Adaptive Control for Backward Quadrupedal Walking
V. Mutable Activation of Bifunctional Thigh Muscles

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SUMMARY AND CONCLUSIONS

1. In this, the fifth article in a series to assess changes in posture, hindlimb dynamics, and muscle synergies associated with backward (BWD) quadrupedal walking, we compared the recruitment of three biarticular muscles of the cat's anterior thigh (anterior sartorius, SAA; medial sartorius, SAM; rectus femoris, RF) for forward (FWD) and BWD treadmill walking. Electromyography (EMG) records from these muscles, along with those of two muscles (semitendinosus, ST; anterior biceps femoris, ABF) studied previously in this series, were synchronized with kinematic data digitized from high-speed cine film for unperturbed steps and steps in which a stumbling corrective reaction was elicited during swing.

2. During swing, the relative timing of EMG activity for the unifunctional SAM (hip and knee flexor) was similar for unper- turbed steps of FWD and BWD walking. The SAM was active before paw lift off and remained active during most of swing (75%) for both forms of walking, but there was a marked decrease in EMG amplitude after paw off during BWD and not FWD swing. In contrast, the relative timing of EMG activity for the SAA and RF, two bifunctional muscles (hip flexors, knee extensors), was different for FWD and BWD swing. During FWD swing, the SAA and the RF (to a lesser extent) were coactive with the SAM; however, during BWD swing, the SAA and RF were active just before paw lift off and then inactive for the rest of swing until just before paw contact (see 3). Thus the swing-phase activity of the SAA and RF was markedly shorter for BWD than FWD swing.

3. Activity in SAA and RF was also different during FWD and BWD stance. The RF was consistently active from mid-to-late stance of FWD walking, and the SAA was also active during this period in some FWD steps. During the stance phase of BWD walking, however, the onset of activity in both muscles consistently shifted to early stance as both muscles became active just before paw contact (the El phase). Activity in RF consistently persisted through most of BWD stance. The duration of SAAa recruitment during BWD stance was more variable across cats with offsets ranging from mid- to late stance.

4. The activation patterns of the biarticular anterior thigh mus- cles during stumbling corrective reactions were, in general, similar to their different activations during FWD and BWD swing. The initial response to a mechanical stimulus applied to the dorsum of the paw that obstructed FWD swing was an augmentation of knee flexion and increased activity in ST and SAM. A mechanical stimulus applied to the ventral surface of the paw to obstruct BWD swing resulted in an initial conversion of hip extension to flexion and a slowing of knee flexion. There was a corresponding recruitment of SAA and RF and an enhancement of background activity in SAM.

5. The two forms of walking are differentiated by posture and limb dynamics, yet muscles participating in the basic flexor and extensor synergies are unchanged. Although central pattern gener ating (CPG) circuits determine the basic timing of these synergies, changes in the duration and waveform of muscle activity may depend on unique interactions among the CPG, supraspinal inputs that set posture and the animal's goal (to walk BWD or FWD) and motion-related feedback from the hindlimb. Output mutability to each muscle may depend on the balance of this tripartite input; muscles with immutable patterns may rely heavily on input from CPG circuits, whereas muscles with mutable patterns may rely more on form-specific proprioceptive and supraspinal inputs.

INTRODUCTION

Unlike different gaits of forward (FWD) locomotion, in which basic muscle and joint synergies are preserved, there is an uncoupling of hip motion relative to the knee and ankle during backward (BWD) walking; the hip extends rather than flexes during BWD swing and flexes rather than extends during BWD stance (Buford et al. 1990; Perell et al. 1993). Contrary to predictions (Grillner 1981; Miller and Scott 1980) that there would be an uncoupling of muscle syn- ergies, Buford and Smith (1990) found that basic flexor (swing-related) and extensor (stance-related) muscle syn- ergies are similar during the two forms of walking. Thus the success of BWD walking depends on major changes in the cat's posture and hindlimb dynamics rather than a reorga- nization of the locomotor central pattern generator (CPG). Of the eight hindlimb muscles tested in two previous studies in this series (Buford and Smith 1990; Perell et al. 1993), motor patterns of two ankle muscles [tibialis anterior (TA) and soleus (SOL)] were so similar that it was difficult to determine what direction the animal was walking by observ- ing the burst waveforms or relative timing of electromyo- graphic (EMG) activity. However, whereas the basic swing- and stance-related synergies were similar for FWD and BWD walking, there were significant form-related changes in burst duration and/or waveform in six muscles [medial and lateral gastrocnemius (MG and LG), vastus lateralis (VL), anterior biceps femoris (ABF), semitendinosus (ST), and illoposas (IP)]. In most cases, changes in muscle activation patterns were consistent with changes in the limb kinetics, specifically the muscle torque data for the hip, knee, and ankle associated with BWD walking (Perell et al. 1993) (also see DISCUSSION).

Although changes in the muscle torque data were gener- ally consistent with changes in the EMG motor patterns, there were some inconsistencies. This led us to ask whether form-specific changes in the activity of muscles not yet tested during BWD walking could account for two apparent
inconsistencies between muscle activity patterns and limb kinetics during the swing and stance phases of the two forms of walking. To this end, we assessed the motor patterns of three biarticular anterior thigh muscles, rectus femoris (RF) and the anterior (SAa) and medial (SAm) regions of the sartorius muscle. SAa and RF are bifunctional muscles that flex the hip and extend the knee, whereas SAm is a unifunctional muscle that flexes the hip and knee. These conventional classifications, based on each muscle's anatomic connection to the skeleton, are used in this report to be consistent with the current literature but without presumptions that these anatomic relationships predict or define muscle function, especially in nonsagittal actions (Pratt and Loeb 1991; Pratt et al. 1991; Smith and Zernicke 1987; Zajac and Gordon 1989).

Our first question focused on the swing phase of BWD walking. During BWD walking, hip flexion is initiated at the end of stance by activity in IP (Buford and Smith 1990), a multiarticular flexor of the hip and lumbar spine. In midswing, hip extension is initiated largely by a gravitational torque that is partially counterbalanced by a flexor muscle torque at the hip that continues through the end of swing (Petell et al. 1993). Because IP activity diminishes early in BWD swing (Buford and Smith 1990), it is unlikely to be the source of the flexor muscle torque at the hip in mid-late BWD swing; however, this torque component is a "residual term" in the inverse-dynamics formulation and includes forces arising from active muscle contraction and passive deformations of musculotendinous and periarthritis tissues (Smith and Zernicke 1987; Zernicke and Smith 1996). Passive-elastic forces alone could contribute to the torque component, making recruitment of hip flexor muscles (such as the IP) unnecessary. We predicted, however, that at least one of the cat's hip flexor muscles would be active because the range and rate of hip joint extension at the end of BWD swing appeared insufficient to supply the necessary force from tissue deformation alone.

Both SAa and SAm are active with IP from late stance through most, but not all, of FWD swing (Engberg and Lundberg 1969; Halbertsma 1983; Hoffer et al. 1987a,b; Pratt and Loeb 1991; Rasmussen et al. 1978). In contrast to its anatomic synergist, SAa, RF is typically recruited during FWD stance, although a second burst of activity sometimes is also present during the extensor (E1) phase of FWD swing (Engberg and Lundberg 1969; Hoffer et al. 1987b). Thus RF could contribute to the hip flexor muscle torque in late BWD swing if it were recruited similarly in both forms of walking, but SAa and/or SAm activity at the end of BWD swing would be evidence of a kinetics-related, form-specific activation.

Our second question focused on the stance phase of the two walking forms. Despite the fact that the hip extends throughout most of FWD stance and the knee extends through most of BWD stance, there is a point midway through stance when the muscle torque shifts from extensor to flexor at the hip for FWD stance and at the knee for BWD stance (Petell et al. 1993). The development of these flexor muscle torques appears necessary to counterbalance shifts in the orientation of the ground-reaction force vector at the hip and knee joints and serves to decelerate the rate at which the hip extends during FWD stance and the knee extends during BWD stance. Although the IP is inactive and could not contribute to the flexor muscle torque at the hip during FWD stance, the bifunctional muscles, RF and SAa, may because these muscles are also active during stance (Engberg and Lundberg 1969; Hoffer et al. 1987a,b; Pratt and Loeb 1991; Rasmussen et al. 1978). Likewise, during BWD stance, activity in bifunctional ankle extensor-knee flexors (LG and MG) contributes to the flexor muscle torque at the knee, with occasional assistance from ST. If SAm were active late in BWD stance, it could also contribute to the knee flexor torque.

The third question addressed in this study is whether there is a parallel reorganization of the stumbling corrective reactions in muscles that have mutable activation patterns during the two forms of walking. Specifically, the ST responds powerfully when FWD swing is obstructed (ventral paw tap) but is slightly suppressed when BWD swing is obstructed (Buford and Smith 1993). We wanted to determine whether the bifunctional antagonists of the ST, SAa and RF, also have opposite responses during perturbed FWD versus BWD step cycles. Preliminary results of this study have been published in abstract form (Pratt et al. 1992).

METHODS

Training and surgical procedures

Three young, laboratory-raised female cats (Felis domesticus, 2.2-3.6 kg) were trained as previously described (Buford and Smith 1993) to walk FWD and BWD on a motorized treadmill (30 x 80 cm) at slow walking speeds (0.4-0.6 m/s). Training sessions were conducted 5 days a week for 3-10 mo before surgery. Affection and food rewards were used to provide positive reinforcement for appropriate behavior.

Electrodes to record electromyograms (EMGs) were implanted surgically with the animal under pentobarbital sodium anesthesia (25 mg/kg iv) and following standard aseptic procedures. A long-acting antibiotic was given the day before surgery, and three preanesthetic agents were administered just before surgery: atropine sulfate (0.05 mg/kg sc), acepromazine maleate (0.2 mg/kg im), and ketamine hydrochloride (13 mg/kg im). A respiratory stimulant (Dopram 5 mg/kg im) was given at the end of surgery. Animals were placed in an incubator for the 1st 12-24 h of postsurgical recuperation and were placed in their regular cages once they had regained independent locomotion. An analgesic (Talwin, 1-3 mg/kg im) was given as needed during the week after surgery. Standard postoperative care also included the administration of oral antibiotics and cleansing of all incision sites with 10% povidone iodine (Betadine scrub solution). Treadmill training was resumed after the cat had recovered fully from surgery, typically within 3-5 days. A combination of bipolar intramuscular wire and epimysial patch electrodes was used in this study to record EMGs. Both types of electrodes were made with the use of a pair of 38-gauge, Teflon-insulated, multistranded wires (Cooner Wire, AS632). The patch electrodes and their implantation have been described in detail elsewhere (Hoffer 1990; Loeb and Gans 1986; Pratt and Loeb 1991). Briefly, one or two pairs of wires were sewn into custom-sized sections of Dacron-reinforced Silastic material (Dow Corning 501-1). In each electrode pair, the exposed contacts were 5 mm long with a 5-mm interelectrode separation. A two-electrode patch array on a 15 x 50-mm sheet of silastic was used to record from the anterior (SAa) and medial (SAm) margins of sartorius. The SAa and SAm electrode pairs were separated by 20-22 mm. The array was placed between the sartorius and the underlying quadriceps muscles with the exposed electrode contacts facing up against
the under surface of sartorius. The ends of the array were wrapped around to the ventral surface of sartorius and anchored to the fascial sheath. The array was oriented along the transverse axis of sartorius, and the electrode contacts were oriented with the dipole parallel to the muscle fibers. The patch electrode, which provides a dielectric shield of potential cross talk from adjacent muscles, has proven to be an excellent design for recording from SA and SAM (Hoffer et al. 1987a; Pratt and Loeb 1991), which is a very thin, sheetlike muscle (Pratt and Chanaud 1986).

Patch electrodes were used to record SA and SAM activity in cats 1–3, RF activity in cats 2 and 3, and ST activity in cat 3. Intramuscular wire electrodes were used to record EMGs from ABF in cat 1 and ST in cat 3. A 1-to 2-mm section of insulation was removed from each wire, and the bare areas were inserted deep in the muscle belly so that the exposed contacts were 3–5 mm apart and oriented parallel to the muscle fibers. Each wire was anchored by sutures to the fascia overlaying the muscle. All electrode wires and a common ground wire were passed subcutaneously to a multipin connector secured to the skull by screws and dental acrylic.

**Data collection and analyses**

During recording sessions a flexible, lightweight cable connected the EMG preamplifiers with the connector on the animal's head. The EMG signals were amplified (×1,000), high-pass filtered at 100 Hz, and recorded on FM tape (18.75 cm/s) along with an identifying binary code. The EMGs were digitized off line at 1,000 samples/s on an IBM PC/AT and stored on disk. A data analysis software program (Datapac II, Run Technologies) was used to full-wave rectify the data, generate event-triggered averages (see Fig. 3), and measure burst durations and burst onset and offset times. Criteria for burst detection were user-defined and included specification of threshold voltages and filters for minimum and maximum burst durations. Automated computer detections of burst onsets and offsets were visually inspected and edited manually, if necessary.

Before filming, black and white circular (5 mm diam) paper markers were glued on the shaved skin over the following hindlimb sites: iliac crest, greater trochanter, lateral malleolus, head of the fifth metatarsal, and the estimated axis of rotation for the knee joint. For each animal, bouts of 10–15 FWD and BWD walking steps were filmed (100 frames/s) within the same recording session with a motor-driven, pin-registered 16-mm camera (Photosonics 1PL). To synchronize the film and EMG records, a light placed in view of the camera was activated intermittently during recording, and a voltage pulse from the light was simultaneously recorded on FM tape. An overhead projection system (Vanguard M16C, Numonics 1220) interfaced with a microcomputer (IBM PC/AT) was used to digitize the rectangular coordinates of the circular markers in serial film frames. Noise was removed from the digitized joint coordinates with a fourth-order, zero-lag Butterworth filter, and the filtered values were used to calculate linear and angular displacements. Knee joint coordinates were calculated trigonometrically, as described previously (Buford et al. 1990). Paw off (PO) and paw contact (PC) times were recorded in terms of film frame numbers and then converted to time (ms) with the use of a regression equation generated from the synchronization of the light pulses on film and FM tape. A minimum of three consecutive step cycles of FWD and BWD walking were digitized for each animal.

**Stumbling corrective reactions**

Stumbling corrective reactions were elicited in cats 2 and 3 with the use of techniques described by Buford and Smith (1993). A force-sensitive rod was used to obstruct the motion of the hindlimb during swing for BWD and FWD walking. Stimuli were manually directed to contact the tarsal segment of midpaw, contacting the dorsum of the paw for FWD swing and the ventrum of the paw for BWD swing. Output from the force-sensitive rod was recorded on FM tape with EMG data to provide an analog record of stimulation. Reactions were videotaped for cataloging and filmed for kinematic analysis. The period of stimulus contact was determined from the film record. Only perturbed steps that were preceded and followed by three good, unperturbed steps were analyzed.

**RESULTS**

**Hindlimb kinematics for FWD and BWD walking**

Hindlimb joint actions and trunk postures for FWD and BWD treadmill walking were similar to those described by Buford et al. (1990). Because the focus of this paper is on the activity of thigh muscles, we focus specifically on hip and knee joint kinematics (but see Fig. 5 for ankle motions). Typical hip and knee joint actions during FWD and BWD walking for cat 1 are presented in Fig. 1. As previously described (Buford et al. 1990; Perrell et al. 1993), hip and knee joint motions during swing were appreciably different for FWD and BWD walking with regard to range and duration. During FWD walking (Fig. 1A), both the knee and hip flexed from the onset of swing, and the knee reversed from flexion to extension (F-EI transition) midway through swing, whereas the hip continued to flex through most (95%) of swing. In contrast, during BWD walking (Fig. 1B), the knee flexed for most (80%) of swing, whereas the hip flexed for only the 1st 15% and then extended throughout the remainder of swing.

The principal hip joint motion was opposite during stance of FWD and BWD walking; the hip extended for most of FWD stance (Fig. 1A) and flexed for most of BWD stance (Fig. 1B). Immediately after paw contact during FWD walking, the knee joint flexed (yielded, E2 phase), but the yield was usually absent or minimal during BWD walking. For both walking forms, the knee joint extended during stance, but the range of extension was usually >50° for BWD walking (Fig. 1B) and typically <20° for FWD walking (Fig. 1A). Generally during FWD stance there was a midstance plateau during which the range of extension was minimal (Fig. 1A). For both walking forms, a transition from extension to flexion occurred just before the end of stance. Cat 2 had an atypical flexor motion at the knee during FWD stance (Fig. 2A), but this kinematic pattern did not represent an impaired gait.

**Comparison of FWD and BWD muscle activation patterns**

Data were recorded from SA and SAM in all cats (Figs. 1–3) and from RF in two cats (Figs. 2 and 3). Also, EMGs were recorded from the ABF in cat 1 (Fig. 1) and ST in cats 2 and 3 (Figs. 2 and 3). At comparable speeds, cycle durations were shorter for BWD (505 ± 69 ms, mean ± SD, n = 92) than for FWD (707 ± 67 ms, n = 74) walking (also see Buford et al. 1990). To facilitate comparisons of activation patterns across different cycle periods, burst onsets and offsets during FWD and BWD walking were expressed relative to normalized step cycles that started with paw off (0.0 = PO; 1.0 = the next PO). Normalized EMG averages for cat 3, triggered relative to paw off, are presented
in Fig. 3, and averages for all records are illustrated schematically in Fig. 4.

**SWING-RELATED EMG PATTERNS.** Typically the swing-related activity in SAa, SAM, and ST began during late FWD (0.92–0.95) and BWD (0.80–0.87) stance before paw off (Figs. 2 and 3); the onset of swing-related activity in SAa and SAM coincided with paw off in cat 1. This activity during swing, often referred to as “flexor-related” activity (Grillner 1981), coincided with the onset of hip and knee flexion that initiated swing for both walking forms (Figs. 1

**FIG. 1.** Electromyographic (EMG) activity (in mV) of 2 biarticular hip flexors [anterior sartorius (SAa) and medial sartorius (SAM)] and a uniaxial hip extensor [anterior biceps femoris (ABF)] related to kinematics of the hip (bold lines) and knee joints for 2 steps of forward (FWD; A) and backward (BWD; B) walking from cat 1. Each record starts with paw off (↑); downward arrows (↓) mark paw contact. In this and other figures the swing phase extends from paw off to paw contact; the stance phase extends from paw contact to the next paw off. Both FWD and BWD walking were recorded at the same treadmill speed (0.6 m/s).

**FIG. 2.** EMG activity (in mV) of 3 biarticular hip flexors [SAa, SAM, and rectus femoris (RF)] and a biarticular hip extensor [semitendinosus (ST)] related to kinematics of the hip (bold lines) and knee joints for 2 steps of FWD (A, 0.6 m/s) and BWD (B, 0.5 m/s) walking from cat 2. Upward arrows mark paw off (↑); downward arrows (↓) mark paw contact.
FIG. 3. Averaged EMG activity (in mV) of 3 biarticular hip flexors (SAA, SAM, and RF) and a biarticular hip extensor (ST) for a normalized step cycle of FWD (A, 0.6 m/s) and BWD (B, 0.5 m/s) walking from cat 3. EMG data were averaged around the time of paw off (upward arrow). Asterisks (*) in A and B indicate the approximate time of paw contact. For FWD walking (A), paw contact would normally occur near the end of the second ST burst, ~250 ms after paw off. For BWD walking (B), paw contact would normally occur near the end of the single, prolonged ST burst, ~200 ms after paw off. Six steps were included in the average for each direction. With the gains in B taken as 1, the gains in A are 1.25 for SAM, 1.5 for SAa, 2.25 for RF, and 2.75 for ST.

and 2). Although these swing-related bursts generally had similar onsets, they were differentiated by distinct waveforms and burst durations.

Both SAa and SAM were active throughout most (80-85%) of FWD swing while the hip flexed (Figs. 1-3A). They were usually recruited during late (0.9) stance (Figs. 2 and 3A), but in cat 1 they were recruited just after paw off (Fig. 1A). During BWD walking, in contrast, the two regions of sartorius were recruited differently; SAM was active throughout most (70%) of swing, whereas SAa activity ceased just before (Figs. 1 and 3B) or after (Fig. 2B) paw off. In fact, the pattern of SAM recruitment during BWD swing more closely resembled ST activity than SAa activity (Figs. 2 and 3B), and the pattern of SAa activity more closely resembled IP recruitment than SAM activity. Marked changes in the waveform of SAM activity were evident,
however, during the two forms of walking; the amplitude of SAm activity was greater and tended to progressively increase during FWD swing but was lower and tended to steadily decrease throughout BWD swing. The decreased recruitment level of SAm during BWD swing is especially evident in Figs. 1 and 3 in which the EMG records for SAm for both directions of walking are presented at the same gains.

The onset of swing-related activity tended to occur later in RF than in SAA and SAm, either near (Fig. 3A) or after (Fig. 2A) paw off. This is consistent with Engberg and Lundberg’s (1969) observation that RF, unlike other muscles that flex the hip, typically was not active before paw off during FWD walking. During BWD walking, however, the onset of RF activity typically coincided with the onset of activity in SAA and SAm. The RF and SAA bursts had similar durations and ended around paw off at the start of BWD swing (Figs. 2B and 3B).

During FWD walking, a brief swing-related burst in ST began in late stance (0.97 ± 0.04) along with the onset of hip and knee flexion and the onset of activity in SAm and SAA. The swing-related burst in ST was relatively brief and ended early (0.04 ± 0.04) in FWD swing (Figs. 2A and 3A). In contrast, during BWD swing ST displayed a single prolonged burst that had an early onset (0.8 ± 0.17) and lasted most of the swing phase (Figs. 2B and 4B).

STANCE-RELATED EMG PATTERNS. Although the unifunctional SAm exhibited negligible stance-related activity during FWD or BWD stance, the two bifunctional muscles of the anterior thigh (SAA and RF) had distinct bursts during stance, often referred to as “extensor-related” activity (Grillner 1981). At the relatively slow FWD walking speeds of 0.5–0.6 m/s analyzed here, SAA exhibited variable amounts (Fig. 4A, shaded bar) of low-level activity during late (0.68–0.84) stance (Figs. 1A-3A). For example, SAA in cat 2 was not recruited during stance in the first step of the record but was in the second (Fig. 2A). This variability is consistent with previous reports that the stance-phase activity in SAA during FWD walking is speed dependent (Engberg and Lundberg 1969; Pratt and Loeb 1991). In contrast to SAA, RF was consistently recruited from midstance (0.47) to late (0.90) stance in both cat 2 (Fig. 2A) and cat 3 (Fig. 3A). The stance-related burst in RF had an earlier onset (0.47 ± 0.23) than SAA’s (0.68 ± 0.02) and was longer in duration (0.52 ± 0.23 vs. 0.16 ± 0.04).

Although SAA and RF were also active during BWD stance, there was a significant shift in the timing of their stance-related activity. The SAA burst that occurred around paw contact during BWD walking is best illustrated in the averaged records in Fig. 3B. The onset of stance-related activity in SAA and RF occurred much earlier during BWD than FWD walking, preceding paw contact (0.35 ± 0.06) and the reversal from hip extension to flexion (Figs. 1–3B). Activity in SAA ended in early BWD stance (0.47 ± 0.17), whereas activity in RF continued throughout the stance phase along with knee extension. The duration of RF’s stance-related activity was greater during BWD walking (0.75 ± 0.07) than FWD walking (0.52 ± 0.23), as shown in Fig. 4.

ST had a very brief burst that began in late FWD swing (0.27 ± 0.04) and ended just before paw contact (0.31 ± 0.05), as shown in Figs. 2A and 3A. Although ST usually was not active during early and midstance of FWD or BWD walking (Figs. 2 and 3), on occasion, the ST exhibited low-level activity from about midstance to the onset of the large-amplitude, swing-related ST burst during BWD walking (Fig. 2B).

The uniarticular hip extensor, ABF, was active during both FWD (Fig. 1A) and BWD (Fig. 1B) stance, as described previously by Buford and Smith (1990). Typically, the onset of ABF activity occurred just after paw contact during FWD walking (Fig. 4A) and before paw contact during BWD walking (Fig. 4B). However, in some cats, including cat 1, the onset of ABF activity during FWD walking occurred near midstance. During BWD walking, the ABF burst had an earlier onset and longer duration than during FWD walking, but its basic pattern of activation was similar in the two forms of walking.

Participation in stumbling corrective reactions

Mechanical stimuli were applied with a force-sensitive rod to obstruct the swing phase of walking in both directions. Dozens of stumbling corrective reactions were elicited in cats 2 and 3 as they walked in each direction. Reactions during FWD walking were consistent, but as described by Buford and Smith (1993), stumbling corrective reactions during BWD walking did not always result in successful negotiations of the obstacle. The data illustrated in Fig. 5 are examples of stumbling corrective reactions that succeeded in overcoming the obstacle.

After a mechanical stimulus to the dorsum of the paw obstructed FWD swing (Fig. 5B), there was a powerful ST response as hip flexion was retarded and knee flexion was augmented. The ST was normally inactive during this phase of forward swing (Fig. 5A). Often SAm responded with ST, and this is illustrated in Fig. 5B by an augmented EMG, because SAm was usually active during this phase of forward swing. Activity in SAA and RF appeared to be unaffected at the stimulus onset, but their activity was briefly extinguished as knee flexion continued to draw the limb away from the stimulus. SAm activity also decreased at this time. As the stimulus-evoked knee flexion neared its peak, the ST response ceased and activity resumed in SAm and especially in SAA and RF as the hip flexed and the knee extended to prepare for paw contact.

After the ventral stimulus obstructed BWD swing (Fig. 5D), there were brief responses in SAA and RF as the hip reversed from extension to flexion, and there was a pause in knee flexion. These two muscles were normally inactive during this phase of BWD swing (Fig. 5C). The stimulus-induced activity was associated with the retardation of the rearward progress of the swinging limb, as hip extension and knee flexion were slowed. ST and SAm also responded at the stimulus onset; this is illustrated by an augmentation of the control EMG, because these muscles are normally active during midswing of BWD walking. During the stimulus application, there was a pause in ST and SAm activity followed by another burst; this pause occurred at a time when both muscles were usually active (Fig. 5C), and it appeared to be a consistent response to the stimulus. After the response in SAA and RF, a strong response in ST and SAm followed as knee flexion and hip extension resumed to raise the paw over the obstacle and prepare for paw contact.
DISCUSSION

In the present study, the unifunctional flexor, SAm, and the unifunctional extensor, ABF, had activation patterns during FWD and BWD swing and stance, respectively, that were consistent with classic flexor and extensor synergies. Both unifunctional muscles exhibited one burst per step cycle, the timing of this burst was synchronized with the activity of other flexor or extensor muscles, and the pattern of activation was similar for both forms of walking. Although the timing of the SAm burst was similar for FWD and BWD walking, the EMG waveform was not; specifically, the amplitude of swing-phase activity tended to progressively increase during FWD walking and decrease during BWD walking. Changes in the EMG waveform have also been noted for other unifunctional muscles; for example, the duration of VL activity is similar, but its waveform increases in amplitude during BWD stance and decreases during FWD stance (see Fig. 2 of Buford and Smith 1990).

In contrast to the stereotypic timing of unifunctional muscle activity, motor patterns of the three bifunctional muscles (SAa, RF, and ST) were independent of basic flexor and extensor muscles synergies; each typically displayed more than one burst per step cycle, and the timing of their motor patterns was different for the two forms of walking. These results suggest that the timing of bifunctional muscle activity during locomotion is more mutable than that of unifunctional muscles. Evidence from previous studies of ST activity during different speeds and gaits of FWD locomotion, reviewed in Smith et al. (1993), reveals a close correspondence be-
between the mutability of ST activation and task-specific intersegmental dynamics. For example, several studies have shown that the amplitude of the ST burst that occurs just before paw contact increases with locomotion speed during FWD walking and trotting (Chanaud et al. 1991; Engberg and Lundberg 1969; English and Weeks 1987; Smith et al. 1993). Wisleder et al. (1990) found that the speed-related increase in the amplitude of this stance-related ST burst is consistent with the need to decelerate the limb before paw contact by counterbalancing motion-dependent inertial torques that act to flex the hip and extend the knee. Furthermore, recent evidence from Perell et al. (1993) indicates that the ST burst associated with paw off also is related to limb dynamics and not invariably part of the flexor synergy. The amplitude of the swing-related (before paw off) ST burst is usually (but see Fig. 2) larger than the stance-related (before paw contact) burst during walking (see Figs. 3 and 5) and trotting (Chanaud et al. 1991; Engberg and Lundberg 1969; Smith et al. 1993), but the reverse is true during the gallop. The swing-related ST burst, in fact, can be absent during fast galloping (Smith et al. 1993). The shift in the relative amplitudes of the two ST bursts is related to the hindlimb kinetics associated with the different locomotor gaits; inertial torques, unique to the gallop, are primarily responsible for sustaining knee flexion, thereby reducing the need for a knee flexor muscle torque (Smith et al. 1993).

Is the mutability of bifunctional anterior thigh muscle activity during FWD and BWD walking also related to the different hindlimb dynamics associated with the two forms of walking? As outlined in the introduction, two specific questions were posed to address this issue. To answer these questions, mutable muscle activation patterns will be related to results of kinetic analyses of FWD and BWD walking that were presented in the preceding paper in this series (Perell et al. 1993). To facilitate this discussion, schematic summaries of hip and knee muscle torque data from Perell et al. (1993), joint motion, and averaged muscle activation patterns from this and a previous study (Buford and Smith 1990) are presented in normalized form in Fig. 4.

**Relationship between mutable activation of bifunctional anterior thigh muscles and limb dynamics**

The development and maintenance of a flexor muscle torque at the hip during most of BWD swing is one of the unexplained findings from Perell et al. (1993) mentioned in the introduction. Activity of IP that continues for just the 1st 20% of the swing phase (Buford and Smith 1990) does not account for this torque component. However, the combined activation of the biarticular anterior thigh muscles does: SAm is active for the 1st 67% of BWD swing, and then SAa and RF are both recruited for the last 23% of BWD swing. The transition between activity in the knee flexor (SAm) and the knee extensors (SAa and RF) coincides with the reversal of knee flexion to extension (67% of BWD swing). The sequential activation throughout BWD swing of hip flexors with opposing actions at the knee, appropriately timed to effectively contribute to forces at the knee, results in a continued flexor muscle torque at the hip. The recruitment of SAa and RF at the end of BWD swing is particularly noteworthy because the onset of SAa and RF stance phase activity was shifted from the second half of stance during FWD walking to just before paw contact during BWD walking.

To slow the limb before paw contact at the end of swing for both directions, there is a need to decelerate inertial forces caused by motion-dependent torques. At the end of FWD swing, there is a need to decelerate hip flexion and knee extension. As discussed earlier, there is evidence that the individualistic activation of ST at the end of FWD stance coincides with hip extensor and knee flexor muscle torques that counterbalance inertial forces and decelerate the limb before paw contact (Wisleder et al. 1990). Only the bifunctional ST has a specialized recruitment at the end of FWD swing to decelerate hip and knee motion; neither of the potential unifunctional contributors, ABF or SAm, is active in late FWD swing (Fig. 4B).

In contrast to FWD swing, there is a need to decelerate hip extension and knee flexion before paw contact during BWD swing (Perell et al. 1993). Activity of uniaxial knee extensors (such as the VL) during the El-phase of BWD swing (Buford and Smith 1990) appears to contribute to the extensor muscle torque at the knee. In addition, the recruitment of SAa and RF late in BWD swing allows these bifunctional muscles to contribute both to the knee extensor muscle torque and the hip flexor muscle torque at the end of BWD swing, as well as the initial loading response at the onset of BWD stance. There were differences, however, in the stance-related activity in SAa and RF. Activity in RF continued from before paw contact through the end of BWD stance; in contrast, the SAa stance-related burst ended in early stance and did not appear in every BWD step cycle (Fig. 4B, shaded bar). The brief, paw contact-related burst in SAa during BWD walking resembled the paw contact-related burst observed in ST during FWD walking. These results suggest that the timing of the onset of stance-related activity in the bifunctional antagonists, ST versus SAa and RF, is adjusted to slow and reverse limb motion in preparation for paw contact in BWD and FWD walking, respectively.

Our second question addressed the possible sources of the flexor muscle torques present during the second half of FWD and BWD stance at the hip and knee, respectively (Perell et al. 1993). The transition from an extensor to a flexor hip muscle torque occurs at midstance during FWD walking, but the unifunctional hip extensor, ABF, remains active. At the slow walking speeds used in this study, RF was consistently active, and SAa was occasionally active in mid-late FWD stance, so these biarticular muscles could have contributed to the hip flexor muscle torque at the end of FWD stance.

During BWD stance the transition from an extensor to a flexor muscle torque at the knee occurs as the ground-reaction force vector passes from a posterior to an anterior position relative to the knee at midstance, but the unifunctional knee extensor, VL, remains active (Buford and Smith 1990). The initiation of the knee flexor muscle torque coincides with the steady increase in the amplitude of MG and LG activity (Perell et al. 1993), bifunctional muscles with knee flexion and ankle extension actions. In some steps (Fig. 2B) we have also observed low-level activity in ST in the latter half of BWD stance, reminiscent of that observed by Barbeau
et al. (1987) during BWD treadmill walking in spinal cats. The unifunctional flexor, SAm, is not recruited in midstance during BWD walking and cannot contribute to the initiation and maintenance of the 1st 60% of the knee flexor muscle torque. SAm was recruited before paw off and could have combined with ST to contribute to the knee flexor muscle torque in late BWD stance.

Again, differential recruitment of the two bifunctional (SAA and RF) anterior thigh muscles, not the unifunctional (SAm) muscle, was consistent with the stance-phase kinetics at the hip during FWD walking. Likewise, at the knee, differential recruitment of bifunctional muscles (ST and MG) (Buford and Smith 1990), not the unifunctional muscle (SAm), was consistent with the knee joint kinetics for BWD stance. These data are consistent with the proposal that bifunctional muscle activity is more closely matched to limb dynamics than is activity in unifunctional muscles.

Parallel reorganization during stumbling corrective reactions in bifunctional thigh muscles

To overcome dorsal obstacles during FWD walking, the limb was drawn back (avoidance), lifted over (upswing), and advanced beyond the obstacle into position for the ensuing stance phase (recovery). A parallel strategy was used for BWD walking, although the avoidance, upswing, and recovery phases were not as distinct. Responses in ST are dramatic during the avoidance and upswing phases during FWD stumbling corrective reactions (Buford and Smith 1993; Forssberg 1979; Wand et al. 1980). We had postulated that SAA and/or RF could serve similar roles, and as expected, SAA and RF were recruited after the ventral obstacle during BWD swing. During the recovery, ST was reengaged after a slight suppression of activity during the stumbling corrective reaction for BWD swing, but SAA and RF were recruited for the recovery during FWD swing. In these ways the responses were opposite for BWD and FWD walking.

Looking at the synergistic relationships among the biarticular muscles, however, a slightly different picture emerges. For stumbling corrective reactions during FWD walking, the patterns in SAm, SAA, and RF are grossly similar, with ST standing out as different. For BWD walking, in contrast, RF stands out alone, whereas ST, SAm, and SAA look basically similar. Thus not only were the responses different for stumbling corrective reactions during BWD and FWD walking, the alliances among the biarticular muscles were reorganized, as well. Once again, this demonstrates the mutability of the synergies.

Implications for neural control

On the basis of the observation that the timing of EMG activity for unifunctional muscles was similar during FWD and BWD walking, Buford and Smith (1990) proposed that the same locomotor CPG organizes a basic flexor-extensor synergy that is common for both walking forms. While the timing and EMG waveform may be similar for some muscles, such as the SOL and TA, the EMG waveform of other unifunctional muscles is form dependent and consistent with the limb dynamics. The motor patterns of the SAm fit this scheme because timing was similar for both walking forms but the EMG waveform was not. Mechanisms responsible for determining these waveform characteristics are not clear, but motion-dependent feedback may be important.

The CPG output to bifunctional muscles has never been well defined, and our EMG data for the SAA and RF, as well as other muscles (ST, LG/MG, and IP), suggest that the timing of EMG activity, as well as the waveforms, are mutable and consistent with changes in the limb dynamics. The change in timing of the IP at the onset of swing, for example, is similar to that of the SAA; neither the IP nor the SAA burst continues after paw off, and this is consistent with the lack of a hip flexor muscle torque at the onset of BWD swing (Fig. 4). Burst durations of the LG and MG (knee flexor; ankle extensor) increase during BWD stance, and the increased activity at the end of stance coincides with a need for a knee flexor muscle torque to counterbalance knee extensor inertial forces (Fig. 4). Given that changes in the timing and EMG waveforms are closely associated with changes in the limb dynamics, it is unlikely that CPG inputs alone can account for the altered activity patterns observed in these bifunctional muscles.

The best indication of inputs from the CPG to SAA and RF motoneurons comes from experimental preparations in which locomotion is induced without the administration of drugs, which can bias the pattern of locomotor activity (Dubuc et al. 1986; Harris-Warrick 1988; Pearson and Rossignol 1991), and without phasic or tonic afferent inputs from the limb. Phasic (but not tonic) afferent inputs from the limb are eliminated in paralyzed animals that can be induced to locomote (fictive locomotion). Extensor activity has never been observed in SAA motoneurons during fictive locomotion that either occurred spontaneously in decorticate cats (Perret 1983; Perret and Cabelguen 1980) or was evoked in decerebrate cats by stimulation of the mesencephalic locomotor region (C. Pratt and L. Jordan, unpublished results). Extensor-related activity could be evoked in SAA during fictive locomotion in chronic spinal cats with either clonidine administration or perineal stimulation (Pearson and Rossignol 1991). In contrast to SAA, normal-like flexor and extensor bursts were seen in RF during spontaneous locomotion in deafferented (Perret 1983) or paralyzed (Perret 1983; Perret and Cabelguen 1980) decorticate cats.

These results suggest that the isolated locomotor CPG distributes flexor and extensor commands to RF and only a flexor command to SAA. The notion that the swing-related activity in SAA is primarily produced by CPG inputs and the stance-related burst is primarily produced by motion dependent feedback is consistent with the demonstration that different task groups of SAA motor units are recruited during the swing and stance phases of FWD locomotion (Hoffer et al. 1987a; Hoffer et al. 1981) when SAA actively shortens and lengthens, respectively (Hoffer et al. 1987a; Pratt and Loeb 1991). The evidence from fictive locomotion studies that different neural inputs may be primarily responsible for the activity in RF and SAA during stance is consistent with our observations that, although SAA and RF were both active during FWD and BWD stance, there were distinct differences in their activation patterns. Indeed, RF activity during both FWD and BWD stance was more consistent with participation in a basic extensor synergy than was SAA activity. In contrast, stance-related SAA activity was more similar to the
individualistic stance-related bursts seen in ST during FWD walking and appeared independent of any classic synergy.

Even though central circuits appear to generate an extensor command to RF, the shift in timing of the RF (and SAA) stance-related burst during BWD walking, in conjunction with altered limb dynamics, suggests that the precise timing cues for these and other mutable bursts are provided by motion-dependent afferent inputs. The characteristic activation patterns observed in uni- and bifunctional muscles can be explained by a single tripartite neural control model consisting of inputs to motoneurons from three sources: a locomotor CPG that organizes basic flexor and extensor synergies; posture- and goal-dependent inputs from supraspinal centers; and motion-related feedback. Within this model, all motoneurons receive inputs from all three sources, but the relative strengths and complexity of these inputs may reflect the mechanical complexity of the muscle units. Thus unifunctional muscles may receive strong flexor or extensor inputs from CPG modules (Jordan 1991) or “generators” (Grillner 1981) and segmental afferents, whereas bifunctional muscles may receive complex mixtures of flexor- and extensor-related inputs from central and peripheral sources (reviewed in Van Ingen Schenau et al. 1994).

This proposal is consistent with recent evidence that segmental afferent systems typically have multiple parallel excitatory and inhibitory pathways connecting them to hindlimb motoneurons (Baldissera et al. 1981; Hagbarth 1952; Jankowska 1992; McCrea 1986; Pearson and Collins 1993; Pratt 1995). However, unifunctional and bifunctional muscles appear to differ in their responsiveness to these complex inputs. For example, a recent study of low-threshold cutaneous reflexes in thigh muscles during FWD walking showed that there was a close correspondence between the complexity of locomotor activation patterns and responses to cutaneous inputs. Unifunctional muscles were consistently recruited as either flexors or extensors, but bifunctional muscles that produced multiple bursts of activity during a step cycle exhibited complex mixtures of excitatory and inhibitory reflex responses (Pratt 1992; Pratt et al. 1991). The similar close correspondence between locomotor activation patterns and stumbling corrective reactions observed in the present study indicates that tonic feedback and/or supraspinal influences related to postural differences typical of FWD and BWD walking (Buford et al. 1990) may exert parallel biomechanical and afferent influences on regional activation of the activity in the hindlimb of the cat during unrestrained locomotion. Acta Physiol. Scand. 75: 614–630, 1969.

Moreover, the relative strength of peripheral inputs may be stronger than central inputs to motoneurons innervating bifunctional muscle units, which may also contribute to their mutability and relative independence of classic synergies. The relative timing of unifunctional muscle activation may be similar for both FWD and BWD walking because their motoneurons are primarily driven by either flexor- or extensor-related inputs from central and peripheral sources. However, the EMG waveforms of unifunctional muscles may be mutable and different for FWD and BWD walking; thus form-specific descending and afferent inputs can modify muscle activity within a basic synergy, as observed for the SAm (shown here) and other unifunctional muscles, such as the VL (Buford and Smith 1990).

The fact that the activation patterns of most (9 of 11) muscles tested thus far during FWD and BWD walking exhibit form-specific modifications indicates that customizing individual muscle activation patterns to meet the mechanical demands of the task is the rule rather than the exception. Although the activity of functionally complex muscles may exhibit more mutability than uniaxial or unifunctional muscles within a task, comparative studies of varied multitasked subjects with different mechanical challenges have revealed dramatic, task-related mutability in muscle synergies and activation patterns (Pratt and Loeb 1991; Pratt et al. 1991; Smith et al. 1985), even in uniaxial muscles (Smith et al. 1985). Additional studies of this kind are needed to fully appreciate the mutability of muscle activation and its relationship to task-specific dynamics.

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