Contribution of Cutaneous Inputs From the Hindpaw to the Control of Locomotion. I. Intact Cats

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INTRODUCTION

Experiments by Sherrington in the early 1900s (Sherrington 1910) suggested that cutaneous inputs do not play a major role in the control of locomotion in quadrupeds. Indeed, having removed all cutaneous nerves of the hind and fore paws, Sherrington concluded that this procedure impaired “walking so little as to make it highly unlikely that the loss of receptivity of the feet destroys any large factor in the reflex basis of these acts.” Sherrington also reported that, in decerebrate or chronic spinal cats with similar cutaneous denervation, bilateral rhythmic movements of the hindlimbs could still be induced by perineal stimulation or extension of the hips (air stepping).

That the generation of the fundamental rhythm of locomotion does not depend essentially on peripheral afferent inputs (proprioceptive or cutaneous) has now been quite well established. Indeed, the basic locomotor pattern can be expressed after neuromuscular paralysis that removes all movement-related phasic sensory inputs in spinal cats injected with L-dihydroxyphenylalanine (Grillner and Zangger 1979) or after dorsal rhizotomy in decerebrate cats walking on a treadmill (Grillner and Zangger 1984).

However, several lines of evidence suggest that afferent inputs may play a regulatory role (Rossignol 1996; Rossignol et al. 1988). For instance, direct measurements (Stein et al. 2000) indicate that the stretch reflex might contribute ≤30% of the ankle extensor activity during normal walking. In an attempt to understand such a specific role of afferents, this study and its companion will concentrate specifically on the role of cutaneous inputs of the hindpaws in the control of locomotion in intact and spinal cats.

It is known that stimulation of the foot skin or afferent nerves gives rise to complex phase-dependent responses involving several muscles and several joints and which are well integrated within the step cycle so as not to impede locomotion, but yet efficiently modify the limb trajectory to avoid obstacles (Rossignol 1996). These responses not only recruit muscles active during a given phase but also antagonist muscles at several joints to make these responses appropriate (Drew and Rossignol 1987). Work in humans (Zehr and Stein 1999) not only corroborates these observations but also suggests quite specific roles for reflex responses evoked by stimulation of the various receptive fields so as to remove the foot from a potentially damaging obstacle. Such a fine “local sign” control is also suggested by work in rats (Schouenborg and Kalliomaki 1990), cats (Levinsson et al. 1999), and humans (Van Wezel et al. 1997; Zehr and Stein 1999). Therefore cutaneous afferents are undoubtedly involved in compensating for perturbations of the locomotor cycle (reviewed in Rossignol 1996; Rossignol et al. 1988).

Chronic recordings from dorsal root ganglia in freely walking cats (Loeb et al. 1977) show that cutaneous inputs from the paw provide a variety of information to the CNS. Some of the recorded units are phasic, discharging mainly around touch down and toe off, whereas others are tonic, discharging throughout stance (Loeb et al. 1977). Moreover, studies performed during fictive locomotion show that there also exists a sophisticated phase-dependent control of cutaneous afferents at presynaptic (Gossard et al. 1989, 1990) and premotoneuronal (Burke et al. 2001; Degtaryenko et al. 1996) sites during
locomotion, suggesting again that these inputs might have some role to play in the regulation of locomotion.

Given that cutaneous inputs give rise to elaborate responses to perturbation, that cutaneous receptors are activated during normal locomotion, and that there is a complex pre- and postsynaptic control of cutaneous afferents, what are the consequences on locomotion of removing these cutaneous inputs? Previous work using anesthesia of the pads (Engberg 1964; Forssberg et al. 1977; Wand et al. 1980) or partial neurectomy (Duy [223x49]sens and Stein 1978) also confirms Sherrington’s observation that few deficits are observed (Duy [217x39]sens et al. 2000). The question we ask here is whether these deficits become apparent only when using more elaborate analysis methods and also more demanding locomotor situations in which these cutaneous inputs may be crucial.

Another fundamental aspect that motivated the present investigation on the role of cutaneous inputs of the paws during locomotion is our long-lasting interest in understanding the mechanisms that control the recovery and expression of locomotion in cats spinalized at T13 (Rossignol 1996; Rossignol et al. 2000). Indeed, spinal cats might depend even more critically than normal cats on sensory cues to bear weight and to adapt their walking speed to the treadmill speed, functions they use without difficulty. The peripheral cutaneous neurectomy model used here makes it possible to quite readily compare the same denervated cats in the intact condition and after spinalization.

Our results are presented in 2 companion studies. This first study describes the effects on locomotion of depriving the hindpaws of some or all cutaneous inputs in the otherwise intact cat. Chronic multimuscle electromyographic (EMG) recordings combined with movement kinematics are used to document treadmill locomotion in cats before and over the weeks after a bilateral hindpaw cutaneous denervation (complete or incomplete). More demanding locomotor situations such as walking on a horizontal ladder, inclines, and walkway with embedded force platforms complement our observations. By comparing the details of the locomotor movements, motor patterns and force distribution to the ground in the presence and absence of skin feedback from the hindpaws, we obtained valuable information on some aspects of the role of cutaneous inputs in the adaptation of locomotion. In this first study we will conclude that the deficits observed in the otherwise intact cats are minimal in undemanding locomotor tasks (treadmill) but important in more demanding tasks (incline treadmill, ladder walking) at least for several weeks after denervation. The companion study (Bouyer and Rossignol 2003b) will report the effect of spinalization at T13 on the same cats, performed several weeks after recovery from the denervation. Cats that were well adapted to the denervation before spinalization could not place the foot properly after spinalization, suggesting a critical role of cutaneous inputs for the correct expression of spinal locomotion. Parts of these results were previously presented in abstract form (Bouyer and Rossignol 1997, 1998a,b).

**METHODS**

**Animals and general procedures**

Three adult cats of either sex (weight 3.7–4.5 kg) were used in this study, for a total of 101 recording sessions. The 3 cats (“Denervated–Spiralized” DS1, DS2, DS3) were first selected for their ability to walk on a treadmill and then trained several times a week to walk at a constant speed on the treadmill. They were subsequently implanted with chronic EMG electrodes, allowed to recover from the implantation, and then recorded to obtain baseline data for EMG recordings and kinematics. After several controls were obtained, cats were denervated (see following text for specific protocol) and recorded again at different times after the cutaneous denervation under several conditions: on the treadmill (with or without slopes), on a horizontal ladder with rungs of different sizes, and on a walkway instrumented with force platforms. After a period of recovery, the same animals were spinalized, as will be reported in the companion study.

The experimental protocol was in accordance with the guidelines of the animal Ethics Committee of the Université de Montréal. All surgical procedures were carried out under general anesthesia and aseptic conditions in a dedicated operating room. After premedication [atratvet 0.1 mg/kg subcutaneously (sc), glycopyrrolate 0.01 mg/kg sc, and ketamine 5–10 mg/kg, sc], cats were intubated and maintained under gaseous anesthesia (isoflurane 2%), while monitoring heart rate and respiratory. After surgery, analgesic (buprenorphine HCl, 0.005–0.01 mg/kg sc) was given every 6–8 h for 1–2 days. No recordings were made while cats were under analgesics.

**Implantation of electromyographic electrodes**

EMG electrodes were implanted chronically in selected muscles of the hindlimbs. Implantations were not identical for all cats. DS1 and DS2 were implanted with an emphasis on extensors, and DS3 on ankle flexors (see results section). The different muscles implanted and main function were: sartorius anterior (Srt, hip flexor/knee extensor), semitendinosus (St, knee flexor/hip extensor), vastus lateralis (VL, knee extensor), tibialis anterior (TA, ankle flexor), extensor digitorum longus (EDL, ankle flexor), medial gastrocnemius (GM, ankle extensor), lateral gastrocnemius (GL, ankle extensor), soleus (ankle extensor), and extensor digitorum brevis (EBO, toe flexor). For each muscle, a pair of Teflon-insulated multistrain fine wires (30 μm diameter; AS633, Cooner Wire, Chatsworth, CA) was led subcutaneously from head-mounted multipin connectors (CINCH Connectors, TTI, Pointe-Claire, Canada) and sown into the belly of the muscle for bipolar EMG recordings.

**Cutaneous denervation**

Below the ankle, the skin of the paw is innervated by 5 nerves that cover distinct, complementary territories (Crouch 1969). Their name, abbreviation, site of neurectomy, and receptive fields are listed in Table 1. Except for the tibial and deep peroneal n., cutaneous nerves are purely sensory below the ankle. Cutting cutaneous nerves at the level given in Table 1 therefore causes little direct impairment in muscle function. Neurectomies consisted of making a small incision in the skin, exposing the nerve by gently separating it from the adjacent connective and vascular tissues using hemostats, suturing the proximal and distal parts using silk thread, cutting the nerve, and capping its proximal end with flexible vinyl polysiloxane (Reprosil, Dentsply International, Milford, DE) to prevent regrowth. The nerve was then put back in place and the opening closed.

In all cats, neurectomies were performed symmetrically in both hindlimbs. The neurectomies were made according to the following protocols: for cat DS1, all 5 cutaneous nerves were cut bilaterally in a single procedure, causing a complete denervation of the hindlimb paws. Cat DS2 was only partially denervated, keeping the deep peroneal nerve intact on both sides. Cat DS3 was denervated in 2 stages. Initially, the deep peroneal nerve was left intact, whereas all other nerves were cut. In a 2nd procedure 13 days later, the cutaneous branch of the deep peroneal nerve (DPc) was cut. Care was taken not to damage the motor branch of this nerve, which innervates EDB. Therefore 2 cats eventually had a complete denervation (DS1 and

3626 L.J.G. BOUYER AND S. ROSSIGNOL

J Neurophysiol • VOL 90 • DECEMBER 2003 • www.jn.org
TABLE 1.  Cutaneous nerves of the hindlimb paw, site of neurectomy, and receptive field

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>Site of Neurectomy</th>
<th>Receptive Field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superficial peroneal n.</td>
<td>SP</td>
<td>About 1 cm above the transverse</td>
<td>Dorsum of the paw from tip of digits to ankle</td>
</tr>
<tr>
<td>Tibial n.</td>
<td>Tib</td>
<td>Behind the calcaneal tendon</td>
<td>Hairy skin of the planter surface of the paw, central</td>
</tr>
<tr>
<td>Caudal cutaneous sural n.</td>
<td>CCS</td>
<td>Surface of the belly of lateral</td>
<td>Skin on the lateral surface of the paw and over the</td>
</tr>
<tr>
<td>Saphenous n.</td>
<td>Saph</td>
<td>Along the saphenous vein, just above the</td>
<td>calcaneus</td>
</tr>
<tr>
<td>Deep peroneal n., cutaneous branch</td>
<td>DPC</td>
<td>On the metatarsal bones, distal to the</td>
<td>Skin on the medial surface of the paw and anterior</td>
</tr>
</tbody>
</table>

DS3) and 2 cats had a partial denervation, one (DS2) for 76 days and the other (DS3) for 13 days. This was seen as the optimal combination to reduce the number of chronically implanted animals. The completeness of the denervation was also evaluated clinically by gently pinching the skin at different locations on the paw.

**EMG and kinematic recordings during treadmill locomotion**

Cats were trained to walk regularly on a motorized treadmill under 3 conditions: level, 15° pitch up and 15° pitch down, at speeds varying from 0.3 to 0.7 m/s for level walking and 0.3 to 0.5 m/s for incline walking. Reflective markers were placed on the left hindlimb over the iliac crest, greater trochanter, lateral epicondyle, lateral malleolus, metatarsophalanegal (MTP) joint, and the tip of the 4th toe. Recording sessions consisted of acquiring video images simultaneously with the EMG data during treadmill locomotion, to fully describe the walking pattern. Filtered and amplified EMG signals (100 Hz–3 kHz bandpass, gains of 500 to 20K) from the implanted muscles were recorded on VHS tape using a 16-channel Vetter Digital 4000a PCM recorder (1.25-kHz bandwidth/channel). Kinematic and EMG data were synchronized using an SMPTE time code generator (Skotel).

**Ladder walking**

Cats were also trained to walk regularly on the rungs of a 2-m long × 35-cm wide horizontal ladder. Three types of rungs were used: round (2.5 cm diameter), small flat (2.5-cm width), and large flat (6.5-cm width). Only video images were recorded during this task.

**Ground reaction forces during overground walking**

Cats DS2 and DS3 were also trained to walk across a 3-m long × 0.6-m wide walkway. A 3-axis force platform (AMTI, model ORS6-5-1) was installed flush with the surface of the walkway to record vertical, anteroposterior, and mediolateral ground reaction forces generated by one paw during walking. A thin opaque plastic mat was placed over the entire walkway, such that the cat could not see where the force platform was located. Force and moment data were acquired at 1.2 KHz and synchronized to video images of the cat walking across the walkway.

**Analyses**

**KINEMATIC ANALYSIS.** Joint angles and foot lifts/contacts were reconstructed off-line frame-by-frame from the video images using a Peak Performance motion analysis system (Englewood, CA) with a resolution of 60 fields/s. The knee angle was mathematically corrected for skin slippage by triangulation using postmortem leg segment lengths (femur and tibia). The step cycle was divided into 4 sections, according to Philippson (1905): the swing phase was subdivided into flexion (F) and the 1st extension phase (E1), whereas the stance phase was divided into 2 extension phases, weight acceptance (E2) and push off (E3) (see Fig. 1D).

Double hindlimb support was defined as the percentage of total cycle time spent with both hindlimbs in contact with the treadmill belt and evaluated from the videotapes. In addition, the duty cycle, percentage of total cycle time with 2, 3, or 4 paws on the ground was sometimes quantified. Video segments where all 4 limbs were visible over about 10 consecutive steps were analyzed. These segments were not necessarily the same as used for double hindlimb support analysis because the camera was usually zoomed onto the hindlimbs to have a better resolution for kinematic analysis.

**KINETIC ANALYSIS.** Ground reaction forces were measured off-line from the data obtained during locomotion on a walkway with embedded force platforms. Trials were selected for analysis only when the walking speed across the walkway was constant and within the range of 0.35–0.55 m/s (measured using the video images) and when the cat placed only one paw on the platform. Voltage signals from the force platforms were low-pass filtered at 50 Hz using a 2nd-order Butterworth filter, calibrated using the platform’s calibration matrix provided by the manufacturer (AMTI), and converted to newtons. Trial data were then normalized for walking direction, as reported previously (Lavoie et al. 1995). Finally, data for each limb were grouped, synchronized on paw contact, and averaged using custom software.

**EMG ANALYSIS.** Electromyographic data recorded on tape were played back off-line and printed out using an electrostatic plotter (Gould ES-2000), along with their SMPTE time stamp. Data segments consisting of ≥10 consecutive steps at constant speed were chosen using the EMG printouts and videotapes of the experiments. EMG data of these chosen segments were then digitized using custom software at 1,000 samples/s per channel on a 200-MHz Pentium computer. Burst duration, amplitude, and relative timing of chosen data segments were then measured by manually placing cursors using custom analysis software.

To compare EMG patterns between sessions (e.g., Fig. 1), EMGs were rectified, normalized to 256 points per step, and averaged over ≥10 consecutive steps. Data from 2 sessions were then superimposed after normalizing to mean step duration.

The amplitude of EMG activity in extensors was quantified by integrating the area under each rectified EMG burst and dividing it by the burst duration, a measure called mean amplitude. For flexors, it was noticed when comparing averaged EMG activity, that the changes caused by the denervation in activation amplitude were spiky (e.g., St in Fig. 1, F and G). Therefore because the increase in amplitude did not last for the entire burst duration on most occasions, mean amplitude was not the ideal method to assess the changes in amplitude related to the denervation. For this muscle, and also for the other flexors, peak amplitude was therefore used to quantify changes in activity instead of mean amplitude. This method gave very consistent measurements.
Individual time courses of compensation

Kinematic and EMG recordings on the treadmill were continued until each cat had recovered the ability to walk across the most challenging situation (i.e., the round rungs). This explains why the abscissa on the time course graphs presented in this study is different for each cat.

Statistics

To measure statistical differences after the denervation, data from ≥3 separate controls were pooled and compared with data obtained on each of the many postdenervation tests using a one-way ANOVA followed by Dunnett’s post hoc test for many comparisons against a control group. If data failed normality and equivariance tests, an ANOVA on rank (Kruskal–Wallis method) followed by Dunn’s post hoc test was applied instead (Glantz 1992).

RESULTS

Overall, cats recovered very well from the denervation. Surprisingly they showed very little slippage of the feet, even on the laboratory floor, which was more slippery than the treadmill belt. However, lateral stability was not as good as predenervation. In addition, in early days, the cats presented a
more cautious type of walking; while standing or walking, the hindlimbs tended to be abducted and the hindpaws everted. Pinching of the skin of the paw produced no withdrawal response.

**Level treadmill walking**

Although the cats showed some obvious deficits in foot placement during ladder walking (see following text), one of the most striking observations was the absence of any major deficit during level treadmill walking after the cutaneous denervation. All cats, partially or completely denervated, appeared—at least to the naked eye—to walk normally on the treadmill. However, a more detailed analysis revealed several consistent changes in the locomotor movements and EMG activity.

**Kinematics and EMGs**

Figure 1 presents an overview of the kinematic and EMG changes observed during level treadmill locomotion after the cutaneous denervation. This figure summarizes the main changes present short term (2 days) and long term (41 days) postdenervation by using stick figures, angular excursion plots, and averaged EMGs of the control and the denervated conditions.

Two days after the complete denervation (Fig. 1B), swing was faster but stride length was similar to that of the control before denervation (Fig. 1A). Using foot contact as the synchronizing event, Fig. 1D represents angular displacements at the hip, knee, ankle, and MTP joints, with a superposition of control and early postdenervation conditions. At the knee, flexion during the swing phase increased both in amplitude and velocity, as shown by a steeper slope of the angular excursion (cf. arrow). The changes at the ankle result in part from a more crouched posture. This figure also shows that the overall cycle duration was reduced after denervation. This was mainly attributed to the more rapid swing phase, whereas stance was hardly affected. So although stride length was maintained, cycle time was decreased. Averaged rectified EMGs (Fig. 1F) show that distal flexor activity was significantly increased, mainly in amplitude for EDL (ankle flexor), and both in amplitude (see asterisks indicating the increase of both bursts) and duration for St (knee flexor). These changes corroborate the changes in kinematics.

The recovery of the cats was monitored for several weeks after the denervation. Late after the denervation (Fig. 1C), step duration remained shorter than control. Knee flexion excursion returned to normal (Fig. 1E) but knee flexion velocity remained above control (steeper slope). Figure 1G shows that the increased activity persisted in St and EDL, concomitant with the maintained increased knee velocity and shorter swing duration.

**Time course of compensation.** The 3 cats did not follow the same pattern of neurectomies, to serve as reciprocal controls (see METHODS). Cat DS1 was completely denervated in one surgical procedure, whereas cat DS2 was only partially denervated (cutaneous branch not cut from deep peroneal n.) and cat DS3 was first partially denervated and 13 days later, the denervation was completed. During the several weeks that followed the neurectomies, animals were periodically tested on the treadmill, to establish a time course of compensation. Data obtained during this extended period, as well as interanimal differences, are presented in Figs. 2 to 7.

Figure 2 describes the changes in step cycle duration (A–C) and double hindlimb support (D–F). The main change observed in the early days after the denervation was a reduction in swing duration, as seen in all 3 cats. Note that in DS3 this change was more apparent when the denervation was completed (see data points after 2nd vertical dashed line) at which time the changes were almost identical to those observed in DS1. DS2 also showed a decrease in swing duration after the partial denervation.

Stance duration, on the contrary, was hardly affected. It was not statistically different in any session for cat DS3 and only different in 1/5 sessions in cat DS1. DS2 showed a temporary increase in stance duration on days 2, 3, and 7. These changes were only transitory, given that at the 49-days session and beyond, the situation was similar to that of the other cats.

The denervation significantly increased \( P < 0.05 \) the percentage of time spent in double hindlimb support (Fig. 2, D–F) by 5 to 10% of total cycle time. This increase in double support augments the stability of walking. Not only was this increase present early after the denervation, but it also persisted for the duration of the postdenervation testing period.

To measure the effects of increased double hindlimb support on quadrupedal walking, we also measured the time spent with
2, 3, or 4 paws on the ground in cat DS3 (duty cycle; see METHODS). Segments were taken from a total of 5 walking sessions: 3 controls, 1 early (8 days) post complete denervation, and 1 late (34 days) post complete denervation. The results are summarized in Table 2, for a walking speed of 0.5 m/s. Before denervation, cat DS3 duty cycle was distributed the following way: 0.6% of cycle duration was spent on 4 limbs, 70.4% on 3 limbs, and 29.0% on 2 limbs. Early after the denervation, the time spent on 3 limbs was significantly increased to 79.4% (P < 0.05) and the time spent on 2 limbs significantly reduced to 20.4% (P < 0.05). Time spent on 4 limbs was unchanged, remaining essentially null (0.2 ± 0.4%). Late after the denervation, part of these changes in duty cycle remained: the time spent on 2 limbs was 25.0%, remaining significantly below control (P < 0.05), whereas the time spent on 3 limbs was 73.9%, which, although nonsignificantly higher than control, nevertheless showed a tendency to be higher.

Figure 3 illustrates the modifications that occurred in the trajectory of the hindpaw. Horizontal paw position relative to the hip (Fig. 3A) is shown at toe off (l1) and at foot contact (l2) for each cat in B–D. The distance between l1 and l2 represents stride length. After the complete denervation, cats tended to lift their hindpaws at a somewhat more caudal position (l1), that is, with the hindlimb extended further backward. Paw positions at foot contact showed some variation from cat to cat, however. After the denervation, cat DS1 tended to contact the ground more caudally, cat DS2 more rostrally, and cat DS3 at the same place as predenervation. The consistent finding across cats was that stride length was not changed by the denervation.

Paw clearance, evaluated by measuring the peak vertical position of the MTP joint during the swing phase (Fig. 3E), was significantly larger (P < 0.05) in the 3 cats postdenervation (Fig. 3, F–H). This measure represents the net flexion of the whole limb. Contrary to other measures of the kinematics of locomotion, the postdenervation increase in paw clearance was maintained for more than 10 days in cat DS1 and permanently in the 2 other cats, thereby showing that hindlimb flexion was strongly affected by the denervation.

Figure 4 looks in detail at the changes in knee kinematics for all cats. A summary of knee angular excursion during the swing phase is presented in Fig. 4, A–C. In cat DS1 (Fig. 4A) there was a significant increase in amplitude immediately after the denervation that persisted throughout the testing period. In DS2 (Fig. 4B), there was tendency toward an increase early after the partial denervation, but it did not reach statistical significance and was not maintained over time. The findings in cat DS3 (Fig. 4C) confirm both of these observations by showing that a robust increase in knee flexion amplitude appeared only after the denervation was completed. The rest of Fig. 4 looks at the rate of change of knee angular position, separately for the F (flexion; Fig. 4, D–F) and E (extension; Fig. 4, G–I) parts of the swing phase. This more detailed analysis reveals that the velocity of knee movements is significantly increased in all cats after the denervation, regardless of whether it was partial or complete. The fact that mainly velocity, not displacement, was increased explains why very little deficit was visible by the naked eye. The changes in knee velocity persisted for several weeks.

**EMG Changes after Cutaneous Denervation.** Figures 5 to 7 describe the changes in amplitude (peak for flexors, mean for extensors; cf. METHODS) as well as burst duration in several muscles for the 3 cats. Because the denervation was bilateral, muscles from both limbs were superimposed when available. The most consistent change seen across all cats was an increase in amplitude of the knee flexor semitendinosus, which persisted throughout the period of observation. This corroborates very well the kinematics in which knee flexion amplitude and/or velocity were increased (Fig. 4) and paw clearance was larger (Fig. 3). In cat DS3, EDL (recorded only in this cat) also showed a persistent increase in amplitude. Burst duration of these flexor muscles varied over time, with a larger duration early after denervation. The hip flexor/knee extensor sartorius activity did not significantly change except in the very early period after the denervation.

Regardless of extensors, at least one prime extensor EMG activity was significantly increased in each cat, and this increase was maintained for several days. However, it was not the same muscle in all cats. For cat DS1, VL (knee extensor) EMG activity was increased for several days (Fig. 5C), whereas GM (ankle extensor) activity remained essentially constant (Fig. 5D). SOL, another ankle extensor, showed opposite changes in activity in the left and right hindlimbs on the first test postdenervation, followed by a small reduction in activity long term postdenervation (Fig. 5E). In cat DS2, overall, both GM and SOL activity were increased (Fig. 6, C and D). On the first test postdenervation, however, the right SOL presented a punctual decrease in activity (Fig. 6D). Finally, cat DS3 showed a significant increase in VL activity after the partial denervation followed by a return to control amplitude (Fig. 7D).

**Summarizing the Evolution of Locomotor Parameters after Partial and Complete Denervations.** Inspection of Figs. 1 through 7 shows that overall changes in the kinematics of locomotion were larger after the complete than the partial denervation, but that in all cases most parameters gradually returned statistically toward predenervation values after several days (depending on the cat). The parameters that remained changed on a long-term basis were: the percentage of double support, toe clearance (a measure of total limb flexion during swing), and knee flexion amplitude and velocity during the F phase (complete denervation). Factors that did return to predenervation values were: step cycle and swing durations, toe position at foot contact, knee flexion amplitude, and velocity during the F phase (partial denervation).

**TABLE 2. Duty cycle during quadrupedal walking for cat DS3 at a walking speed of 0.5 m/s**

<table>
<thead>
<tr>
<th>State</th>
<th>n</th>
<th>4-Limb Support (°/cycle)</th>
<th>3-Limb Support (°/cycle)</th>
<th>2-Limb Support (°/cycle)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>25</td>
<td>0.6 ± 1.4</td>
<td>70.4 ± 6.6</td>
<td>29.0 ± 6.5</td>
</tr>
<tr>
<td>8 days post complete denerv.</td>
<td>17</td>
<td>0.2 ± 0.4 (NS)</td>
<td>79.4 ± 4.4 (*)</td>
<td>20.4 ± 4.3 (*)</td>
</tr>
<tr>
<td>34 days post complete denerv.</td>
<td>14</td>
<td>1.1 ± 1.4 (NS)</td>
<td>73.9 ± 2.4 (NS)</td>
<td>25.0 ± 1.8 (NS)</td>
</tr>
</tbody>
</table>

Values are ° cycle duration ± SD; n = number of steps. * P < 0.05, ANOVA testing against control; NS, not significantly different.
applied to the ground than level walking and can therefore be
requires more subtle control of force amplitude and direction
these are fairly easy slopes, walking on inclined surfaces
with the treadmill belt inclined 15\degree
Treadmill walking with pitch slopes

\begin{align*}
\text{Distance between} & \quad \text{represents horizontal distance between hip and toe markers at foot contact.} \\
\text{represents horizontal distance between hip and toe markers at toe off;}
\end{align*}

\begin{align*}
d & \quad \text{ds}2. \\
H & \quad \text{ds}2.
\end{align*}

\begin{align*}
\text{H} & \quad \text{ds}3. \\
\text{ds}3 & \quad \text{ds}3.
\end{align*}

**FIG. 3.** Details of metrics of left hindpaw during treadmill locomotion.

**A–D:** stride length and paw position relative to hip. **A:** line drawing; \( l_1 \)
represents horizontal distance between hip and toe markers at foot contact. Distance between \( l_1 \) and \( l_2 \) is a measure of stride length. **B:** cat DS1. **C:** cat DS2. **D:** cat DS3. **E–H:** vertical elevation of paw during swing phase. **E:** line drawing representing how peak vertical position of metatarsophalangeal (MTP) joint with respect to treadmill surface was measured. **F:** cat DS1. **G:** cat DS2. **H:** cat DS3. For all graphs in this figure, each point represents mean \( \pm \) SD. Horizontal dashed lines represent mean predenervation value. Vertical dashed lines represent time of denervation. \(*P < 0.05, \text{one-way ANOVA against predenervation control.}\)

**Treadmill walking with pitch slopes**

In addition to level walking, cats where also trained to walk
with the treadmill belt inclined 15\degree up and 15\degree down. Although
these are fairly easy slopes, walking on inclined surfaces
requires more subtle control of force amplitude and direction
applied to the ground than level walking and can therefore be
considered an additional challenge for the locomotor control
capabilities of our animals.

Before denervation, all cats could easily walk at 0.5 m/s in
either condition. Early postdenervation, the maximal speed was
reduced to 0.4 m/s for cats DS1 and DS2. Above this speed,
cats could not maintain a regular pace but showed hesitation
and stopped walking every 3–4 steps. Because control data
were collected at 0.3, 0.4, and 0.5 m/s, data analysis was
therefore performed on walking segments obtained at 0.4 m/s.

Figure 8 presents the kinematics of the locomotor adapta-
tions that occurred in the control situation, 1 day after and 23
days after the denervation in cat DS1 for up and down slopes.
Joint excursion data obtained while walking on the incline
(down) are superimposed on data obtained during level
walking on the same day (gray traces). Using this approach,
the joint adaptations required between level and incline walking
are emphasized. By comparing the differences between control
and postdenervation, it is possible to identify the initial deficit
and extent of recovery performed by the animal. The data from
this cat are representative of all 3 animals.

**UPWARD SLOPE.** Figure 8, **A–C** summarizes the performance
of cat DS1 walking 15\degree upward. The kinematics are presented
as angular displacements separately for each hindlimb joint. In
the control situation, when comparing between walking with a
15\degree up slope and level walking (Fig. 8A), modifications are
present at the hip, knee, and ankle. The hip extension is
increased at the end of stance. At the knee, changes are more
complex. There is a larger extension at the end of stance,
followed by a more rapid flexion during the F phase and a
reduced extension during E1, leading to a more flexed knee
posture at foot contact that is gradually reduced through the
rest of the stance phase. The situation is similar at the ankle as
at the knee: slightly larger extension at the end of stance, rapid,
and in this case a larger joint flexion during the F phase leading
to a more flexed ankle posture that is gradually reduced over
the first half of the stance phase. The MTP joint displacements
are very similar. With respect to timing, flexion is initiated later
at all joints and so is E1 at the knee and ankle.

One day after the denervation, the cat was not at ease during
slope walking, and some important differences were present
when comparing level to upslope walking. By comparing Fig.
8A and 8B, the following observations can be made. The hip
joint is more flexed throughout swing, resulting in an over-
exed hip at foot contact that gradually disappears during the
first half of stance. The onset of swing is no longer delayed
compared with the level walking situation. At the knee, the
onset of swing is no longer delayed, E1 extension is exagger-
ated, and the knee angle during stance is not more flexed than
level walking. At the ankle, the main difference with control is
a lack of extra flexion during F, such that the ankle joint angle
is similar to level walking at foot contact. This joint, however,
yields almost immediately as the leg starts to bear weight. The
collapse at the ankle can also be seen at the hip and MTP joints
(cf. arrows). For the MTP, a smaller joint angle is observed
around and after foot contact, indicative of a more plantar-
exed paw position. In summary for the 1-day postdenervation
situation, the cat is not producing the smooth and gradual
changes at all leg joints that are normally observed in the intact
state. Instead, the hip is more flexed, the knee is locked during
stance, and the ankle yields on foot contact.
Twenty-three days after the denervation, the cat had an easier time performing the uphill walking task, although the deficit was only partly compensated. At the hip, knee, and ankle (Fig. 8C), the extra extension at the end of stance was still missing. Aside from this deficit, the knee joint behavior was similar to control. At the ankle, the prefoot contact angle was normal in amplitude, but still wrong in timing and the weight acceptance phase was near normal. The MTP joint

![Cat DS1](image)

**Fig. 5.** Summary of EMG activity for cat DS1. Black circles: muscles of left leg. White circles: muscles of right leg. A and B: peak amplitude and burst duration for hip flexor sartorius (A) and knee flexor semitendinosus (B). C–E: mean amplitude and burst duration for knee extensor vastus lateralis (C), ankle extensor medial gastrocnemius (D), and ankle extensor soleus (E). For all graphs, each point represents mean ± SD. Horizontal dashed lines delineate predenervation value. Vertical dashed lines represent times of denervation. *P < 0.05, one-way ANOVA against predenervation control.
showed, however, that the paw was now more dorsiflexed throughout stance, an indication that some lack of fine control of leg position present at foot contact remained throughout stance.

**DOWNWARD SLOPE.** Figure 8, D–F superimpose 15° downward slopes to level walking on the same days. In the control situation (Fig. 8D), modulation is present at multiple joints. The downward slopes, instead of requiring extra push off at the end of stance, need a good control mainly during the weight acceptance phase, E2. Predenervation (Fig. 8D), hip joint angular displacement is hardly different from control. At the knee, the small extension at the end of stance is lacking, and joint extension is larger during E1. The knee remains slightly overextended during early stance. At the ankle, the yield after foot contact is prolonged until the end of stance, and ankle extension at push off is reduced. This increased yield at the ankle is accompanied by a reduction in MTP angle throughout stance representing a more dorsiflexed paw.

One day after the denervation (Fig. 8E), the hip joint is essentially unaffected. The knee joint displacements are almost normal except that the end of stance extension, normally suppressed during down slope, is now present. The main deficit is at the ankle joint. The gradual yield observed after foot contact in the control situation is no longer present. This is confirmed by a lack of reduction of MTP angle throughout stance.

Twenty-three days after the denervation (Fig. 8F), the recovery was incomplete. The modulation of ankle yield improved, but as shown by the MTP joint data, the paw remained more plantarflexed than control. All 3 cats exhibited similar changes in slope adaptations.

In summary, although the cats could manage the slopes, and improved their performance over time after the denervation, the slope adaptations were different from those in the predenervation condition. In addition, cats DS1 and DS2 never recovered the ability to walk at 0.5 m/s on inclines.

**CHANGES IN EMG PATTERNS ASSOCIATED WITH INCLINE WALKING.** EMG activity from several muscles was also obtained during these walking sessions. Figure 9 shows the superimposition of the control and early postdenervation locomotor pattern for up slope, separately for each of the 3 cats. These averages were obtained over many steps (>20) and synchronized on the end of the sartorius burst, a reliable timing cue close to foot contact. For postdenervation data to be considered statistically different from control, they had to fall outside of the 95% confidence interval boundaries of the control data. Contrary to the changes in kinematics, the changes in EMG activity of the implanted muscles during incline walking were small, and differed from one cat to the next, and even between the 2 legs in the same cat. For example, cat DS2 left GM increased its activity after denervation, whereas its right GM decreased (Fig. 9B). Slope walking itself did greatly modulate activity in extensor muscles, however. This normal modulation associated with incline walking caused much greater changes in the EMG locomotor pattern than denerva-
tion itself. Data for down slopes presented the same characteristics of large modulation attributed to the treadmill incline, but no consistent deficit across cats postdenervation (not shown).

Walking on a horizontal ladder

To increase even more the demand for fine locomotor control, the cats were also tested on a horizontal ladder. Contrary to treadmill walking, ladder walking was greatly impaired early after the denervation. Most of the time, cats even refused to walk on the ladder. Thus early postdenervation, none of the 3 cats could stand on the rungs of the ladder, even if helped by the experimenter and allowed to view their hindlimbs. The best that could be obtained was a temporary maintenance of posture if the paws were manually placed on the rungs and no external perturbation applied. After a few seconds in this position, the cats would start to sway laterally and lose balance.

With time, ladder walking recovered almost completely in each cat. After partial or complete denervations, the paw placement strategy differed.

**COMPLETELY DENERVATED CATS.** Cat DS1 was documented 3 times on the ladder after the denervation: at 3, 18, and 24 days. At 3 days, it could not even quietly stand on the rungs of the horizontal ladder if not helped by the experimenter. At 18 days, quiet standing was possible, as well as walking on the large flat rungs. It was at 24 days that the ability to walk on the round rungs returned. However, the way the cat placed the paw on the round rungs was different from control. Predenervation, DS1 stood and walked on the plantar cushions, with the paw parallel to the ground (Fig. 10A). Postdenervation, it now stood and walked on the tarsal bone, with the toes plantarflexed (Fig. 10B). This posture made the paw look like a cock spur. Cat DS1 switched to the “cock spur” way of walking after the 2nd denervation only (complete denervation). The latter was able to walk on the round rungs only 41 days after this 2nd denervation. Therefore the training obtained after the partial denervation did not carry over to the complete denervation situation.

**PARTIALLY DENERVATED CATS.** Cat DS2 was documented more often than cat DS1 in the early days after the denervation, to look for a more rapid functional recovery, although it did not recover faster. Only at 7 days was cat DS2 capable of quiet standing on the large flat rungs. Complete recovery was observed 49 days postdenervation. Contrary to completely denervated cats, DS2 (and DS3 after the 1st denervation) walked with the paw dorsi- flexed when crossing on the round rungs (Fig. 10C).

Ground reaction forces during overground walking

Ground reaction forces during overground locomotion were evaluated in cats DS2 and DS3 once before the denervation, and a 2nd time more than a month after surgery. Figure 11 summarizes the changes for the completely denervated cat (DS3), before and 37 days after the complete denervation.
Looking at all 4 limbs, it can be seen that the main effect was a large statistical increase in the mediolateral force (3/4 legs). The positive going force indicates that more lateral force is produced after denervation. The right hindlimb (Fig. 11D) shows a somewhat different strategy, with a reduction in propulsive force (less positive anteroposterior force) rather than a large increase in mediolateral force. Nevertheless, even for this limb there was a tendency for the mediolateral force to be increased after the denervation. In all limbs, vertical forces after denervation were very similar to predenervation, suggesting that the cat did not use a general strategy of transferring a positive going force in the mediolateral direction.

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**Fig. 9.** Rectified average EMG activity obtained before denervation (thin lines: 95% confidence intervals) and early after denervation (thick lines) during 15° upslope walking. Data are synchronized on end of sartorius burst. A: cat DS1, control and 1-day post complete denervation. B: cat DS2, control and 3 days post partial denervation. C: cat DS3, control and 8 days post complete denervation. See text for muscle abbreviations. i, left; co, right.

**Fig. 10.** Line drawing of hindpaw made from video images showing characteristic paw placement on rungs during ladder walking. A: before denervation. B: after complete denervation. C: after partial denervation.

**Fig. 11.** Ground reaction forces during stance phase of overground walking on a walkway for each of the 4 paws of cat DS3. Gray traces: predenervation control. Black traces: 37 days postdenervation. Thin lines: 95% confidence intervals on mean. A: left forelimb. B: right forelimb. C: left hindlimb. D: right hindlimb.
larger proportion of its weight to the forelimbs, which have intact sensory feedback (cf. Brustein and Rossignol 1998). Therefore overall, only the mediolateral component of the force distribution pattern during stance remained modified late after the denervation. The peak value of this component was increased by more than 200% compared with predenervation.

The results of the partially denervated cat 71 days postdenervation (not shown), were qualitatively similar but of smaller amplitude. Statistical increases were measured in lateral force generation on the left side fore-and hindlimbs, and no change on the right side. There was no change in anteroposterior or vertical forces in any leg.

DISCUSSION

These experiments show that the absence of cutaneous inputs from the hindpaws in otherwise intact cats does not prevent the expression of the locomotor rhythm in undemanding situations such as level walking on a treadmill. This corroborates the observations by Sherrington on hindpaw denervation (Sherrington 1910) and later works showing that nerve cuts (Duysens and Stein 1978) or foot pad anesthesia (Engberg 1964; Forssberg et al. 1977; Prochazka et al. 1978; Wand et al. 1980) had practically no effect on locomotion, at least to the naked eye. However, our results show that even in such undemanding conditions there are consistent long-term changes such as increases in vertical paw trajectory and knee flexion velocity accompanied by an increase in the peak amplitude of knee and ankle flexor muscles. Furthermore, there is a significant increase in the percentage of the locomotor cycle spent in double support. The deficits become more apparent in more demanding locomotor situations and suggest that cutaneous afferents from the paw are used for fine control of foot placement. When cats are required to walk on incline planes, the normal compensatory modifications of joints to accommodate for the slopes are reduced. Furthermore, our results suggest that the cutaneous inputs are particularly involved in locomotor conditions demanding a precise positioning of the foot such as ladder walking. In the initial period postdenervation, cats are unable to walk on a horizontal ladder. Later on, they develop a strategy of “cock spur” posture, which allows them to grasp the rungs and perform the task at a slower pace. The normal elegant walk on the rungs seen before denervation never recovers. Finally, when walking on a walkway with embedded force platforms, cats tend to exert larger mediolateral forces even long term postdenervation, again suggesting that the loss of cutaneous inputs results in permanent abnormalities of the walking pattern, even if subtle to the naked eye.

Two questions are raised by these observations. First, what locomotor deficits could have been predicted from the known connectivity of cutaneous afferents with the spinal circuitry? Second, are the changes specific to the cutaneous deprivation or do they represent a switch to a locomotor strategy that produces a more stable walking pattern and, as a result, offsets the insecurity introduced by the sensory loss?

Predicted and observed deficits

THE DIRECT EFFECT OF THE DENERVATION. As mentioned in the introduction, experiments by Sherrington (1910) suggested that cutaneous inputs from the paws do not play a major role in the control of locomotion in quadrupeds. However, in the further description by Sherrington, it is clear that some important functional locomotor deficits were present in his cats after the cutaneous denervation. They included doubling of the toes underneath the planta, foot drag during swing, and a higher lift during stepping. Animals would not correct this misplacement because they seemed unaware of it. Sherrington did not come to a clear conclusion on the reason for the doubling of the toes but discarded the possibility that cutting the innervation to small intrinsic foot muscles such as EDB (innervated by the deep peroneal nerve) could be responsible, given that a specific denervation of this muscle did not result in doubling of the toes.

The cats presented in this study, despite having some deficits in foot placement on the ladder in the first few days after denervation, could all perform quasi-normal locomotor movements on the treadmill without foot drag or toe underturning. However, they exhibited a higher lift of the paw during the swing phase, similar to Sherrington’s cats. We have been careful in our own experiments to dissect the cutaneous branch of the deep peroneal nerve free from its motor innervation to EDB before the denervation, and cut only the cutaneous branch to ensure that the deficits observed would not be attributable to a direct damage to the muscle’s innervation. In addition, in cat DS3, EDB had been implanted with chronic EMG electrodes to ensure that the motor innervation remained functional after the surgery. This will become a crucial point in the companion study where the same denervated cats are trained to walk after spinalization because it will allow us to discard the possibility that the deficits observed in that condition are attributable to local damage to the innervation of the intrinsic foot musculature.

THE ABOLITION OF CUTANEOUS REFLEX PATHWAYS. A challenging question in the field of locomotor control is to establish the role of specific afferent feedback in the normal, unperturbed locomotion. One of the main findings in this report was that the cutaneous denervation caused an increase in knee and ankle flexor activity during the flexion phase of locomotion.

It is known from nerve recordings (Duysens and Stein 1978; Popovic et al. 1993) that there are discharges in the cutaneous nerves at different points in the step cycle. Chronic unit recordings in dorsal root ganglia (Loeb et al. 1977) also clearly indicate discharges of single units that are not necessarily linked to clear kinematic events such as foot contact, but may represent skin stretches during joint movements. These discharges contributing to the locomotor pattern, such as has been suggested for proprioceptive inputs from ankle extensors that may contribute to more than one third of the muscle output during decerebrate walking (Stein et al. 2000)?

Regarding extensor muscles, before and after injecting a local anesthetic into the central foot pad, Engberg (Engberg 1964; Engberg and Lundberg 1969) found no change in the EMG activity of flexor digitorum brevis (FDB), a toe extensor acting during the stance phase of locomotion. The results presented in this study further suggest that the load inputs from the cutaneous receptors contribute relatively little essential feedback to the normal locomotor output of the ankle extensor muscles despite the well-established excitatory connections between cutaneous afferents and ankle extensor motoneurons (LaBella et al. 1989; Wilson 1963). Based on the latter work, the cutaneous denervation was expected to produce a marked
decrease in leg extensor activity. On the contrary, activity of at least one prime extensor was significantly increased in each cat for several days after denervation (Figs. 5–7). Whether this resulted from an increase in the gain of compensatory proprioceptive reflexes of the ankle extensors or to an increase in central drive is unknown. Perhaps an experiment similar to that reported by Stein et al. (2000) using an imposed force profile on the output of ankle extensors during decerebrate walking after a cutaneous denervation could shed some light on this difference.

On the basis of cutaneous nerve stimulation we could have expected larger deficits in the walking pattern of our cats after denervation. Early work (Duysens 1977; Duysens and Pearson 1976) showed that cutaneous stimuli could significantly prolong the stance phase. In normal cats, Halbertsma (1983) showed that as the speed of walking increases, the hindlimb paw is gradually lifted off the ground at a distance closer to the hip, whereas the foot contact position relative to the hip remains remarkably constant across a wide range of speeds. After denervation, our cats did not show a reduction in stride length nor an important modification of paw position relative to the hip at paw lift or contact. The movement was simply executed faster, and sometimes with a greater flexion at the knee, which would simply lift the paw higher off the ground without affecting lift or contact position. Although we saw a decrease in cycle duration in all 3 cats, the shortening was attributed to a decrease in swing duration (faster swing), whereas stance duration remained more or less the same. Similarly, the stride length was preserved, suggesting that cutaneous inputs contribute little to the overall duration of the stance phase or the overall metrics of the step cycle in the otherwise normal cat.

Another strategy that could have been used by the cats would have been to shift the weight control over to the forelimbs, as previously reported after large lesions of the ventral and ventrolateral spinal tracts (Brustein and Rossignol 1998). This was not the case, given that measurements of vertical forces in all 4 limbs did not show such a weight shift (Fig. 11).

Regarding flexor muscles, nerve stimulation studies during locomotion have shown that stimulating the dorsum of the paw [superficial peroneal (SP) n. receptive field] gives rise to a multiaxial response that normally brings the paw up and around an obstacle hit during the swing movement (Drew and Rossignol 1987; Forssberg 1979). This response is inhibited during stance (Drew and Rossignol 1987). Using spatial facilitation during fictive locomotion Degtarenden et al. (1996), recording from TA and EDL motoneurons, showed the presence of an elaborate excitatory and inhibitory short-latency set of connections between cutaneous afferents from the paw and flexor motoneurons that is powerfully modulated by the central pattern generator (CPG) during locomotion. According to these authors, during flexion, EDL motoneurons receive disynaptic inhibitory postsynaptic potentials from SP stimulation, whereas TA motoneurons receive no inhibition. On the other hand, stimulation of the medial planar nerve, a cutaneous branch of the tibial nerve, produces essentially no response during swing. These results are compatible with the neural organization needed to prevent claw protrusion during the stumbling reaction (Degtarenden et al. 1996). However, we cannot easily predict how elimination of paw cutaneous feedback during unperturbed swing would lead this circuitry to increase EDL peak EMG activity to 350% of control (cf. Fig. 7C). Therefore the increase in EMG activity of flexor muscles reported in this study could not have been easily predicted by the removal of any of the known cutaneous pathways from the paw and probably results from an increase in central drive.

Moreover, recent work in rats (Schouenborg and Kalliomaki 1990; Schouenborg et al. 1992, 1994), cats (Burke et al. 2001; Degtarenden et al. 1996; Levinsson et al. 1999), and humans (Van Wezel et al. 1997) suggests that skin inputs may also be involved in a fine “local sign” control. Another interpretation of our results could therefore be that the loss of such fine control probably induces cats to adopt a safer walking strategy where the limb is lifted higher (in case there would be obstacles) and faster to increase the percentage of time spent on the ground (increase in double support). Such a change in walking strategy would require an increase in flexor EMG activity. Furthermore, this interpretation is supported by the increase in mediolateral force measured during stance (cf. Fig. 11), which probably represents an additional way to increase stability in the absence of fine control of the distal limb.

Short-term and long-term compensations

One of our general objectives was to study the adaptive capacity of the locomotor system to a permanent reduction in skin feedback. To address this objective, we studied the denervated animals for several weeks after the denervation and measured functional improvements over time.

With respect to level treadmill walking, the small deficits in knee flexion amplitude were rapidly compensated. The increased knee flexion velocity remained and the ankle and knee flexor muscle activity gradually diminished but remained significantly above control level. Therefore careful inspection of the kinematics of walking and motor pattern showed some permanent modifications. The persistence of these modifications rules out their presence as being related to a change in motor strategy associated with pain or other aspects related to the denervation procedure.

The second important result in this study was that the animals showed extensive compensation during ladder and slope walking over the several weeks that followed the denervation. This compensation was gradual, which is suggestive of motor learning rather than switching to an already existing alternate motor strategy. Although functionally extensive, however, compensation was nevertheless incomplete, as shown by: 1) the differences in joint modulation on slopes between control and 23 days postdenervation; 2) the late ladder walking motor strategy (“cock spur” paw position); and 3) the >200% increase in mediolateral ground reaction force during overground locomotion.

Therefore although the locomotor system of the adult cat is capable of compensating for the removal of hindpaw cutaneous inputs, it cannot regain fine control of the movement in their absence. In summary, the lack of long-term compensation for the deficits in lateral force production during level walking, in joint adaptations during slope walking and in paw placement during ladder walking, suggests that cutaneous inputs are essential for the fine control of locomotion and become more useful as the locomotor task becomes more demanding.

PARTIAL VERSUS COMPLETE DENERVATION. There were more similarities than differences in motor deficit and adaptive stra-
egy between animals having undergone a partial or a complete cutaneous denervation. During ladder walking, the time courses of recovery on the rungs were equivalent. During incline walking, the reduction in joint angular modulation was also similar. Overground, the increase in mediolateral force was of the same magnitude and direction. The only difference between the partially and completely denervated cats was at the level of the knee hyperflexion, which appeared transiently only after the complete cutaneous denervation. The 2-stage denervation in cat DSL3 nicely shows the similarities and differences between the partial and complete denervations and strengthens our findings.

COMPENSATORY MECHANISMS. The extensive compensation after the complete hindpaw cutaneous denervation is in contrast to cats having undergone a complete deafferentation through a dorsal rhizotomy (Goldberger 1977, 1983; Hiebert and Pearson 1999; Wetzel et al. 1976). After such a procedure, which abolishes feedback from all sources of sensory information originating from the whole limb, cats tend not to use the deafferented limb (however, for acute decerebrate cats with mesencephalic locomotor region (MLR) stimulation see Grillner and Zanger 1974). However, if a single dorsal root is spared, cats gradually recover the ability to use the experimental limb. These experiments suggest that central reorganization can occur after small or large reductions in sensory feedback, provided some feedback from the limb remains. In the case of the cutaneous denervation, remaining feedback could be obtained from muscle and joint receptors, as discussed above.

However, in addition to these peripheral signals, some central mechanisms could also participate in compensation. The corticospinal system could be involved in the locomotor compensation after a complete or incomplete cutaneous denervation and increase the central locomotor drive. Preliminary data from experiments involving a cutaneous denervation performed on motor cortex–lesioned cats show no increase in St amplitude after the denervation and the presence of foot drag (Bouyer et al. 2000), supporting a role for the motor cortex in the compensation process.

The limit of the denervation protocol is that the deficit observed even immediately after the neurectomies is the outcome of a combination of 2 factors: 1) the missing contribution of the removed input and 2) the immediate compensation from the remaining neural circuits. The long-term compensation gradually occurring over the following weeks on the other hand results from the adaptive capacity of the system. In this study, we have used chronic recordings to compare early and late locomotor compensation after a complete or incomplete cutaneous denervation originating from the whole limb, cats tend not to use the deafferented limb (however, for acute decerebrate cats with mesencephalic locomotor region (MLR) stimulation see Grillner and Zanger 1974). However, if a single dorsal root is spared, cats gradually recover the ability to use the experimental limb. These experiments suggest that central reorganization can occur after small or large reductions in sensory feedback, provided some feedback from the limb remains. In the case of the cutaneous denervation, remaining feedback could be obtained from muscle and joint receptors, as discussed above.

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ROLE OF CUTANEOUS INPUTS DURING LOCOMOTION IN INTACT CATS


