INTRODUCTION

The maintenance of equilibrium in quiet stance requires not only that the body be supported against gravity but also that the body’s center of mass be maintained within the base of support in the horizontal plane. As quadrupeds, cats have an intrinsically stable musculoskeletal framework (Gray 1944). Nevertheless, active control of the limbs and trunk is required to maintain stance and balance. The sensorimotor system must interact with the external environment to maintain stability and orientation across changing terrain.

We have examined previously the determinants of postural orientation in intact cats during quiet stance at various interpaw distances (Fung and Macpherson 1995). Postural orientation refers to the relative position of the body segments with respect to each other and with respect to environmental coordinate reference frames (e.g., gravity vector). Intact cats use a strategy of orienting the trunk parallel to the support surface and changing orientation of the limbs at the pectoral and pelvic girdles to accommodate changes in stance distance. The sagittal plane ground reaction force (GRF) vector is aligned closely with the limb axis, and both change their angle as fore-hind stance distance changes, whereas intralimb geometry is held constant.

As a result, the distribution of joint torques is constrained and the effort of stance has a local minimum at a stance distance near the cat’s preferred distance. We postulate that the adaptation to changes in stance distance is determined by both mechanical and neural constraints. Mechanical constraints are dictated largely by viscoelastic properties of muscles and joint ligaments, whereas neural elements consist mainly of spinal reflexes such as la and lb pathways.

The degree to which the isolated spinal cord circuitry can maintain and adapt postural orientation is not known. With adequate training, cats can recover full weight-bearing and stepping capability in the hindlimbs after a complete spinal cord transection (Barbeau and Rossignol 1987; Carter and Smith 1986; Lovely et al. 1986, 1990; Smith et al. 1982), but the metrics of quiet stance have not been quantified. Our preliminary work (Fung et al. 1995; Macpherson et al. 1997; Pratt et al. 1994) showed that the chronic spinal cat can maintain normal positioning of the hindlimbs during brief periods of stance, suggesting that postural orientation may have a significant spinal component. The purpose of this study was to determine whether the chronic spinal cat can adapt to stance distance changes and use similar strategies as intact cats in maintaining equilibrium during quiet stance.

METHODS

Subjects and surgical procedures

Four adult male cats were used in this study (Ru, 3.9 kg; Ni, 4.8 kg; Re, 3.8 kg; and Go, 4.36 kg). The experimental protocol was approved by the local Institutional Animal Care and Use Committee and conformed to National Institutes of Health guidelines regarding the care and treatment of animals. The cats were trained daily (5 day/wk) using food reward and verbal encouragement to stand quietly on four small treads of a force platform (Fig. 1A). The “preferred” stance distance was determined...
from the natural paw-separation distance assumed by each cat on the floor. A mean of 10 measurements was taken as the cat stood still intermittently while roaming freely over the tiled floor of the laboratory. This preferred stance distance (Fig. 1B, vertical dashed line) was found to be quite similar among the four cats (29 cm for Ru and Ni; 28 cm for Re and Go). Setting the fore-hind plate distance at the preferred distance was useful to ensure a comfortable stance posture for initial training and for the purpose of comparing stance distances among cats. The training program consisted of discrete trials of 1–5 s in length in which the cat was required to distribute its weight about equally between the left and right sides (with the difference in loading forces to exceed no more than 10% of body weight) to receive the food reward.

Once trained, each animal was implanted with chronically indwelling electrodes for recording electromyographic (EMG) activity from fore- and hindlimb muscles on the left side of the body. Cats were anesthetized with Saffan (0.75 ml/kg consisting of 9 mg/ml alphaxalone and 3 mg/ml alphadolone acetate), and implantations were performed under aseptic conditions. Electrodes consisted of bipolar multistranded stainless steel wire insulated with Teflon (Cooner AS632). The proximal ends of the wires were drawn up under the skin and attached to a connector, which then was mounted on the skull. These electrodes provide consistent recordings for many months. Cross-talk was minimized by placing the electrodes well within muscle boundaries, baring a small length of wire within the muscle (2–3 mm), and spacing the electrodes <5 mm apart. At the time of implantation, morphometric measures were taken of limb segment lengths and joint widths for subsequent inverse dynamics calculations.

After control data were collected, cats were spinalized (complete transection) at the T6 level. A midline incision was performed through the skin and fascia from T4 to T8. After retracting the skin and fascia, another midline incision was performed through the back muscles overlying the T5–T7 vertebrae. The muscles attached to the dorsal part of the T6 vertebra were scraped away and retracted. The T6 spinous process was removed, and a partial laminectomy was performed to expose the spinal cord in the vertebral canal, taking care not to disrupt the intervertebral joints. The dura was opened sufficiently to allow application of a few drops of lidocaine directly onto the spinal cord. After 5 min, the spinal cord with dural sheath was hook-lifted from the exposed canal and cut completely through. The space between the retracted caudal and rostral stumps was packed with Gelfoam, and the wound was closed in layers. Antibiotics were administered 1 day before surgery and continued for 7–10 days after spinalization.

After spinalization, the cats were maintained on a thick layer of absorbent bedding material to prevent pressure sores. The bladder was expressed manually twice daily. Stretching exercises, passive range of motion, and massage were administered daily to the hindlimbs. Stance training was begun within 1 wk of the surgery, and data collection resumed as soon as the animal was able to support all its own weight. Data collection proceeded with an assistant behind the cat to provide lateral stability as needed and to prevent falling. Once the cat was stable and bearing full weight during standing, manual assistance was removed and the trials of independent quiet stance data were acquired. The cat was killed when data collection was completed. Postmortem dissection was conducted, without histological investigations, to verify the sites of muscle implantation in each cat.

**Data collection**

After cats recovered from the implantation surgery, control data were collected. The cats were tested at five different fore-hind plate distances (Fig. 1). The five plate separation distances consisted of the preferred distance, two increments, and two decrements, each of 5 cm. Thus a total range of 20 cm was examined, from the shortest to the longest fore-hind plate distance. The recording sessions used similar force stabilization routines as the training sessions. The cats were freely standing and
unrestrained, the only restriction being to remain upright (not crouched) and to keep each paw on a force plate. The order of plate distance variations was randomized. At each plate distance, a total of three sets of five trials, consisting of 2 s of quiet stance were collected for Ru and Ni. We noted that after spinalization, it was often difficult for the first two cats to maintain independent stance for the entire duration of 2 s without assistance, especially at extreme stance distances. Assistance often was needed near the middle or end of the trial to prevent the cat from falling as it was distracted or moving the head. Thus only the initial 100 ms of each trial of quiet stance was used for data analysis. For the subsequent two cats (Re and Go), quiet stance data consisted of the 100-ms background period before perturbations. Forty to 80 of these trials were collected each day.

The recorded data included the three linear forces from each of the four force plates (12 force channels), eight 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 Optotrac system (Northern Digital) with infrared emitting markers (IREDs) fixed over bony landmarks of the fore- and hindlimbs on the left side (see Fig. 1). 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.

Data analysis

The various data types were all imported into one file for each trial and subsequent analysis was performed using Matlab (Mathworks). Force, EMG, and joint-position data were averaged within each trial. Only unsupported trials of independent quiet stance were accepted for data analysis. Joint radius, skin depth, and IRED base thickness were subtracted from the x-axis joint positions to approximate joint centers of rotation. The actual fore–hind paw separation distance was obtained by calculating the distance between the metacarlo–phalangeal (MCP) and metatarsal–phalangeal (MTP) joint markers. This was termed ante–posterior (AP) stance distance and was used subsequently as the independent variable in all regression analyses.

Forces were analyzed in the three cardinal planes (sagittal, frontal, horizontal) as well as in three dimension. The vertical (Fz), longitudinal (Fx), and lateral (Fy) force components under each paw were summed in pairs to obtain the planar vectors. Center of pressure (CoP) in the AP and lateral directions was calculated by summing, respectively, Fz’s of the front paws and Fz’s of the right paws, with each normalized as a percentage of the summed Fz’s of all four paws. Under static conditions and averaged over time, the CoP is equivalent to the position of the center of mass projected onto the horizontal plane.

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 power spectrum analysis of representative kinematic data. Joint and segment angles were computed for the forelimb axis, the line joining the shoulder (glenohumeral) joint and MCP joint; the hindlimb axis, the line joining hip and MTP joints; and the trunk axis, the line joining shoulder and hip joints. Net joint torques were computed for fore– and hindlimbs using inverse dynamics from the kinematic and ground reaction force data, body weight, 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.

Force, kinematic, and kinetic variables were graphed against AP distance as scatter plots and smoothed by a function using locally weighted least squares of sums (LOWESS). A tension of 0.8 was used in all the LOWESS smoothing procedures. The LOWESS lines were helpful in determining the choice of curve-fitting. When the LOWESS line appeared linear, a linear equation was fitted to the data. When the data showed significant linear regressions (\( P < 0.01 \) and \( R^2 = 0.70 \)), the slopes and elevations of the regression lines were compared by t-tests (Zar 1984) with Bonferroni adjustment. All statistical and smoothing procedures were done using Systat (SPSS).

RESULTS

Recovery of stance capability and adaptability after spinalization

Although equal amounts of intensive daily physical therapy and stance training were given to all four cats, there were two distinct paths of recovery that seemed to depend on the development of muscle tone in the hindlimbs after spinalization. Muscle tone at each hindlimb joint was recorded daily as the amount of resistance perceived when the examiner passively moved each hindlimb joint through the full range of flexion and extension at varying velocities. Clasp–knife response was considered present when a joint suddenly yielded into flexion as it resisted being flexed from a fully extended position. Immediately after spinalization (within the 1st week), cats Ru and Re had muscle tone not noticeably different from the prespinalization period, whereas cats Ni and Go were completely flaccid in the hindlimb muscles. By day 10 postspinalization, Ru and Re were standing independently and intermittently, with full weight-bearing capability. In contrast, Ni and Go required perineal stimulation or tail clamping, to prevent the hindquarters from sagging to a squatting position. Hindlimb muscle tone progressively increased in all four cats such that after 1 mo, Ru and Re had developed considerable hypertonia and spastic features, including increase in resistance to passive stretch and clasp–knife responses. Spasms, clonus, and stepping behavior frequently interfered with quiet stance. In contrast, at 1 mo, Ni and Go had developed sufficient muscle tone to maintain brief periods of independent stance without perineal stimulation. However, hindlimb muscle tone in these two cats remained low and the hindlimbs yielded from time to time during quiet stance, causing the hindquarters to descend into a crouch. None of the spasticity–like features observed in Ru and Re were present in Ni and Go.

Stance data in the spinalized cat were acquired from the second week up to 3 mo after spinalization. Because of the different time course of tone development, more stance data were obtained from Ru and Re during the early period (between 2 and 6 wk), whereas more stance data were obtained from Ni and Go during the later period (between 2 and 3 mo). Figure 1B shows the individual means and variations of AP stance distance at each plate separation before spinalization (closed black circles) and during the 3 mo postspinalization (open grey circles). Also shown in Fig. 1, B is the entire range of unsupported, independent stance distances achieved by each cat during the prespinalization period (black bars) and in the 3 mo after spinalization (gray bars). Three of the four cats (Ru, Ni, and Re) could adapt to standing at a variety of stance distances after spinalization, although the range of distances was smaller and skewed toward the shorter distances as compared with the
preferred distance before spinalization (dashed vertical lines). 

Cat Go could manage to stand independently only at the shortest plate distance (20 cm) even at 3 mo after spinalization and not at any longer stance distances.

The relative distribution of loading on the limbs can be observed from the position of center of pressure (CoP) in the medio-lateral (x) and antero-posterior (y) axes, before (filled black circles) and after spinalization (open gray circles) in each cat (A–D). E: data were binned as indicated and averaged across all 4 cats. Gray zone in the CoP-Y graph denotes the range of CoP-Y predicted by assuming that all the weight loss postspinalization was from the hindquarters.

greater proportion of body weight was borne by the forelimbs after spinalization than before. The average anterior shift in CoP-Y was within the range predicted by a simple model of redistribution of body mass (Fig. 2E, gray zone), which assumed that all the weight loss was from the hindquarters.

**Strategies and determinants of postural orientation**

All four cats could maintain relatively normal orientation of trunk and hindlimb axes, as well as hindlimb GRF vector during quiet stance after spinalization. As observed in the intact cat, the trunk axis was generally parallel to the support surface, the forelimbs were almost fully extended, and the hindlimbs were semiflexed in quiet stance. Significant changes were observed postspinally in the orientation of the forelimb axis and the pelvis. Figure 3 shows the sagittal plane forelimb and hindlimb postures together with the alignment of the ground reaction forces in cat Ni. At the preferred (intermedi-

![Figure 2](https://example.com/figure2.png)

**FIG. 2.** Center of pressure (CoP) plotted as a function of AP stance distance. CoP along the mediolateral (x) and longitudinal (y) axes, before (filled black circles) and after spinalization (open gray circles) in each cat (A–D). E: data were binned as indicated and averaged across all 4 cats. Gray zone in the CoP-Y graph denotes the range of CoP-Y predicted by assuming that all the weight loss postspinalization was from the hindquarters.

![Figure 3](https://example.com/figure3.png)

**FIG. 3.** Averaged sagittal plane limb geometry (stick figures) and ground reaction force (GRF; arrows) of cat Ni standing at 3 different AP distances. Vertical dashed lines through the figurines represent the earth vertical. Stick figures were aligned at the MTP joint for the hindlimb and at the MCP joint for the forelimb to contrast the postures at different stance distances and for comparison before (black) and after spinalization (gray).
As a consequence, the hip and ankle were more flexed, whereas the knee was more extended than in the control case. Nevertheless both the GRF vector and the hindlimb axis maintained the same alignment as in the control. The forelimb axis was anteriorly tilted relative to control especially at the shorter stance distance.

The three spinalized cats that could adapt to changes in stance distance (Ru, Re, and Ni) used similar strategies as intact cats by maintaining a constant horizontal trunk orientation while changing limb orientation. The GRFs remained closely aligned with the limb axes. As illustrated by the example of Ni in Fig. 3, both the fore- and hindlimb axes as well as the GRFs became more inclined from the vertical as the stance distance increased from shortest to longest. The GRFs after spinalization (gray arrows) remained parallel to those before spinalization (black arrows) although the vector amplitudes were smaller for the hindlimb. The significant linear relationships (P < 0.001) among the various parameters of postural orientation with AP stance distance are illustrated further in Fig. 4 (A–F). In the forelimb, the AP stance distance could account for most of the changes in orientation of the limb axis (Fig. 4A, r² pre = 0.96; r² post = 0.90) and of the GRF vector (Fig. 4E, r² pre = 0.96; r² post = 0.88), whereas the GRF vector angle varied closely with the limb axis (Fig. 4F, r² pre = 0.94; r² post = 0.88). No significant difference in slope was found for these hindlimb variables before and after spinalization. However, the regression of the hindlimb axis onto stance distance in the spinal cat was offset compared with prespinal, indicating a slightly more inclined posture than in the intact animal at each stance distance. The orientation of the trunk axis, as well as the vertical height of the shoulder and the hip joints, remained constant across all stance distances (Fig. 4, G–I). There were no differences before versus after spinalization, indicating that the strategy of constraining trunk geometry was preserved in the spinal cat. These findings, which are illustrated for cat Ni with low muscle tone, were similar to those for the cats with high tone (Ru and Re).

Although body axes of the spinal cat were similar to control,
the intralimb geometry was significantly different. Figure 5 shows the proximal and distal segment angles as well as the joint angles of the forelimb and hindlimb of Re for stance at different AP distances. In the forelimb, the scapula was oriented closer to vertical postspinalization especially at the shorter stance distances. The elbow was more flexed and the wrist was more extended at the shorter stance distance. The forepaw segment became less dorsiflexed at shorter stance distances and more dorsiflexed at longer ones. In the hindlimb, the pelvis of the spinal cat was angled more forward than control at the short stance distance and did not show the strong increase in angle with increase in stance distance that characterized the control pelvis angle. In contrast, the hip joint in the spinal cat was more extended at longer distances than in the control and showed a strong increase in extension with increase in stance distance unlike the control hip angle, which tended to remain constant with stance distance. Thus before spinalization, the hindlimb axis rotated at the pelvic segment as stance distance changed while the hip joint angle remained constant. After spinalization, the pelvic segment remained relatively constant while the hindlimb axis rotated at the hip joint. The knee joint was more extended and the ankle more flexed across all stance distances in spinal versus control stance. The hindpaw segment maintained a similar relation with AP stance distance, but it was more plantarflexed in the spinal cat across all distances.

**EMG and joint torques**

In the spinal cat, tonic EMG activity during stance generally was elevated in forelimb extensors and diminished in hindlimb extensors. Figure 6 shows examples of the average background EMG activity plotted against AP distance in different cats. Supraspinatus (Fig. 6A, Re), an upper arm extensor, was activated at a markedly larger amplitude in the spinal cat throughout all stance distances. Teres major (Fig. 6B, Re), an internal rotator and arm adductor, was not recruited at any stance distance in the intact cat, but became tonically activated across all stance distances in the spinal cat. In contrast, vastus medialis (Fig. 6C, Ni), a knee extensor normally activated at longer stance distances, and lateral gastrocnemius (Fig. 6D, Re), an ankle plantarflexor normally recruited at shorter stance distances, became markedly diminished at all stance distances in the spinal cat.

Figure 7 shows a cost function for the hindlimb of three cats, computed by summing the squared three-dimensional joint torques. This function is related to the “effort” required in maintaining the stance posture (Nubar and Contini 1961). As reported previously (Fung and Macpherson 1995), this function has a curvilinear relation with AP stance distance in the normal cat with the minimum cost function at or near the preferred stance distance. In each spinal cat, this function generally was diminished throughout all stance distances, indicating that less torque or effort was generated by the hindlimb. The diminished cost function was related to the decreased load borne by the hindlimbs postspinalization and remained relatively constant across stance distance.

Figure 8 (cat Ru) illustrates the pattern of torque distribution...
during stance that was common to all cats. There were considerable differences in the pre- and postspinal net torques at each of the hindlimb joints because of the difference in vertical force between the two conditions. Therefore sagittal torque at each joint was normalized as a percentage of the summed torque to allow comparison of the relative distribution of torque across the joints of each limb before and after spinalization. This was considered a valid normalization because there was a linear relationship between the sum of the net torques across all joints of the limb and the loading force (Fz), for both forelimb and hindlimb (Fig. 8A). Data from all stance distances were included. The slopes of the linear regressions were similar, pre- versus postspinally, for both the fore- and hindlimb. However, for the forelimb, the postspinal function was shifted upward, indicating a significantly greater value of summed torque at each given force level in the spinal cat. Although the values of summed torque for the hindlimb were lower postspinally, so too were the loading forces, indicating a simple downward shift along the same linear function.

In the forelimb (Fig. 8B), a higher percentage of extensor torque was distributed at the elbow joint, compared with the shoulder, before spinalization. After spinalization, torque was more evenly distributed across shoulder and elbow joints. Distribution of moments in the wrist and MCP were similar pre- versus postspinalization. In the hindlimb (Fig. 8C), redistribution of joint torques was observed mainly at the hip and ankle. Before spinalization, the extensor torque was greater at the hip compared with the ankle, whereas after spinalization, extensor torque was greater at the ankle than at the hip. The torque distribution changes with stance distance were not affected by spinalization. Before and after lesion, the percentage of extensor torque at the hip and ankle decreased with increasing stance distance, whereas the extensor torque at the knee increased. The relative distribution of moments at the knee and MTP joints did not change with spinalization. The same findings were observed in the other two cats (Re and Ni) with different presentations of muscle tone. Thus the net torque distribution after spinalization was not affected by the degree of muscle tone present in the hindlimb.

**DISCUSSION**

The present study shows that the chronic spinal cat could maintain relatively normal body geometry during quiet stance and could, to a lesser degree, adapt to changes in interpaw distance. Those cats that could adapt retained the strategy of a constant horizontal trunk alignment while tilting the limb axes together with their ground reaction forces. However, marked changes in intralimb geometry were noted in the hindlimb as well as the forelimb and especially in the proximal segments. These differences may be due to postspinal changes in the development of force in the muscles of the hindquarters, as well as compensatory changes in the forequarters.

The decision to transect the spinal cord at the T 6 level, rather than at the thoraco-lumbar junction (as conventionally done), was based on two factors. We previously found that the epaxial trunk muscles subdivide into two functional groups, upper thoracic and lower thoracic/lumbar, based on their response to translation in the horizontal plane (Macpherson and Fung 1998). The transition from one response type to the other occurs in a relatively discrete region between T10 and T 12 , where the trunk extensors respond to almost all directions of translation. Therefore the muscles near the thoraco-lumbar junction may be particularly important for postural stabilization. Second, our recent X-ray study (Macpherson and Ye 1998) showed that during stance, the lower thoracic and upper lumbar vertebrae assume a strong dorsiflexion curvature and the T12 to T13 joint is near maximal flexion. Thus laminectomy at the T 13 level may result in significant destabilization of the spine by disrupting critical trunk extensor muscles and by mechanically weakening the vertebra and its articulations. Such destabilization could compromise the ability of the T13-spinal cat to control the trunk during stance. To avoid this possibility, we decided to transect the cord more rostrally, at T 6 .
Control of body axes

Postural orientation, or the relative positioning of body segments with respect to each other and to the environment, is one of the two major behavioral goals underlying postural control (Horak and Macpherson 1996). The other goal, postural equilibrium, is the focus of the accompanying report (Macpherson and Fung 1999). Spinalization did not affect the alignment of either the trunk axis or the hindlimb axis during quiet stance even though forelimb and hindlimb geometry were somewhat different from control. Furthermore the trunk remained aligned to horizontal at different stance distances as previously shown in intact cats (Fung and Macpherson 1995).

Thus we conclude that the rudimentary neural processes for attaining postural orientation of the hindquarters in quiet stance are manifested in the spinal cord.

Trunk axis orientation is a function of the heights of both the shoulder and the hip joint above the support surface and therefore is affected by the degree of extension of forelimbs and hindlimbs. The forelimb in the cat is considerably shorter than the hindlimb and, during stance, the forelimb is held habitually near maximum extension while the hindlimb is semiflexed. In the spinal cat, the forelimb is also near maximum extension, so trunk axis orientation depends critically on the height of the hip which, itself, depends on the amount of extension at knee, ankle, and MTP joints. The extension at each joint is a function of the tonic activation level in the antigravity muscles.

In the spinal cat, the angles at all the hindlimb joints were different from control, yet the overall height of the hip was maintained as in the control. The decrease in joint angle at MTP and ankle were compensated by an increase at the knee, and these relationships were maintained across all stance distances. Even though hindlimb joint angles and loading forces were different after spinalization, the percent of total extensor torque developed at the MTP and knee were similar to control, whereas that at the ankle was higher. These findings suggest that spinal circuitry contains global set points regarding limb geometry, that is, the setting of some function related to the length of the extensor muscles at knee, ankle, and MTP joints, combined. Changes in extensor muscle length at any of the joints will result in changes in joint angle that are compensated at the other joints according to the global function that ultimately determines hip height and therefore trunk orientation in space.

Orientation of the trunk in space is an important controlled variable (Gurfinkel and Levick 1991) not only in the regulation of quadrupedal stance, but also of bipedal stance, as shown by psychophysical experiments in humans (Mittelstaedt 1983; Young et al. 1984). It further has been demonstrated that subjects use the trunk as a reference to estimate head position in space, head position relative to the trunk, and trunk position in space (Mergner et al. 1993). Multiple senses, including vestibular, visual, proprioceptive, and perhaps mesenteric afferents from receptors in the kidney capsules (Mittelstaedt and Fricke 1988) contribute to the determination of trunk position relative to the base of support. The isolated lumbosacral cord in the chronic spinal cat clearly lacks access to the entire body schema (Gurfinkel and Levick 1991) that is constructed from all these sources of sensory input. Nevertheless some of the feedback mechanisms regarding trunk orientation may be available at the spinal level, thereby allowing trunk orientation to be maintained even at different interpaw distances.

In the chronic spinal cat, the central, internal representation of body posture may have changed postspinally with the loss of all sensation caudal to the mid-thoracic level. The cat may have experienced the hindquarters as a “dead weight” pulling from behind, causing the cat to constantly pull the shoulders and anterior trunk forward as a counterbalancing strategy. Thus the change in forelimb orientation that was observed in the spinal cat may have been a compensation for the change in body image. Not only was the limb orientation changed, but so too was the distribution of extensor torque between elbow and shoulder. Alternatively, the change in forelimb orientation may have been an active strategy to redistribute the increased loading force between elbow and shoulder extensor muscles.

Muscle tone and stiffness regulation in stance

The degree of muscle tone, or resistance to passive stretch, in the spinal cat likely has a strong influence on stance capability. Hypotonia in hindlimb extensors causes the limbs to collapse under the influence of gravity. At the other extreme, hypertonia can trigger spasms and stepping responses, which interfere with quiet stance. Early behavioral studies (Burke et al. 1972; Eidelberg 1981; Wiesendanger 1985) reported a gradual development of extensor tonus in the hindlimbs after a complete spinal cord transection, giving rise to moderate increase in stretch reflexes and clasp-knife responses in the chronic stage. Two of our chronic spinal cats (Ru and Re) manifested similar changes. The other two (Ni and Go) also had gradual increase in extensor tone but showed no signs of spasticity even at 3 mo postspinalization. In fact, Go remained hypotonic, which may have been related to its inability to adapt to stance distance changes.

Stance in the spinal cat is accomplished partly through spinal reflex mechanisms that set stiffness levels for extensor muscles and provide length and force corrections within narrow limits (Grillner 1972). Bennett et al. (1996) showed that during low level tonic contractions, the triceps surae stretch reflex loop gain was ~1 in spinal or decerebrate cats, contributing to about half of the total hindlimb muscle force generated during low-level postural corrections. Such a high gain indicates that a stretch on the muscle spindles produces an equal amount of muscle shortening under isotonic conditions. Spasms or tremor would occur if the gain were to increase further (Bennett 1994).

In the present study, there were several characteristics that distinguished stance in the spinal cat from that in the intact cat. Even at the preferred stance distance, the postspinal intralimb joint angles were different from prespinal, suggesting changes in the working length of the tonically active muscles and shifts in the working region of the length-tension curves. In addition, the amplitude of the hindlimb GRF was lower after spinalization, making the total muscle force requirement lower as well. It is also interesting to note that the ankle extensors were likely more stretched in the spinal cat than in the intact animal because the ankle joint was held in a more flexed position across all stance distances. Ankle stretch reflexes are enhanced in the chronic spinal cat due to a large increase in homonymous and heteronymous Ia excitatory postsynaptic potentials in the ankle extensor motoneurons (Hochman and McCrea 1994).
The augmented stretch of the ankle extensors and the enhanced stretch reflex gain postspinalization may both contribute to ensuring continued antigravity support in the spinal cat as the limb is loaded and unloaded with small shifts in center of mass.

**Center of pressure**

Stability in quiet stance is maintained by adjusting the distribution of load on the limbs such that the horizontal plane projection of the body’s center of gravity is maintained within the base of support (Winter et al. 1996). A reasonable approximation of the horizontal plane position of the center of mass during quiet stance can be determined from the center of pressure averaged over the time period of the trial. In the chronic spinal cat, the center of pressure was displaced forward, compared with control, at all distances. However, the amount of forward displacement could be accounted for entirely by the amount of weight loss that the animal experienced postspinally, assuming that the loss was due to wasting of the hindquarters only. Intact cats also adjust to a redistribution of body mass by changing the load borne by each limb and allowing the center of pressure to move to a new position. Previous studies showed that when body mass in the standing cat was artificially redistributed anteriorly by applying external loads to the forequarters, the center of pressure shifted forward (Lacquaniti and Maioli 1994; Lacquaniti et al. 1990). We observed that increasing stance distance also caused the center of pressure to be shifted progressively more forward in both intact and spinal cats. However, this may have been a behavioral strategy, to keep the head close to the food bowl.

**Adaptation to stance distance changes**

The intact cat accommodated to stance distance changes primarily by changing the angle of the paw and pelvic segments (Macpherson 1994). As stance distance increased, the iliac crest of the pelvis became progressively tipped down, whereas hip joint angle remained nearly constant. In the chronic spinal cat, the pelvis was tipped down even at the short stance distance. Unlike the intact cat, the pelvis angle did not change with stance distance, whereas the hip angle was significantly modulated. The abnormal position of the pelvis in the spinal cat may be due to the significant loss of muscle mass around the pelvic girdle and a reduced capacity to generate force in the hip extensor muscles. However, it is not clear which pelvic muscles are tonically active during stance and how pelvic angle is maintained even in the intact cat (Macpherson and Ye 1998). This change in geometry of the pelvis and hip joint may help explain the difficulties of the spinal cat in standing at the longer stance distances.

Quiet stance often was disrupted at the longer distance by stepping movements of the hindlimbs. The stepping response may have been facilitated by the hip’s extended position, which was more pronounced in the postspinal cat. Previous studies showed that when the hip was extended beyond a critical angle during treadmill locomotion, a phase switch from extension to flexion was triggered in chronic spinal and in decerebrate cats, (Andersson and Grillner 1981, 1983; Grillner and Rossignol 1978). Unloading the hindlimb in the spinal cat also caused a phase resetting from stance to swing in spinal locomotion (Duysens and Pearson 1980; Pearson et al. 1992). Thus the observed decrease in loading force under the hindlimbs with increasing stance distance in the spinal cat also could have contributed to stepping responses during stance.

Another limiting factor, in accommodating to increased stance distance after spinalization, may have been the decrease in tonic activity in hindlimb extensors. Restricted output and limited adaptation of extensor activity also were noted in chronic spinal cats walking at different treadmill speeds (Belanger et al. 1989) or on an inclined surface (Belanger et al. 1988). The maximum walking speed was limited to 0.8–1.0 m/s after spinalization, in contrast to 2.5 m/s before spinalization (Belanger et al. 1989). Although the chronic spinal cat could manage to walk on surfaces inclined in pitch, it could not cope with more than a few degrees of roll without manual assistance (Belanger et al. 1988). One interesting observation of spinal locomotion is the reduction in step length, which can be attributed to the restricted distance of forward paw placement relative to the hip position at the onset of stance (Belanger et al. 1996).

It must be emphasized that the capacity to adapt to stance distance changes postspinalization is attainable only with training, and still, one of four cats could not accommodate stance distance changes, even after 3 mo of intensive stance training. Our results support the idea that a certain degree of functional adaptation, or plastic change, can be achieved after spinalization. Recent studies showed that the ability to stand or walk after spinalization depended not only on the intensity, but also on the specificity of the training (Edgerton et al. 1997). Spinal cats which were trained to stand had better stance performance than cats trained to walk and vice versa. Spinal cats that received stance training had a fivefold increase in stance endurance compared with untrained cats (de Leon et al. 1998a), and those trained to walk could achieve maximal walking speeds, three times that of untrained cats (de Leon et al. 1998b).

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