Control of Frontal Plane Motion of the Hindlimbs in the Unrestrained Walking Cat

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Submitted 7 April 2006; accepted in final form 28 June 2006


INTRODUCTION

The neural control of walking has been largely studied from a sagittal view. In most limbed animals, the largest movements related to locomotion and the forward progression of the body occur in this plane. Consequently, walking in cats and other mammals is usually described in terms of the flexion and extension movements of the step cycle following the Philippson step cycle (Philippson 1905). From this perspective, the concept of the central pattern generator for stepping and the factors that regulate the basic stepping pattern have been extensively described (Pearson 2004; Rossignol 1996). However, the flexion and extension actions associated with the forward stepping movement are alone inadequate to generate functional locomotion. For example, cats that have received a spinal transection can be trained on a treadmill to produce adequate flexion and extension actions in the hind legs to enable walking with full weight support; however, walking is only achieved if lateral stability is maintained externally (Bar-bau and Rossignol 1987). Correspondingly, neuromechanical models of cat walking fail unless hip adductors and abductors are included (O. Ekeberg, personal communication). Thus for a full understanding of the neural mechanisms controlling walking, there is a need for greater understanding of the control of frontal plane motion.

Currently we know the basic patterns of activity displayed by most of the abductor and adductor muscles during walking (Engberg and Lundberg 1969; Pratt et al. 1991; Rasmussen et al. 1978; Rossignol 1996). Overall it appears that many of the abductors and adductors are active during the late portion of the swing phase (E1) (Philippson 1905) and for much of the stance phase similar to the timing of activation of extensor muscles of the leg, such as medial gastrocnemius or vastus lateralis. Consequently, the abductors and adductors are often described as leg extensors. In fact, the pattern of gracilis (a hip adductor and extensor) nerve activity in a fictive locomotion preparation was so consistent with extensor nerve activity that gracilis was used as a stable indicator of extensor phase activity in a study investigating the modulation of the stepping cycle by afferent input (Kriellaars et al. 1994). Indeed anatomically most hip abductors and adductors may also be hip extensors (Crouch 1969). As a result, the role of muscles such as adductor femoris and gluteus medius in adducting and abducting the hip during gait has been largely overlooked. There have been no studies that document the actions of hip adductor and abductor muscles during the cat step cycle with the frontal plane motions of the hind leg. Moreover, the walking behavior of the cat from the frontal plane has yet to be described.

The purpose of the present study is to characterize the patterns of hip adductor and abductor muscle activity from the cat hind leg and describe the cat step cycle in terms of the frontal plane motions of the leg. In addition, we introduced medial-lateral perturbations of the walking surface to challenge stability to further delineate the role of these muscles. From this, we have gained a better understanding of the functional role of the abductor and adductors muscles of the hip in maintaining stability during walking, and can begin to understand the differential neural control of these muscles. Portions of these results have been described in abstract (Misiaszek 2003).

METHODS

Animals and training

A total of 5 adult female cats (weight: 2.5–3.5 kg) were used in this study. Each animal was trained daily for ≤6 wk to walk across a...
custom-built walkway (8 ft long, 2 ft wide). The cats were trained to walk from one end of the walkway to a food reward at the other end. Once the animals walked consistently for $\geq 20$ min/session (yielding between 20 and 60 passes, depending on the temperament of the cat), the animals were then implanted with chronic indwelling electromyographic (EMG) electrodes. The animals were then permitted to recover ($\sim 2$ days) from the implantation surgery. Subsequently, we recorded EMG and kinematic data from the walking cats daily for $\leq 6$ wk. The experimental procedures were approved by the University of Alberta Health Sciences and Animal Welfare Policy Committee in accordance with the Canadian Council on Animal Care.

**Implantation of EMG electrodes**

Pairs of EMG electrodes were implanted into selected muscles of the hindlimbs. The muscles were not identical for each cat. In all cats, the medial gastrocnemius (an ankle extensor and knee flexor, MG) and tibialis anterior (an ankle flexor, TA) muscles were implanted in the right leg. Adductor femoris (a hip adductor and extensor, AF) was implanted in three of the cats, gracilis (GR) in two cats, gluteus medius (a hip abductor and extensor, GM) in four cats, and tensor fascia lata (a hip abductor and extensor and knee flexor, TFL) in one cat. In addition, right vastus lateralis (a knee extensor, VL), right semitendinosus (a hip extensor and knee flexor, ST) and left (or contralateral) MG (coMG) were recorded in various animals. The EMG electrodes were comprised of a multi-stranded stainless steel wire (Cooner Wire, No. AS632) Teflon insulated except for a 3–4 mm length positioned in the muscle. The wires were secured to a 21-gauge needle so as to be passed through the belly of the muscle. The pair of wires were then knotted together and secured to the muscle with a silk suture. The other ends of the electrodes were attached to a multipin connector, which was secured to the skull of the animals with dental acrylic bonded to stainless steel screws. At the time of the implantation small squares of Velcro (hook portion) were sutured over the joints of the legs. These Velcro patches were used to affix reflective markers over the joints during recording sessions for recording of the cinematic data. This technique ensured the markers were replaced in the same positions from day to day.

After implantation, EMG and video recordings were made daily for several weeks. The EMG signals were amplified (1,000–8,000 times) and filtered (30–3,000 Hz, P511 amplifier, Grass Instruments) prior to storage onto magnetic tape (VHS, Vetter 4000A PCM recording unit). Selected sequences of data were later digitized at 1,000 Hz using a 12-bit A/D converter (DAQcard AI-16E-4, National Instruments) and a custom-written acquisition routine (LabView 5.1, National Instruments). The movements of all four limbs, the head and the caudal spine of the cats were recorded using a four-camera video capture system (Motus 8.0, Peak Performance Technologies). The cameras recorded at 30 fps, and the video signals were later de-interlaced to yield a sampling frequency of 60 Hz. The shutter speed was set at 1/250. Small three-dimensional reflective markers (8-mm head wrapped with reflective tape) were placed on the Velcro patches over the joints of the cat and were easily visible in the cameras. Markers were secured to the metacarpal-phalangeal joint of each forepaw, bilaterally on the iliac crest and hip joints, bilaterally at the metatarsal-phalangeal joints, at the lateral malleolus of the right ankle, over the tibia 2–3 cm proximal of the malleolus and at three points along the spine. In addition, a marker was glued to the headpiece of the cat. The knee joint was not marked. Instead, the length of the tibia was obtained, and a virtual knee point was created with the Motus acquisition software by extending the tibia from the malleolus through the marker placed on the shank. The video records from the four cameras were synchronized using SMPTE time code generators. To synchronize the EMG data with the video records, an event marker was placed on the EMG tape and the video records during each pass across the walkway.

**Medial-lateral translation of the walking surface**

In this study, we wished to determine the role of abductors and adductors during locomotion. We hypothesized that these muscles are important in regulating medial-lateral stability. Consequently, we speculated that medial-lateral perturbations to stability would assist in delineating the role of these muscles. To induce medial-lateral challenges to stability our walkway was equipped with a sliding platform. The central 2-Ft portion of the walkway was separate from the remainder of the walking surface and mounted on a ball-bearing slide. The moveable portion of the walkway was attached to a linear motor (Model CF04B, Baldor Motors), which permitted the platform to be translated perpendicular to the direction of travel of the cat. The platform was rigid when the motor was not activated. During the recording sessions, the cats would walk from one end of the walkway to the other. Periodically, approximately once every 10–15 passes, the central platform of the walkway would be moved while the cat walked over it. The motion of the platform was controlled by computer and triggered by one of the EMG signals. For this study, we used translations timed to approximate the onset of the stance or swing phases of the right leg. Consequently, the onset of the right MG burst plus an 80-ms delay was used to initiate the platform movement at about stance onset (Gorassini et al. 1994). To approximate swing onset, we used either the ST burst with a 30-ms delay, or the coMG burst with a 100-ms delay. The motor allowed for perturbations of variable amplitudes and accelerations. For this paper, the perturbations used were 5-cm displacement with 0.6g peak acceleration. These disturbances produced an obvious adaptation in the walking pattern in all of the animals. The direction of perturbation (left or right with respect to the cat) was randomized. The timing of the perturbation onset (right stance vs. right swing onset) was consistent for any given recording session, but was varied across days. A single-axis accelerometer (Model 1210 Analog Accelerometer, Silicon Designs) affixed to the platform was used to record the onset of movement.

**Data analysis**

Post hoc, the video records of each recording session were screened for the walking behavior of the cat and any passes in which the cat did not walk straight, turned its head, or varied its walking speed and pattern were excluded from analysis. Subsequently, those passes for which the cat walked consistently were then captured for video analysis. The markers of the cat were digitized for all four cameras, and the three-dimensional location of the markers was calculated. Using a custom-written routine, the walking speed of the cat was calculated using the forward motion of the head marker.

The EMG data for those passes that were selected based on the video screening were then selected using custom written software (LabView 5.1, National Instruments). For each step analyzed, a 1,200-ms segment was selected. The EMG traces were digitally full-wave rectified and low-pass filtered (50 Hz, 2nd-order dual-pass Butterworth filter). One full step cycle, when the cat was in the center of the walkway, was analyzed for each trial. This was done to ensure that the walking velocity was stable (neither accelerating nor decelerating) and that the cat was in the optimal position for the video record with respect to the calibration volume. Screening the walking trials in this way resulted in $\sim 60–90$ steps per animal being included in the analysis of the control, undisturbed steps. The perturbation trials were also screened to ensure that the cat was fully supported by the moveable platform for the duration of the perturbation. Any trials where one or more paws were supported by a stable portion of the walkway were excluded from further analysis. This screening resulted in $\geq 10$, and $\leq 30$, perturbed steps per direction (left and right), per point in the step cycle and per animal being included for analysis.

The video data were used to calculate step parameters including fore and hind limb step width (medial-lateral distance between paws...
during double-support), step length, medial-lateral paw excursion (displacement of the paw in the frontal plane over the step cycle), medial-lateral hip excursion (displacement of the hip marker in the frontal plane over the step cycle) as well as three-dimensional kinematics of the right hind leg. Selected segments of the video records were digitized and stored to computer. The reflective markers were then automatically identified frame-by-frame for each camera view using automated tracking software (Motus 8.0, Peak Performance Technologies). The sagittal plane joint angles were calculated for the hip, knee, and ankle of the right leg. The frontal plane joint angle of the hip was also calculated. The EMG activity of undisturbed, control steps was used to calculate the timing, duration, and amplitude of the bursts for the various muscles studied. Burst durations were also calculated for the perturbation trials. In addition, the perturbation trials from each cat were averaged together and compared with the averaged undisturbed trials for that cat to characterize the responses elicited by the disturbance. A response to the perturbation was identified in a muscle if the average EMG trace exceeded the 95% confidence interval around the average trace for the control steps for a minimum of 5 ms. In this way, the EMG of the perturbed trials was identified as being significantly increased or decreased, compared with the undisturbed control steps. Response latency was estimated from the time at which the trace for the averaged perturbed trials began to deviate from the average control trace.

RESULTS

The objective of this study was to characterize the pattern of activity of the abductor and adductor muscles of the hind legs in relation with the motion of the legs in the frontal plane during unrestrained over-ground walking in the cat. The basic pattern of abductor and adductor muscles has been described previously (for review, see Rossignol 1996); however, in the present paper, we expand on this knowledge and describe the activity of the muscles in relation to the frontal plane motion of the hind legs during walking. In addition, the responses of the muscles of the legs to lateral perturbations of the walking surface were introduced to provide further insight into the potential contribution of these muscles to medial-lateral stability during walking.

Basic walking profile

The hip abductors, GM and TFL, and adductors, AF and GR, were typically active during the stance phase of the walking step cycle. To illustrate the timing of the EMG activity in the different muscles, average EMG traces were constructed aligned to the onset of the MG (a traditional extensor muscle) burst for steps of relatively equal walking speed (Fig. 1). Generally, the timing of adductor and abductor muscle activity onset across animals and between muscles is similar. In all cases, the abductors and adductors became active just prior to paw contact, during the E1 phase.

The profile of the EMG activity from the hip abductors GM and TFL was very similar across cats and between the muscles tested. Typically, the burst can be characterized as having two distinct phases of activity. The first phase is a sharp peak at the onset of the burst, followed by a period of lower activity and then a period of sustained activity beginning near the mid point of the stance phase. This pattern was seen in all three cats for which GM was recorded and was also seen in the one TFL recording (Fig. 1). In contrast, the EMG profile for the hip adductors AF and GR was less consistent. In some instances, AF had a relatively sustained tonic level for the duration of its activity (cat 1); in other instances, AF had distinct phases of activity with a sharp peak at the onset and a later sustained level of activity (cat 2). The profile of GR was markedly different from AF with a sharp peak of activity just prior to stance onset and relatively little activity for the duration of the stance phase. In one animal, cat 3, there was often a period of activity in the latter half of the stance phase, but this was not consistently seen from step to step and was not present in the other cat for which GR was recorded.

The angular movements of the hip, knee, and ankle in the sagittal plane were generally similar to what has been reported previously (Rossignol 1996). The hip angular movements in the frontal plane displayed some variation in the specific details of the movement profile, but were generally similar across cats (Fig. 2). Typically, the hip was at its most adducted position at paw contact. Subsequently, the hip abducted through much of the stance phase before adducting slightly just prior to lift off. The hip then abducted briefly during early swing before quickly adducting during the last half of swing. The stick figures in Fig. 2A depict the relative posture of the legs at five points in the step cycle. For clarity, each leg is represented by a single segment, excluding the knee and ankle joints. From
these stick figures it can be seen that the abduction of the hip during stance is related to an elevation of the contralateral hip, whereas the adduction at the end of stance is related to the lowering of the contralateral hip. The abduction during early swing is related to a circumduction of the paw. The overhead view of the trajectory of the paws during swing and the placement of the paws during stance are shown in Fig. 2C for a sequence starting at left paw contact and ending at the second subsequent right paw contact. The paws exhibited a lateral excursion of 2–3 cm during swing phase.

Effect of speed of walking

Although each animal demonstrated other forms of gait, such as trotting and galloping, the animals rarely performed these other forms spontaneously. Consequently, we focused our study on walking. Each animal walked across the walkway at various speeds, ranging from ~0.4 to 1.3 m/s. However, each animal had a preferred walking speed at which they walked most often. Typically this was between 0.6 and 0.8 m/s. The data presented in the preceding section were averaged data from the steps of the preferred walking speed of the cat.

In Fig. 3A, EMG burst durations are plotted against the speed of walking for each trial from one animal. As can be seen, the burst duration decreases with increasing walking speed in all muscles recorded. The Pearson’s r values for each correlation (burst duration vs. walking speed) ranged from −0.54 to −0.86. Specifically, the Pearson’s r for AF and GM were −0.54 and −0.73, respectively, compared with −0.64 and −0.86 for MG and VL, respectively. Similarly strong correlations between burst duration and walking speed were found in all animals and for all muscles tested.

In Fig. 3B, mean burst amplitude for each step is plotted against walking speed for each muscle from one animal. The mean burst amplitude for each of MG, VL, and AF increased with walking speed, showing a strong correlation with Pearson’s r values of 0.52, 0.59, and 0.81, respectively. In contrast, GM burst amplitude remained relatively constant at all walking speeds (Pearson’s r = 0.05). This finding was consistent across all animals. Specifically, mean GM burst amplitude never showed a correlation to walking speed. Consequently, the shorter burst duration and stable burst amplitude with increased walking speed resulted in a weak correlation between GM burst amplitude and walking speed if the integrated amplitude was measured (Pearson’s r = 0.37 for the data in Fig. 3B).

Various step parameters are plotted against walking speed for one cat in Fig. 4. All the animals shared similar results. Increases in walking speeds were accompanied by increases in stride length (Fig. 4A, r = 0.56), but no change in step width (Fig. 4A, r = −0.08). In addition, the lateral excursion of the paw during swing remained consistent across walking speeds (Fig. 4B, r = 0.23); however, there was a marked decrease in the medial-lateral excursion of the hips (side-to-side sway) with increasing walking speed (r = −0.63). The basic pattern of hip motion in the frontal plane, as depicted in Fig. 2, was consistent across speeds. However, the range of motion (ROM, maximum abduction to minimum abduction) of the hip in the frontal plane increased with increasing walking speeds (Fig. 4C, r = 0.71). This was related to small changes in both the maximum and minimum abduction angles. Thus during an increase in walking velocity the side-to-side sway of the animal decreases, whereas the lateral swing of the paw remains unchanged. This is accomplished by increasing the range of tilt of the pelvis as indicated by the increased ROM of the frontal plane hip angle.

Response to medial-lateral translation of the walking surface

To better understand the actions of the abductors and adductors during over-ground walking, we also investigated the
responses in these muscles to medial-lateral translations of the walking surface. The aim of this portion of the study was to characterize the responses of the abductors and adductors and relate these responses to movements of the hind legs observed in the frontal plane. We anticipated that these perturbations would result in differential activation of the abductors and adductors thereby providing insight into the control of these muscles during walking. The responses and behaviors generated by these disturbances were remarkably consistent across animals. In this section, the results of a single animal are described in detail to provide an overview of the behavior that was generated by the disturbance. In addition, some measures are summarized with grouped averages to illustrate the consistency in the responses that was apparent across animals. For the EMG data, the group summaries are limited to those muscles that were recorded in three or more animals. These were MG, TA, GM, and AF.

**Perturbations during stance**

Both the abductor GM and adductor AF are active in the late period of the swing phase (E1), just prior to paw contact and generally remain active for the duration of the stance phase. In this section, we describe the responses of these muscles to medial-lateral perturbations initiated at right hind leg stance onset. The perturbations consisted of a 5 cm ramp displacement, with a peak acceleration of 0.6g. The perturbations were timed to occur 80 ms after the onset of the MG burst, to approximate the time of contact. As can be seen in Figs. 5 and 6, the earliest deflection of the acceleration occurred very near stance onset.

Figure 5 shows the typical reactions elicited with a medial disturbance of the walkway, which slides the right hind paw under the body. The schematic in Fig. 5A shows stick figures of the hind legs of the cat during a perturbed step overlaid on an undisturbed step for five points in the step cycle. As can be
seen, the medial perturbation during stance phase leads to a generalized rotation of the leg-pelvis structure over the stance paw. The left swing paw then adducts toward the ground making contact such that the paws are crossed. Subsequently, the right paw swings laterally from behind the left paw. The paw trajectories associated with this corrective response are shown from overhead in Fig. 5B. For clarity, the hind paws and fore paws are plotted on separate grids. From this overhead view of the corrective response, it can be seen that the left hind leg, which was beginning the swing phase at the onset of the perturbation, has a substantially shorter step length and lands slightly to the right of the paw placement for the control steps. In addition, as shown in the stick figures of Fig. 5A, the left hind paw lands to the right of the right hind paw such that the hind legs are crossed. The subsequent step of the perturbed right hind leg swings the paw to the right avoiding the left paw, before then bringing the paw slightly back toward the left. The right hind paw lands slightly to the right and behind the placement of the control step. The focus of this study is the characterization and control of the movements of the hind legs in the frontal plane. However, as this figure clearly demonstrates, the correction to the balance disturbance involves the actions of all four limbs. At the time of the perturbation, the left fore paw is in stance phase. Consequently, the leftward perturbation results in a lateral displacement of the left fore paw. The right fore paw, which is in swing phase at the time of the disturbance, lands slightly forward and to the right of the control step placement. The subsequent step of the left fore paw swings medially landing slightly to the right of the control step placement. In general, the 5 cm leftward displacement of the support surface resulted in a modest rightward placement of all four paws during the corrective steps. It can also be seen in Fig. 5A that the corrective response restored the medial-lateral position of the pelvis. Thus after the initial rightward displacement, the position of the pelvis (and therefore the body) in space was largely restored to the original path of progression.

The frontal plane hip angular movements associated with the disturbance and subsequent recovery are shown in Fig. 5C along with the responses in the muscle EMGs. Rather counter intuitively, the medial disturbance of the paw at stance onset
led to a greater abduction of the right leg, beginning about midstance. Thus during the initial half of the disturbance no change in the hip angle was induced despite the obvious rotation of the pelvic structure depicted in Fig. 5A. During the latter portion of the stance phase, the hip becomes more abducted and then begins to adduct just prior to lift-off. In contrast to the undisturbed step, where the leg abducts following lift-off, the leg continues to adduct immediately after lift-off before then abducting. Finally, the leg adducts as the paw approaches contact.

As can be seen in Fig. 5C, the translation of the walking surface leads to a considerably shorter stance phase duration and a longer swing phase. The overall step cycle duration is also shortened. In addition, the leg extensors MG and VL show an increase in activity shortly after the onset of the disturbance. The onset of the increased level of activity is 25.5 and 45.0 ms for MG and VL, respectively. The abductor GM also shows a short-latency (33.3 ms) increase in activity with an abbreviated burst duration. The adductor AF shares the abbreviated burst duration, but the amplitude is not changed. In this animal, we also recorded TA, which shows a large contraction during the stance phase beginning 64.6 ms after the onset of the disturbance. This burst continues into the subsequent swing phase activity normally associated with TA. No additional bursts of activity are seen in the abductor or adductor muscles during the subsequent swing phase.

Figure 6, A and B, shows the typical motions elicited with a rightward translation of the walking surface, which slides the right stance paw away from the body. This leads to an abducted angle of the right hip at the time of lift off. In addition, the left leg swings more laterally, leading to a wider stance width and an abducted posture of the left leg at contact. The left paw makes contact to the left and substantially posterior to the paw placement of the control steps. The shorter step length of the left paw is associated with a shorter left paw swing duration, resulting in a prolonged period of hind leg double-support. The subsequent swing of the right leg brings the paw back to the left such that at contact it lands behind but very near the medial-lateral placement of the control steps. With this disturbance, the left fore paw is displaced to the right. Consequently, the right fore paw swings to the left, landing slightly left of the placement of the control steps. The subsequent left step swings leftward, avoiding the right fore paw, and then moves slightly back toward the right. The left fore paw lands behind and to the left of the placement of the control step. In general, the rightward disturbance leads to a modest leftward placement of the paws during the corrective response. The medial-lateral position of the pelvis appears to be relatively unaffected by the disturbance or the subsequent correction.

The frontal plane hip joint angle and muscle responses of the right leg to the rightward translation are depicted in Fig. 6C. As
can be seen, the rightward translation of the right paw leads to an abduction of the right hip. However, despite the very abducted angle of the hip at lift off, the initial portion of the swing phase is characterized by further abduction, before the leg rapidly adducts prior to the subsequent paw contact. The net effect of this hip motion is a paw trajectory that moves toward its placement position with a relatively direct route (Fig. 6B). As with the leftward disturbances, the rightward translations lead to a shortened right hind step cycle and a markedly shortened stance phase. In contrast, the subsequent swing phase duration is relatively unaffected. The muscle responses to the lateral translation reflect the abbreviated stance phase. Each of the MG, VL, and AF burst durations are decreased. In addition, each of these muscles shows a distinct suppression in the EMG amplitude at a short latency after the onset of the translation. The onsets for the reduced activity in each muscle are 31.3, 31.5, and 50.9 ms, respectively. In contrast, the burst duration of GM was not altered after these perturbations despite the reduced duration of the stance phase. In addition, there was a brief burst of increased activity starting 76.3 ms after the onset of the disturbance with a duration of ~50 ms. As with the leftward perturbations, rightward translations also generated a robust activation of TA during the perturbed stance phase beginning 72.4 ms after the onset of the disturbance. No additional bursts were observed in either AF or GM during the subsequent swing phase although the GM burst extended beyond lift off.

In the preceding paragraphs, the average responses evoked in one animal were described. However, the responses evoked in all the cats tested shared a very similar description. For example, the abbreviated stance phase duration described after perturbations in both directions at stance onset was seen in all five animals and was significantly shorter than control steps (paired t-test, P < 0.05, Fig. 7A), whereas the duration of the subsequent swing phase was not affected (P > 0.05). The duration of the MG and AF bursts were also significantly reduced compared with the undisturbed steps (P < 0.05) after both the left and right perturbations (Fig. 8). The GM burst duration was also significantly decreased after leftward perturbations (P < 0.05) but was unaffected by the rightward perturbations (P > 0.05). In addition, leftward perturbations resulted in early activation of MG and GM with a subsequent activation of TA in all animals tested. In contrast, none of the animals tested showed a significant response in AF to these perturbations. Similarly, in all animals tested, the rightward perturbations resulted in early suppression of MG and AF activity and early activation of TA and GM. The response latencies are summarized in Table 1.

Perturbations during swing

Neither the hip abductors nor adductors are active during swing phase, except for the late E1 phase when both muscles typically become active. In this section, the responses of the abductor and adductor muscles to medial-lateral translations of the walking surface initiated near the onset of the swing phase are described. To do this, the disturbances were initiated 30 ms after the onset of the ST burst of the right leg if ST was...
The general behavior of the cats in response to the walking surface translations at the onset of swing are comparable to the behavior described in the previous section (Figs. 5 and 6) but with the legs reversed. Consequently, the description of this behavior will not be repeated here. In Fig. 9A, the frontal plane hip angular movements of the right hind leg are displayed along with the evoked EMG responses after a lateral displacement of the left stance leg. Shortly after the onset of the perturbation, the right swing leg becomes abducted compared with the undisturbed steps. However, prior to ground contact, the leg adducts slightly before then proceeding through abduction for the duration of the subsequent stance phase. The hip remains more abducted for the duration of the subsequent step compared with the undisturbed steps. The duration of the disturbed swing phase is markedly shorter, but the duration of the subsequent stance phase is prolonged. The initial response in the EMG records occurs in the flexors TA and ST with onset latencies of 60.7 and 70.6 ms, respectively, and in GM with a latency of 77.4 ms. A response was observed in AF, but this occurred later at 133.8 ms, which was similar to the onset of the responses in the extensors VL and MG (135.6 and 130.7 ms, respectively). The responses in the MG, VL, and AF were consistent with a later second peak of activity in GM, ST, and TA; this appears to be related to the E1 phase of the abbreviated swing. After stance onset, the extensor muscles return to near normal levels of activity, as does AF. In contrast, GM activity returns to near normal levels early in the subsequent stance phase but becomes more active again toward the middle of the stance phase.

In Fig. 9B, the responses and frontal plane motion of the right hip after medial disturbances of the left stance leg are depicted. These disturbances, the right swing leg adducts slightly immediately with the disturbance but quickly abducts to a near normal hip position. Subsequently, the leg adducts for the remainder of the swing phase to a more adducted position by stance onset consistent with the crossed step depicted in Fig. 5A. Again, the earliest muscles to respond during this swing phase disturbance are the flexors TA and ST at 76.2 and 57 ms, respectively. A response is evident in AF soon afterward (92.9 ms). Subsequently, the extensors MG and VL, along with GM, showed a response at 179, 150.5, and 182.5 ms, respectively. The responses in MG, VL, and GM were consistent with later second bursts of ST, TA, and AF that appear to be related to the E1 phase of the abbreviated swing. Subsequently, each muscle returned to near normal activity levels with the onset of the stance phase, except for GM the activity of which remained elevated for most of the stance phase (note that VL activity appears elevated in the figure because the elevation of VL activity that occurs near the end of stance phase in the undisturbed steps occurs earlier due to the abbreviation of the step).

The responses evoked in all the cats tested shared a very similar description. The duration of the disturbed swing phase was consistently reduced in all five cats for both directions, resulting in significantly shorter swing durations compared with undisturbed controls (paired t-test, P < 0.05, Fig. 7B). The duration of the subsequent stance phase was not different from the control steps (P > 0.05). Leftward perturbations at swing onset resulted in early activation of TA and GM and a later activation of MG and AF in all cats tested. Rightward perturbations also consistently resulted in early activation of

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Left perturbations</th>
<th>Right perturbations</th>
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<tr>
<td>MG (5)</td>
<td>49.3 ± 19.9</td>
<td>41.5 ± 16.4</td>
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<td>TA (5)</td>
<td>59.8 ± 10.2</td>
<td>54.1 ± 12.1</td>
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<td>AF (3)</td>
<td>NR</td>
<td>63.5 ± 16.8</td>
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<tr>
<td>GM (4)</td>
<td>34.5 ± 7.1</td>
<td>63.9 ± 12.1</td>
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Values are means ± SD. For each value listed responses were identified in all cats. NR indicates that no responses were identified in any cat. N, number of animals in which the muscle was recorded is shown in parentheses. Muscle abbreviations are as detailed in the text.

FIG. 7. Group averaged phase and cycle duration data. Steps that received perturbations at early stance (A) and early swing (B) are depicted with control data. In A, the swing phase data represent the swing subsequent to the disturbed stance phase. In B; the stance phase data represents the subsequent stance phase. Each histogram is the mean (n = 5) with SDs. *, significant difference from the controls (paired t-test, P < 0.05).
TA, subsequent activation of AF, and then later activation of MG and GM. The response latencies are summarized in Table 1. The direction-dependent differences in activation times of the hip abductors and adductors after disturbances at the onset of swing were robust. After the rightward displacements of the stance leg, the responses in the swing leg abductors always preceded the onset of the adductor response with an average temporal separation of 53.7 ± 16.1 (SD) ms. After leftward displacements of the stance leg, the responses in the swing leg adductors always preceded the onset of the abductor response by 69.8 ± 17.5 ms on average.

DISCUSSION

We investigated the behavior of the abductor and adductor muscles in conjunction with the frontal plane movements of the cat hindlimb. To date, abductor and adductor muscles of the cat hindlimb have been broadly categorized as hip extensors as both the abductors and adductors tend to be active with the extensor muscles during walking (reviewed in Rossignol 1996). Our results confirm these previous findings. During unrestrained over-ground walking, the abductors and adductors recorded in this study were predominantly active during the stance phase of the step cycle, becoming active in late swing along with the other extensors of the leg. Neither the abductors nor adductors were active during the flexion phase of the step cycle. Thus the general finding that the abductors and adductors are co-active with the extensor muscles suggests that control of these muscles during the step cycle may be regulated by a common mechanism.

There are two major differences between our results and those in the literature. First, Rasmussen et al. (1978) reported that TFL was inactive during walking, becoming active at faster gaits such as the trot or gallop. In the one animal we recorded TFL, the muscle was clearly active during walking. Our recording of TFL activity matched well the description provided in Rasmussen et al. (1978) for the trot, displaying two periods of activity during the stance phase. Perhaps our recording of TFL activity during walking merely reflects inter-animal differences in the recruitment of this muscle. TFL in our recordings appeared very similar to GM records of other cats. Consequently, we are of the opinion that TFL and GM share similar profiles and control features. However, it must be noted that whereas GM crosses only one joint, TFL has actions at both the hip and knee and as such presumably behaves differently in other contexts. Second, Pierotti et al. (1989) describe a modest increase in the mean GM burst amplitude with increasing treadmill walking speed, whereas we report that mean GM burst amplitude remains constant across walking speeds. There may be two explanations for this difference. First, Pierotti et al. (1989) used treadmill walking with the...
treadmill set to specified walking speeds. This may create a task-specific change in the recruitment of GM. Second, the gait pattern used in our study was restricted to walking. Pierotti et al. (1989) specifically included running, and presumably included other gait forms, such as trotting. Some of the effect of speed noted by Pierotti et al. (1989) may be a consequence of the different gait patterns.

**Control of hind leg frontal plane motion**

Each cat demonstrated a slightly different pattern of abduction/adduction motion at the hip. However, the common features of the frontal motions at the hip joint are an abduction of the hip during most of stance, a slight adduction just prior to swing, a brief abduction immediately after lift-off, and a rapid adduction during swing.

The abduction observed during the stance phase is most likely produced by activation of the hip abductors, such as GM. MacKinnon and Winter (1993) demonstrated that in walking humans, a substantial hip abductor muscle torque is required to overcome the gravitational inertial load of the mass of the body and swing leg. Presumably, a similar explanation can be extended to the cat. Alternatively, mechanical events as a consequence of the contralateral propulsion, may also contribute to the abduction of the hip observed during stance. Bouyer and Rossignol (2003) recorded ground reaction forces in all three axes for the step cycle of intact cats. At push-off, there are forces applied posteriorly, laterally, and vertically. Combined these forces may result in a passive accelerational abduction moment about the hip of the stance limb as described during human walking (MacKinnon and Winter 1993). That is, the propulsive forces would not only propel the mass of the body forward but also toward the contralateral supporting limb with the mass rotating about the hip of this limb. It is interesting that with increasing speed of walking, the burst amplitude of the hip abductor GM did not change, whereas the hip adductor AF and the other leg extensor muscles all showed increased burst amplitudes. It would fit that with an increase in extensor activity during the faster walking, there would be a relative decrease in abductor muscle activity as the greater extensor torque would also result in an increase in the passive accelerational abduction moments. It is also important to note that the medial-lateral excursion of the hip (or side-to-side sway of the pelvis) decreased with increasing walking speed. Less sway would presumably increase the efficiency of the extension movements in generating forward propulsion. In contrast, with a slower walking speed, the body mass must be supported for a longer duration by the stance limb, allowing for a greater relative influence of gravity, requiring a relative increase in the hip muscle abductor moments.

If the frontal plane actions at the hip require substantial hip muscle abductor moments during the stance phase of walking (MacKinnon and Winter 1993), why then are both the abductor GM and adductor AF muscles active during the stance phase? As described here and elsewhere, the abductor and adductor muscles of the hip are typically co-activated prior to ground contact, during the E1 phase of the step cycle. Rasmussen et al. (1978) argued the E1 activation of the hip extensors (also adductors and adductors) served to stabilize the hip in anticipation of ground contact and acceptance of loading, similar to the actions of the extensors of the knee and ankle. The responses elicited by medial-lateral translations of the support surface provide support for this putative role. In the present study, both the lateral and medial directed translations of the support surface at stance onset resulted in abduction disturbances of the hip, but only after a period of relatively no disturbance to hip joint motion. Moreover, medial translations at stance onset typically resulted in a generalized rotation of the pelvis and limbs as a unit. This suggests that at the time of the disturbance the hip joint was sufficiently stiff to be able to resist deviations in hip motion during the initial portion of the perturbation. The visco-elastic properties of muscles, determined in part by the level of muscle activation, can provide substantial and immediate resistance to perturbations (Grillner 1972; Rack and Westbury 1974). Therefore the activation of both the abductors and adductors during the E1 phase likely serves to resist perturbations at stance onset by setting the appropriate muscle properties, or “preflexes” (Loeb et al. 1999). Subsequently, throughout the remainder of the stance phase, the abductors and adductors are coactive to extend the hip and maintain body weight support as both muscle groups are also hip extensors. The activity of the abductor and adductor muscle groups could then be weighted so that their net action in the frontal plane results in the appropriate hip abductor moments required for control of frontal plane motion during the stance phase.

The responses elicited by medial-lateral translations of the support surface provide support for the argument that frontal plane motions of the hip may be achieved by weighting the activity between these muscle groups. For example, both medial and lateral disturbances at stance onset resulted in increased hip abduction. The similar initial abduction of the hip is achieved through very different responses in the abductor and adductor muscles. With the rightward perturbation, the abduction is subsequent to a decrease in the ongoing adductor (AF) muscle activity and a transient increase in the abductor (GM) activity. With the leftward perturbation, the abduction is subsequent to an increase in abductor activity but unaltered adductor activity. In essence, the net effect of both responses was a net shift toward abductor muscle activity.

In addition, during the stance phase of the step immediately after the perturbation, that is, the stance phase for the paw that was in swing at the time of the perturbation, the hip abductor (GM) exhibited increased activity regardless of the direction of the perturbation (Fig. 9). This increased activity would serve two distinct purposes in response to two distinct biomechanical needs of the stance limb. In Fig. 9A, the hip is in a more abducted posture throughout the stance phase. Consequently, increased abductor activity would be required to counter the gravitational load with a poorer mechanical configuration of the leg. In contrast, in Fig. 9B, the hip is more adducted at stance onset requiring a greater range of abduction to restore the control alignment of the hip. Taken together, these results suggest that hip abductor activity during stance phase has a prominent role in regulating frontal plane motions of the cat hind legs, consistent with the suggestion of MacKinnon and Winter (1993) for the control of lateral stability in walking humans.

Neither the abductors nor adductors are normally active during the swing phase, except during the late E1 phase. Despite this, the leg moves through a brief abduction followed by a rapid and relatively large adduction. Presumably, these
movements are generated largely by passive accelerational moments. In this study, the cats walked along a straight level walkway. It may be that activity of the hip abductor and adductor muscles during the swing phase will become important when cats walk in a more challenging environment requiring accurate paw placement, such as walking across pegs or the rungs of a ladder. Indeed, activity evoked in the hip adductors and abductors during swing phase appear to be important in correcting for medial-lateral disturbances to stability, as will be discussed in detail in the following text.

Corrective responses to medial-lateral perturbations

The primary purpose of using the medial-lateral perturbations in this study was to probe the functional relevance of the coactivation of the hip abductors and adductors during the stance phase. However, the perturbations also allow for the investigation of the control of balance corrections during locomotion as the perturbations required an active correction on the part of the animals. The active correction involves substantial movements of the legs in the frontal plane along with distinct patterns of activation of the hip abductors and adductors that provide additional insight into the potential mechanisms controlling the activity of these muscles during locomotion. This paper is the first to describe corrective balance reactions to whole-body disturbances during locomotion in the cat.

The medial-lateral perturbations used in this study were applied when all four limbs were on the sliding platform. Subsequently, the disturbance was corrected for with reactions of all four limbs (Figs. 5B and 6B). The corrective reactions of the hind limbs we observed in the cat are comparable with the corrective reactions observed in humans to medial-lateral support surface translations during walking (Oddsson et al. 2004) or stepping in place (Maki et al. 2000). That is, humans will also use a widened corrective step if the stance leg is displaced laterally and a narrowed or crossover corrective step if the stance leg is displaced medially. Therefore the initial corrective reactions of the hind legs in the cat reasonably approximate the reactions of humans, indicating that the cat is a reasonable model to explore the neural mechanisms of lateral stability during walking. There is, however, one main difference between the reactions observed in the cat and those in the human. Humans frequently require multiple steps to regain medial-lateral stability during walking or stepping (Maki et al. 2000; Oddsson et al. 2004). In contrast, the cat appears to be capable of regaining medial-lateral stability within one full step cycle as evidenced by the relatively unaltered EMG patterns observed in the step subsequent to the correction (Figs. 5–7). Presumably, this advantage results from the quadrupedal posture of the cat.

It is also remarkable that the medial-lateral position of the pelvis (and therefore the body) is largely unaffected by the disturbance (Figs. 5A and 6A), despite the rather large corrective movements of the legs. Inertia likely maintains the medial-lateral position of the body in space. Thus the corrective reaction to the disturbance repositions the paws beneath the falling body rather than repositioning the body over the newly translated position of the paws. This is in direct contrast to what is seen in standing balance corrections observed in cats after support surface translation (Macpherson 1988a,b).

Macpherson (1988a,b) showed that standing cats correct for a support surface translation by maintaining the paws in place and generating the necessary muscle moments to reposition the body center of mass over the paws. Thus the force-constraint strategy described by Macpherson (1988a,b) for correcting standing balance cannot be directly translated to the corrective responses required during locomotion. Presumably, therefore the neural mechanisms involved in the corrective responses evoked during locomotion are also substantially different. The paradigm utilized in this study provides a simple and robust means to investigate the neural control of walking balance.

Passive displacement of the limbs might account for some of the motions of the swing leg after the medial-lateral perturbations observed during the corrective step. However, if the primary objective of the corrective responses is to reposition the displaced paws then controlling the medial-lateral motion of the swing leg is critical. In models of human bipedal locomotion, lateral stability has been shown to require active lateral stabilization, achieved in part by medial-lateral foot placement (Bauby and Kuo 2000; Donelan et al. 2004; MacKinnon and Winter 1993; Redfern and Schumann 1994). The corrective responses evoked in the present study involved short-latency motor responses in the muscles of the swing limb with clear differential activation of the hip abductors and adductors (Fig. 9). Therefore it is reasonable to suggest that a portion of the altered medial-lateral swing trajectory results from active control of paw placement. This active control of medial-lateral paw motion during the corrective step is presumably more critical following a medial displacement of the stance paw as the swinging leg must avoid colliding with the other leg to execute a crossover step (Fig. 5). Consequently, these active corrective responses to the medial-lateral disturbances are integrated whole-body reactions that cannot be easily explained by passive mechanical events and are also unlikely to result from activation of simple reflexes alone. This suggests that a complex, integrated response of the hind legs (and presumably the whole body) is initiated by the disturbance (Miaszsek 2006).

From the present study there is little evidence as to the neural mechanisms that might be involved in initiating the corrective responses observed. However, the motor responses evoked in the perturbed stance leg suggest that somatosensory receptors activated by the perturbations would likely be involved in initiating the responses given the relatively short onset times of the corrective responses (<50 ms in many instances). These may include muscle proprioceptors sensitive to load and length changes induced by the disturbance (Lam and Pearson 2002; Pearson 2004) or cutaneous receptors of the pads of the paws sensitive to shear forces and loading (Bouyer and Rossignol 2003; Ting and Macpherson 2004). We cannot rule out potential contributions from vestibular or visual inputs. However, vestibular inputs appear not to be important for triggering balance corrections in the standing cat (Inglis and Macpherson 1995).

The evoked responses typically included activation of the ankle flexor TA, regardless of the direction of the perturbation of the stance leg. This resulted in coactivation of TA and MG during the perturbed stance phase. One possible functional purpose for this activation of TA might be to increase the stiffness of the ankle joint and thereby prevent further disturbances in joint motion (Grillner 1972; Rack and Westbury.
Conclusions

In summary, the hip abductor and adductor muscles share many of the characteristics of other extensor muscles of the leg, particularly related to their timing of activation within the step cycle. Indeed, these muscles also act as extensors of the hip. However, there are several differences in the pattern of activation between the abductor and adductor muscles and the traditional extensors of the leg that are likely related to the complex requirements of these muscles in regulating motions in more than one plane. The distinct behavior of the abductor and adductor muscles was most pronounced when lateral stability was challenged. It will be important in future studies to identify the neural mechanisms involved in regulating the activity of these muscles, particularly given their multifunctional requirements and their role in maintaining lateral stability. With a better understanding of how the hip abductors and adductors are controlled during walking, we may begin to understand why lateral stability remains a limiting factor to functional locomotion after injury and disease.

Acknowledgments

The author thanks I. T. Gordon for assistance with analysis, R. Gramlich for excellent technical assistance, and Dr. K. G. Pearson for providing comments on a preliminary draft of the manuscript.

Grants

This work was supported by the Natural Sciences and Engineering Research Council (Canada).

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