMG data. In the intact animal, postural responses are rapid and time locked to the onset of the disturbance. Evidence suggests that postural reactions in the intact animal are not simple segmental reflexes but reflect more complex processes that encode characteristics of the perturbation such as direction and velocity (Horak and Macpherson 1995). The variable and late timing of EMG activation in the spinal cat suggests that its responses were more reflexive, related to individual muscle stretch or loading. It is likely that such responses contributed much to weight support but little to stability. The reasoning behind this conclusion follows.

In the intact cat, the earliest onset of EMG response is typically 40–80 ms after the onset of platform acceleration. By this time, the animal’s center of mass has moved only a small amount (3–4 mm) relative to the feet (Inglis and Macpherson 1995). Before EMG onset, sensory information about the disturbance enters the CNS and is processed to estimate the direction and velocity of the platform; signals then are generated to activate the appropriate muscles. The actual displacement of the platform at the time the critical sensory signals enter the nervous system is therefore quite small. Given that the body has not yet been destabilized, one might suppose that the nervous system uses the limited sensory information at its disposal to make a best-guess estimate of the impending disturbance to the body’s center of mass to generate a stabilizing response in a feedforward manner. Thus it is not likely that postural reactions are composed of segmental stretch reflexes; instead, they may result from more complex neural processes involving internal representations of the body and the environment (Gurfinkel and Levick 1991; Gurfinkel et al. 1988).

In the control condition, postural equilibrium responses were time-locked to the onset of platform acceleration for both onset and peak of EMG activation. After spinalization, the long latency and the high variability of both onset and peak of EMG activity suggest that the muscle activations were related to events other than the initial acceleration of the support surface. For example, translation of the surface under the cat causes movement of the limbs relative to the trunk and therefore a shift in the center of mass relative to the feet. Those limbs that are moved closer to the body’s center of mass must support more weight; those moved away must support less weight. When a hindlimb is loaded by a particular translation, many of weight support and balance may be controlled by different mechanisms and by different regions of the CNS.

(top right quadrant). Also note the somewhat more restricted trajectories of the forelimb postspinally.

FIG. 11. Stick figures for a series of time points during translation before and after spinalization, plotted relative to earth fixed coordinates. A: sagittal plane segment positions during anterior (180°) and posterior (0°) translations in cat Nl. Direction of translation is indicated by horizontal arrows under the paws. Initial position of the body is shown by the stick figure drawn with heavy black lines. Control and postspinal stick figures are aligned to the position of the metatarso-phalangeal (MTP) joint (vertical dotted line at hindlimb). Similarity in stance distance is indicated by the proximity of the metacarpo-phalangeal (MCP) joints before and after spinalization (vertical dotted line at forelimb). B: frontal plane segment positions during left (90°) and right (270°) translations in cat Ru. Left fore- and hindlimbs are viewed from the rear. Scale in the x direction has been enlarged for easier viewing (see scale bars). Forelimb has been offset along the lateral axis for clarity. Other details as in (A). Figure (top) shows marker positions and the coordinate reference frame. Horizontal axes (x, y) are parallel to the main axes of the force platform. z axis is parallel to the gravity vector. scap, scapular spine at dorsal border; shldr, shoulder; elb, elbow; pelv, iliac crest of pelvis.

In the control condition, postural equilibrium responses were time-locked to the onset of platform acceleration for both onset and peak of EMG activation. After spinalization, the long latency and the high variability of both onset and peak of EMG activity suggest that the muscle activations were related to events other than the initial acceleration of the support surface. For example, translation of the surface under the cat causes movement of the limbs relative to the trunk and therefore a shift in the center of mass relative to the feet. Those limbs that are moved closer to the body’s center of mass must support more weight; those moved away must support less weight. When a hindlimb is loaded by a particular translation, many different somatosensory receptors are likely to be activated, including proprioceptors in muscles and joints and mechanoreceptors, especially in the paw pads. Any of these sensory inputs could give rise to reflex activation of the tonically active
extensors. Indeed, recent studies have shown that mono- and polysynaptic reflexes are elevated in the chronic spinal cat compared with the intact animal (Hochman and McCrea 1994a; Hultborn and Malmsten 1983) probably due to alterations in synaptic mechanisms rather than changes in motoneuron properties (Hochman and McCrea 1994b). The kinetic and kinematic events that accompany translation of the support surface are likely to be rather variable with respect to the onset of platform acceleration depending on the position and velocity of the center of mass at the time of platform onset. Quiet stance is never truly static and as the body sways, the force exerted by each limb continually changes. The state of the sensory receptors and of the motoneuron pools also will vary from trial to trial. Thus reflex activation due to muscle stretch or to cutaneous stimulation could have a variable onset relative to the translation. Furthermore the spinal cat is not stable in stance and the lack of adequate muscle activation early in the translation means that the direction and amplitude of induced body sway will be more variable as suggested by the trajectories of center of pressure (Fig. 8) and position of paws relative to hip in the horizontal plane (Fig. 13). In contrast, the intact cat shows early and robust activation of a group of muscles that is specific to each direction and that likely results in a change in the stiffness of the limb that is directionally specific. This presetting of the stiffness in a directional manner may contribute not only to limiting the amplitude of displacement of the trunk but also focusing the direction of trunk displacement during the perturbation.

**Lack of flexor response to translation**

An aspect of the automatic postural response that is completely lacking in the spinal cat is flexor muscle recruitment. In the intact cat, flexor muscles are activated during platform translation with a specific spatial and temporal pattern, as are the extensors (Macpherson 1988b). None of the spinal cats showed recruitment of any flexors in the first part of the trial although activation near the end was often observed, particularly during falling. Such flexor activity was sporadic and usually too variable to be seen in the averaged traces. Nevertheless, flexor muscles showed robust recruitment in the spinal cats during typical spinal behaviors including flexion withdrawal, paw shake, and airstepping. During stance on the platform, the spinal cats were often highly reactive to the gentle manipulations of the experimenter that would result in one hindlimb stepping off the force plate. Thus the lack of...
early activation of the flexors during translation cannot be attributed to poor recordings or suppressed excitability. The lack of a balancing reaction, particularly in the flexors, is consistent with the behavior of spinal cats described by Hiebert et al. (1994) in their paradigm of “foot-in-hole” during hindlimb stepping on a treadmill. When the intact cat steps into a hole in the treadmill, it shows a robust, large-amplitude recruitment of ipsilateral flexors and contralateral extensors (Hiebert et al. 1994) with a latency (40 – 80 ms) that is similar to the postural response to platform translation that we observe. In contrast, when the hindpaw of the spinal cat enters the hole, there is a long and variable response in the flexors that appears more like the swing phase of the next step. Hiebert and colleagues (1994) concluded that the normal flexor response to the foot-in-hole perturbation requires supraspinal inputs. We suggest that the flexor response to the foot-in-hole perturbation is a form of postural reaction like that elicited by platform translation. As the limb extends, there is an unexpected absence of a support surface and the balance component of locomotion is disrupted. Neither of these postural reactions is organized at the lumbosacral spinal level.

In contrast, the response to disturbances of the stepping component of locomotion remain intact in the spinal cat. Stimulation of the skin or nerves of the paw during locomotion elicits either a flexor or an extensor response in the limb, depending on the phase of the step cycle in which the stimulus is delivered (Duyens and Pearson 1976; Forssberg et al. 1975, 1977) as well as the characteristics of the gait (Buford and Smith 1993). Thus balancing reactions may be organized differently from the reflexes that modify the central pattern generator for locomotion even when the mechanical conditions are similar.

For example, flexor responses to cutaneous stimulation are maximal near the end of the stance phase when the hip and ankle are extending (reviewed in Rossignol 1996). Similarly, the postural response to platform translation in flexors of the intact cat is elicited when the limb is pulled backward with respect to the trunk and the hip and ankle extend. Cutaneous receptors undoubtedly are stimulated during translation by the shear forces between paw and support. Nevertheless flexors are recruited after cutaneous stimulation during stepping in the spinal cat but not during postural adjustments.
Balanced versus unbalanced trials

The strongest evidence that the responses to translation in the spinal cat are not part of the automatic postural response is the similarity in postural variables between balanced and unbalanced trials. If the ability to remain balanced in some of the trials was due to an active mechanism, then one would expect to observe some difference in EMG, kinematic, and/or kinetic variables between the two classes of trials. No differences were seen in the timing of onset or peak of evoked EMG activity, the amplitude or spatial pattern of EMG responses, the pattern and amplitude of forces at the ground, joint torques, or kinematics. These data suggest that the ability of the spinal cat to maintain equilibrium during stance was serendipitous and likely due to passive mechanics combined with segmental loading and unloading reflexes.

Stiffness provides limited stability

How does the chronic spinal cat maintain even limited stability? The cat stands on four limbs that provide a large base of support within which the horizontal projection of the center of mass can move without loss of balance. Furthermore the forelimbs of the spinal cat produce robust and large postural responses to any disturbance (unpublished observations). Forces exerted by the forelimbs along the longitudinal axis of the cat are transmitted through the trunk, which is relatively stiff along that axis due to the structure of the vertebral column, and these forces can compensate to some extent for the lack of a stabilizing response in the hindlimbs. Stability along the lateral axis is more problematic for the spinal cat because of the mobility of the vertebral column not only in lateral flexion, but also in torsion (Macpherson and Ye 1998). Furthermore the base of support is much smaller along the lateral axis than along the longitudinal. The spinal cat appears to stiffen the forelimbs to minimize motion of the forequarters in all directions, but this has minimal effect on the lateral stability of the hindquarters. Back muscles normally may be recruited to stiffen the vertebral column (Macpherson and Fung 1998), but voluntary control in the spinal cats was limited to those segments above T10, the site of the lesion. The majority of torsional motion in the cat occurs between T4 and T11 (Macpherson and Ye 1998) and so would not be under much voluntary control. Stability along the lateral axis at the level of the hindlimbs is most likely due to the tonically active limb extensors which provide weight support. Tonically active muscles are mechanically stiff and resistant to stretch (Grillner 1972). Stiffness is increased by autogenic reflexes (Nichols 1973), which may be enhanced in the spinal cat (Hochman and McCrea 1994a; Hultborn and Malmsten 1983). Furthermore the stretched tendons, fasciae and aponeuroses store elastic energy, which will tend to resist muscle lengthening. In effect, the hindquarters of the spinal cat are supported by two stiff springs that will tend to resist displacement of the trunk.

This passive stiffness is enhanced by segmental reflex activation. When a limb is loaded due to small shifts in center of mass, the tonically active extensors will be stretched, resulting in reflex activation that will cause the limb to extend. The contralateral hindlimb will be unloaded, and the extensors will be shortened, resulting in reduced drive to the motoneurons and decreased activity. The resulting imbalance in forces at the ground will tend to push the trunk toward the unloaded limb and counteract the displacement. Such a mechanism, based on muscle stiffness, is effective within only a very narrow range of displacement and velocity of displacement of the animal’s center of mass, as evidenced by the difficulty in manipulating the spinal animal to the point of balance. As a balancing mechanism, this strategy is not very effective and probably depends critically on a relatively even distribution of weight and muscle tone between the two hindlimbs. Although the stiffness characteristics of the limb also contribute to stability in the intact cat, it is not likely that these reflex mechanisms form the basis of the normal automatic postural response.

Although cats spinalized as adults have poor balance control, kittens spinalized early after birth are purported to have more complete recovery of motor behaviors, including some stability, but the nature of this stability has not been quantitatively examined. Several studies described spinal kittens as being able to stand up and maintain stance independently and to walk over ground for quite a few steps without falling (Grillner 1973; Shurrager and Dykman 1951). Nevertheless detailed studies of the development of locomotion have revealed significant differences in stepping behaviors between intact and spinal kittens (Bradley and Smith 1988a,b). It is difficult to comment on the apparent postural differences between young and adult animals without quantitative analysis of the kittens’ postural behaviors. Nevertheless one can speculate that the local reflex mechanisms, which increase stiffness, could have enhanced the gain and lowered the threshold to sensory input, effectively making the overall mechanical system less compliant. In addition, the broad base of support and relatively low position of the center of mass of the kitten compared with the adult would make the kitten inherently more stable. There also may be differences in the trunk muscles in terms of level of tone and loss of muscle mass after spinalization such that the spinal kitten may have more resistance to bending and rotation of the vertebral column. The possible effect of early postnatal transection on spinal cord development has been well described (Robinson and Goldberger 1986).

Weight support

Unlike balance, good weight support was maintained by all the spinal cats. The reflex mechanisms and stiffness characteristics that affect extensor tonus undoubtedly contributed to the ability of the spinal cat to sustain weight support of the hindquarters. All four cats were able to maintain a normal hip height during those platform translations which loaded one or both hindlimbs. The loading response observed in the hindlimb extensors was often not sufficient to restore the lateral position of the hip relative to the feet (Figs. 8 and 13A), nevertheless the trunk did not sag or lose vertical height unless the cat began to fall. Moreover falling most often was characterized by a sway of the hips to right or left, followed by the proximal trunk, and less often by a vertical drop or loss of weight support. The ability of the spinal cat to maintain weight support dynamically also has been reported for treadmill locomotion. Previous studies have shown that this capacity to support weight can be enhanced by training (Barbeau and Rossignol 1987; deLeon et al. 1998a,b; Lovely et al. 1986; Smith et al. 1982) and by drugs (Chau et al. 1998; Forssberg and Grillner 1973).
Forces and kinematics

In addition to the EMG patterns, the spinal cat showed differences from the intact cat in the forces at the ground, joint torques, and kinematics in response to platform translation. The lower amplitude and diminished rate of rise in vertical force for translations in which the hindlimb was loaded has several possible explanations. First, even though vertical force was normalized to body weight, the spinal cat bore a lower percentage of weight with the hindlimbs as discussed in the accompanying report (Fung and Macpherson 1999). Therefore the change in force with loading may be expected to be somewhat lower than in the control case. The lack of an early activation in the extensor muscles may have contributed to the slower build up of vertical force. However, the fact that the hip height did not drop in the spinal cat suggests that the extensors had sufficient tone to prevent the limb from yielding. The difference in body motion for frontal plane translations also may have contributed to the change in force. In the intact cat, translations with a lateral component caused the trunk to roll about the long axis. As the trunk rolled and the loaded limb was carried under the body, the hip height decreased. The rotational moment about the long axis of the body would tend to increase the amplitude and rate of rise of vertical force under the loaded limb. In the spinal cat, the roll of the trunk was more limited and the loaded hindlimb adducted at the hip. This change in body motion would have reduced the rotational moment of the trunk and therefore the amplitude and rate of rise of vertical force. The increased tendency of the hip joint to adduct also has been observed in spinal cats during locomotion (Barbeau and Rossignol 1987) and may reflect an imbalance of abductor and adductor tonus, perhaps due to wasting of muscles at the pelvic level. The decrease in net joint torque in the spinal cat is primarily due to the decrease in vertical force exerted by the hindlimb against the support. The spinal cat also exhibited an abnormal pelvic position during stance. In the sagittal plane, the iliac crest was less elevated with respect to the ischium than in prespinal stance. This rotated pelvic position occurs normally in intact cats as well but only when they stand at a fore-hindpaw distance that is longer than preferred. At a long stance distance, sagittal plane translations are characterized by hindlimb motion predominating at the hip joint, with the pelvis remaining fixed (Macpherson and Fung 1998), just as observed in the spinal cat. Thus the change in angular rotation of pelvis and hip during translation in the spinal cat merely may reflect the mechanics of the pelvis and hip joint complex. Why the pelvic position was so different in the spinal cat even though it stood at a normal stance distance is not clear. As in the frontal plane discussion in the preceding text, it may be due to loss of muscle mass and therefore loss of tone required to keep the pelvis elevated.

Neural centers for balance

The apparent lack of a postural equilibrium response in the hindlimbs of the chronic spinal cat suggests that the neural circuits controlling stability are located at higher levels of the neuraxis than the spinal cord. This is not surprising if one considers that balance requires the integration of vestibular, visual, and proprioceptive information which is known to occur in brain stem and cerebellum (Horak and Macpherson 1996). Moreover, balance requires the coordinated application of force by all four paws to control the position and velocity of the body’s center of mass. Alternatively, the major circuits for balance may be within the spinal cord but distributed across rostral and caudal segments. Communication among forelimb, hindlimb, and axial spinal centers may be essential for computing appropriate balancing reactions to control center of mass. However, the same argument could be made for hindlimb stepping, which nevertheless is generated by local circuits in the lumbar cord. Locomotion, like posture, requires coordination among the four limbs. Yet unlike posture, the basic unit of stepping is the oscillator at the single joint level, and stepping movements can be elicited in a single hindlimb of the spinal cat (Grillner 1975; Rossignol 1996). Thus the control mechanism for balance appears to be different from that for stepping. Either balance control is critically dependent on propriospinal pathways, unlike stepping, or the control center for balance resides above the spinal cord.

In a balance task, the hindlimb must exert force against the ground of a specific direction and amplitude, which, in combination with the other three limbs, will propel the center of body mass in the appropriate direction to maintain stability. For this to be effective, the trunk also must be stabilized. The requirements of coordination among the four paws and the computation of the appropriate forces based on the estimated impulse on the center of mass due to a disturbance are consistent with a control circuitry that is located above the spinal cord or that, at the very least, depends critically on input from higher centers. The brain stem and/or cerebellum receive afferent inputs from several sensory systems including somatosensory, vestibular and visual, making these areas likely sites for the integration of afferent inputs and the formulation of an internal model of body posture. Even though the response to platform translation seems to depend only on somatosensory inputs, both vestibular and visual signals are known to influence postural orientation and balance under a variety of conditions (Horak and Macpherson 1996).

Finally, this study has important implications for the rehabilitation of patients with spinal cord injury. Our results suggest that the neural control of balance and of weight support involve different mechanisms and different neural structures. It is not likely that balance control can be restored after injury unless the critical ascending and descending tracts to and from postural centers are functional, making the development of artificial devices for stability an important goal in rehabilitation engineering. In contrast, successful training to enhance weight support and to normalize stepping may be less dependent on higher centers and therefore more attainable for a larger number of spinal cord injured individuals.

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