Humeral retractor EMG during quadrupedal walking in primates

Susan G. Larson* and Jack T. Stern, Jr

Department of Anatomical Sciences, Stony Brook University Medical Center, Stony Brook, NY 11794-8081, USA

*Author for correspondence (e-mail: susan.larson@stonybrook.edu)

Summary

The mammalian humeral retractors latissimus dorsi, teres major and caudal parts of the pectoral muscles are commonly thought to contribute to forward impulse during quadrupedal locomotion by pulling the body over the supporting forelimb. While most electromyographic studies on recruitment patterns for these muscles tend to support this functional interpretation, data on muscle use in chimpanzees and vervet monkeys have suggested that the humeral retractors of nonhuman primates are largely inactive during the support phase of quadrupedal locomotion. In the chimpanzee and vervet monkey, in contrast to what has been documented for other mammals, the contributions of latissimus dorsi, caudal pectoralis major, and teres major during quadrupedal locomotion are restricted to slowing down the swinging forelimb in preparation for hand touchdown and/or retracting the humerus to help lift the hand off the substrate at the initiation of swing phase. Based on these results, it has been proposed that unique patterns of shoulder muscle recruitment are among a set of characteristics that distinguish the form of quadrupedalism displayed by nonhuman primates from that of other nonprimate mammals. However, two primate taxa is a limited sample upon which to base such far-reaching conclusions. Here we report on the activity patterns for the humeral retractors during quadrupedal walking in an additional eight species of nonhuman primates. There is some variability in the activity patterns for latissimus dorsi, caudal pectoralis major and teres major, both between and within species, but in general the results confirm that the humeral retractors of primate quadrupeds do not contribute to forward impulse by pulling the body over the supporting forelimb.

Key words: latissimus dorsi, pectoralis major, teres major, electromyography, shoulder, locomotion.

Introduction

Mammalian morphologists typically group the humeral retractors latissimus dorsi, teres major, and caudal parts of the pectoral muscles into a similar functional unit (Davis, 1949; Smith and Savage, 1956; Howell, 1965). These muscles are sometimes referred to collectively as the 'propulsive muscles of the shoulder' (e.g. Ashton and Oxnard, 1963), and are thought to contribute to forward impulse during quadrupedal locomotion by pulling the body over the supporting forelimb (e.g. Davis, 1949; Smith and Savage, 1956). By and large, electromyographic (EMG) studies have supported this conclusion. For example, the latissimus dorsi and major members of the pectoral group are reported to be active during support phase of quadrupedal locomotion in the cat (English, 1978a; English, 1978b), dog (Goslow et al., 1981; Nomura et al., 1966; Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974) and opossum (Jenkins and Weijs, 1979). Teres major is similarly active during support phase in the cat (English, 1978a) and dog (Nomura et al., 1966; Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974). In the opossum, however, the teres major acts only at the initiation of swing phase to retract the humerus as the forelimb is lifted off the ground (Jenkins and Weijs, 1979).

In contrast to the EMG results summarized above, we reported (Larson and Stern, 1987) that the latissimus dorsi and teres major are inactive during the support phase of knuckle-walking in the chimpanzee *Pan troglodytes*. In addition, although the caudal portion of the sternocostal pectoralis major is on occasion active during support phase, we concluded that it performs a function unrelated to propulsion, and suggested that this absence of muscular propulsive effort at the shoulder in chimpanzees is related to a shift in responsibility for body support and propulsion to the hindlimbs as part of a general mechanism for reducing stress on the forelimb during quadrupedal postures and locomotion. We also argued that the need for such stress reduction is due to the fact that even though chimpanzees are frequently quadrupedal, they must at the same time maintain the ability to climb and use their forelimb in overhead supporting and suspensory postures that require enhanced shoulder mobility. The chimpanzee's distinctive pattern of inactive humeral retractors during knuckle-walking is therefore a reflection of its unique compromise morphology.

As a test of this proposal, we analyzed the pattern of recruitment of the humeral retractors in the vervet monkey *Chlorocebus aethiops* (Larson and Stern, 1989), a primate whose primary locomotor mode is quadrupedal walking and running (Rose, 1979). Since the shoulder morphology of the vervet is less derived than that of the chimpanzee, and in many ways more closely resembles that of nonprimate mammalian quadrupeds (see Fig. 1), we predicted that the EMG activity of its humeral retractors would also be more similar to what has been reported for cats, dogs, and opossums (Larson and Stern, 1989). Contrary to this prediction, however, the pattern of humeral retractor muscle use in the vervet was more like that of the morphologically dissimilar chimpanzee than what has been reported for nonprimate mammalian quadrupeds.

One of the possible explanations we offered for similarities in patterns of muscle use among dissimilar species of primates, which also differ from those of other nonprimate mammals, is that neural control mechanisms have been altered in the course of primate evolution (Larson and Stern, 1989). This suggestion,
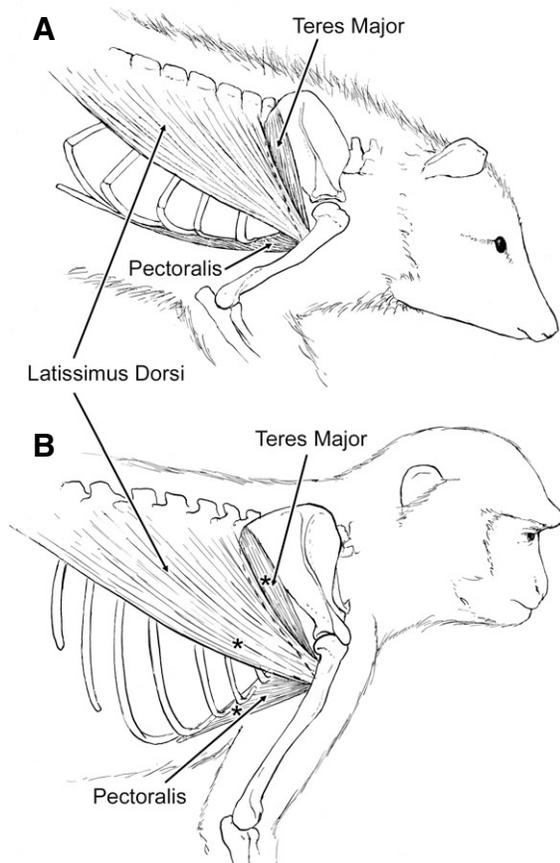

Fig. 1. Schematic drawing of pectoralis, latissimus dorsi, and teres major in a primate (B, vervet monkey) compared to a nonprimate mammal (A, opossum). Although primates tend to have relatively longer limbs and a less crouched limb posture than other mammals of their size, the configuration of their humeral retractors does not differ substantially from that of other mammals. The asterisks indicate approximate positions of EMG electrodes. Opossum redrawn from Jenkins and Weijs (Jenkins and Weijs, 1979).

first enunciated by Vilensky and Larson (Vilensky and Larson, 1989), proposed that use of the forelimb for manipulation and exploration of the environment led to evolutionary changes toward more direct cortical control of forelimb movements. These changes, in turn, may have been associated with alterations of spinal circuitry overriding or eliminating inherited pattern generators governing muscle recruitment patterns, as well as other locomotor characteristics such as gait selection that have also been shown to be unique in primate quadrupeds (Prost, 1965; Prost, 1969; Hildebrand, 1967; Rollinson and Martin, 1981; Vilensky, 1987; Vilensky, 1989; Larson, 1998).

The observation of similarities in patterns of muscle use among nonhuman primates with different morphologies (Larson and Stern, 1989) echoes a proposal made by Goslow and coworkers known as the 'neuromuscular conservation hypothesis' (Goslow et al., 1989; Peters and Goslow, 1983; Jenkins and Goslow, 1983). Noting the similarity in EMG activity of homologous limb muscles in different animals during quadrupedal walking, Goslow et al. proposed that during the evolution of tetrapods, motor patterns of homologous muscles have been maintained, and a primitive organization of neural control components has persisted in derived groups despite differences in morphology (Goslow et al., 1989). In other words, evolutionary modification of limb function is brought about mainly through alteration of musculoskeletal components in such a way that a conserved sequence of muscle recruitment will continue to serve the new function. The point was illustrated by contrasting the patterns of shoulder muscle recruitment in a lizard and an opossum, two rather dissimilar vertebrates (Goslow et al., 1989). Despite differences in limb orientation and shoulder structure, four major muscle groups showed similar patterns of activity during walking, including latissimus dorsi and pectoralis, which were active primarily during support phase, as has been reported for other quadrupeds.

The fact that neither the chimpanzee nor the vervet monkey share this pattern of muscle use, but nonetheless display similar recruitment patterns to each other despite their different shoulder morphologies, suggests that perhaps neural control mechanisms shifted at some point during the course of primate evolution, and have been conserved thereafter (Vilensky and Larson, 1989; Larson and Stern, 1989). There might be a uniquely primate pattern of neuromuscular conservation, a proposition that could have profound significance for understanding primate origins as well as our own neurobiology.

EMG data for two primate species is not a sufficient basis for such far-reaching conclusions, however. We therefore have attempted to expand this database by documenting humeral retractor muscle activity patterns across the diversity of primate taxa available for laboratory study. Here we report on the recruitment of latissimus dorsi, caudal sternocostal pectoralis major, and teres major during quadrupedal walking in four additional anthropoid primate species (patas monkey, spider monkey, howler monkey, and woolly monkey), and four prosimian species (ring-tail lemur, brown lemur, red-belly lemur, and red-ruffed lemur).

Materials and methods

Subjects

The subjects of this study were two female and one male ring-tail lemur (*Lemur catta* Linnaeus 1758), two female and one male brown lemur (*Eulemur fulvus* E. Geoffroy Saint-Hilaire 1796), one female and one male red-belly lemur (*E. rubriventer* I. Geoffroy Saint-Hilaire 1850), three female red-ruffed lemurs (*Varecia variagata* Kerr 1792); three spider monkeys (one female *Ateles belzebuth* E. Geoffroy Saint-Hilaire 1806, one male *A. paniscus* Linnaeus 1758, and one male *A. geoffroyi* Kuhl 1820), one male and one female woolly monkey (*Lagothrix lagotricha* Humboldt 1812), one female howler monkey (*Alouatta seniculus* Linnaeus 1766), one female and two male vervet monkeys (*Chlorocebus aethiops* Linnaeus 1758), one male patas monkey (*Erythrocebus patas* Schreber 1775), and two male chimpanzees (*Pan troglodytes* Blumenbach 1775). The chimpanzees were subadults, but all other subjects were adults. Data for the prosimian species were collected specifically for this study. However, data for the anthropoid species had been collected several years ago in relation to previous studies and complete datasets were not always available. Information on numbers of individuals and step cycles for each muscle is presented in Table 1.

Electrode placement and electromyography

The technique of telemetered electromyography coupled with simultaneous video recording of the subject and EMG has been previously described (Stern et al., 1977; Stern et al., 1980; Susman and Stern, 1979; Larson and Stern, 1989) and will be only briefly summarized here. The procedures have been approved by the Institutional Animal Care and Use Committee of Stony Brook University and Duke University.

Bipolar fine-wire electrodes were inserted with a 25-gauge hypodermic needle into the muscles of choice while the animal was under gas anesthesia (the anesthetic used during the time of the recording sessions on the anthropoid primate species was halothane/nitrous oxide; more recently we have switched to using isoflurane). After withdrawal of the needle, leaving the bared and hooked tips of the 50 μm diameter electrode wires in position, proper placement of each electrode was verified by sending a small (200–500 μA) 50 Hz sinusoidal current through the wires and observing the contraction or movement produced.

Needles were inserted into teres major such that the electrode tips were approximately in the middle of the muscle belly. For sternocostal pectoralis major, electrodes were placed into the caudal edge of the muscle to sample those fibers most likely to be involved in humeral retraction. Similarly, electrodes were placed in the most ventral portion of latissimus dorsi, although in smaller subjects where the muscle is rather thin, electrodes were sometimes positioned subcutaneously in order to avoid passing through the muscle completely. In such cases, the electrode probably samples a somewhat broader muscle fiber distribution. A graphic portrayal of approximate electrode positions is shown in Fig. 1, as well as a depiction of the humeral retractor muscles in a quadrupedal monkey (Fig. 1B) compared to an opossum (Fig. 1A).

The free ends of the electrode wires were connected to a 112 g, 4-channel FM telemetry transmitter (Bio-Sentry Telemetry, Torrance, CA, USA) that was attached to a non-restrictive harness worn by the animal. For the data recording sessions on the prosimian subjects, the transmitted electromyographic signals were detected by a FM receiver that sent its demodulated EMG output to a National Instruments SCXI-1000 A-D converter, whose signal was acquired at a rate of 2700 Hz by LabVIEW version 5.0.1 (National Instruments, Austin, TX, USA) software installed on a 233 MHZ PII Gateway computer using Windows NT4. The LabVIEW software was configured to (i) display the EMG signals on a computer monitor that simulated a storage oscilloscope with a 2 s sweep speed, and (ii) store each 2 s of data in a computer file with a unique name. This name was also displayed on the computer monitor, as was a counter that was set to 0 when each

Table 1. *Numbers of subjects and step cycles included in the analysis*

Species	Number of step cycles (N)		
	Pectoralis major	Latissimus dorsi	Teres major
Eulemur fulvus[1]	125 (3)	100 (3)	70 (3)
Eulemur rubriventer[1]	75 (2)	50 (2)	50 (2)
Lemur catta[1]	75 (3)	100 (3)	100 (3)
Varecia variegata[1]	75 (3)	75 (3)	75 (3)
Ateles sp.[2]	54 (2)	60 (3)	41 (3)
Lagothrix lagotricha[2]	23 (1)	33 (2)	10 (1)
Alouatta seniculus[2]	17 (1)	25 (1)	–
Chlorocebus aethiops[3]	52 (3)	68 (3)	70 (3)
Erythrocebus patas[3]	21 (1)	16 (1)	16 (1)
Pan troglodytes[4]	44 (1)	54 (2)	45 (2)
Total	561 (20)	581 (23)	477 (21)

N, number of subjects.
[1]Prosimian species; [2]New World monkey; [3]Old World monkey; [4]Ape.

sweep began and reached 120 when the sweep ended (thereby giving an indication of time since the beginning of the sweep in intervals of 1/60 s). The complete image displayed on the computer monitor was converted to a standard analog video signal that was superimposed onto a video image of the subject taken by a color camera with an electronic high speed shutter, and the composite image was recorded onto SVHS videotape, thereby permiting direct correlation of the EMG signal with the subject's movements. Using a Panasonic AG-7350 Video Cassette Recorder (Secaucus, NJ, USA) that enables field-by-field playback of the videotape at 60 field s^{-1}, the file number and counter value corresponding to particular behavioral events were recorded in order to collect samples of step cycles.

Data for the anthropoid subjects were collected prior to the acquisition of the digital recording system. For those recording sessions, EMG signals detected by the FM receiver were sent to a 4-channel storage oscilloscope. An image of the oscilloscope screen, detected by a television camera aimed at it, was superimposed onto a video image of the subject's movements taken by a color camera with an electronic high-speed shutter. An electronic circuit eliminated the video picture of the subject for a period of 0.1 s at the end of each 2 s sweep of the oscilloscope beams; this left an unobscured record of the EMG activity that occurred during the sweep. All video information was continuously recorded on VHS videotape for later analysis.

Data analysis

Using field-by-field playback of the videotape record of the experiment, the precise relationship between muscle activity and subject movement can be determined. With the LabVIEW-based data acquisition system, as the videotape record of the experiment was played back, notation was made of the file number and counter-reading of significant locomotor events (e.g. touchdown, midsupport, lift-off, midswing). These were entered manually into a text file, which served as input to a Fortran program (written by J.T.S.) that read the LabVIEW-created EMG data files, identified which data points within such files corresponded to the events of interest, and calculated the Root Mean Square (RMS) (at intervals of 1.85 ms, using a time constant of 41.85 ms) of the EMG for all samples of support and swing phase. A second Fortran program read all the files containing the RMS information for any specified phase, equalized all samples with regard to duration, and calculated at 1% intervals a quartile distribution of the RMS. Activity occurring 75% or more of the time was considered to be the most consistent, while activity observed at least 50% of the time was viewed as frequent but more variable. In text figures, amplitude of muscle activity during locomotion is shown as the level of the RMS relative to the 'maximum burst' RMS value observed during the experiment. These maximum burst values were obtained by reviewing the videotape record of the experiment, and visually identifying those instances when the EMG amplitude appeared to be highest. Three or four examples of high-amplitude bursts were typically collected and quantified, and the average of the highest RMS value for each

was used as the maximum burst for scaling the RMS values observed during locomotion. Not surprisingly, vertical climbing and one-arm hoisting were among the behaviors most frequently eliciting maximum activity levels for the three humeral retractors. Since the focus of our analysis was mainly on presence or absence of muscle activity and on easily recognized major differences in amplitudes, no attempt was made to statistically compare RMS values across species or individuals.

For experiments conducted prior to the acquisition of LabVIEW-based data acquisition system, we noted the timing of activity and estimated relative amplitude by hand digitizing spike heights on paper copies of the EMG interference patterns. Once the interference patterns had been digitized, they were quantified in the same way as those files that had been digitally recorded. EMG activity patterns of latissimus dorsi, pectoralis major, and teres major for the chimpanzees and vervet monkeys have been previously published (Larson and Stern, 1987; Larson and Stern, 1989), but were redigitized so that they could be quantified in the manner described above. Chimpanzees typically overstride when walking quadrupedally, meaning that their foot touches down alongside or in front of their ipsilateral hand (Larson and Stern, 1987). When the foot lands medial to the hand (outside-hand), the shoulder of that forelimb is in a somewhat abducted posture; when the foot lands lateral to the hand (inside-hand), the shoulder of that forelimb is more adducted (see Larson and Stern, 1987). As this difference in shoulder posture is associated with some differences in muscle recruitment, step cycles for inside *vs* outside hands were quantified separately.

Behaviors analyzed

Following electrode insertion, the subject was brought into a large exercise enclosure and allowed to awaken in the presence of a human trainer. Recording would commence once the subject was judged to be fully awake and would typically last 20–30 min. The exercise enclosure is 7.3 m long×3.7 m wide×2.7 m (in one region 3.7 m) high. Installed within the enclosure was a tree trunk 5.3 m long×15 cm diameter, suspended horizontally from the ceiling roughly 1 m above the floor, which was cement covered with an epoxy resin. Only walking steps were analyzed, and attempts were made to include steps from the range of speeds the subjects voluntarily displayed. For any given bout of walking, several sequential steps between the first and last were collected; however, the first or last steps of a series were not digitized as they often included nonsterotypical motions such as turning or rising from a seated posture. For the prosimian and New World monkey subjects, step cycles were collected from walking along the suspended tree trunk. For the Old World monkeys and chimpanzees, step cycles were collected from walking bouts on the enclosure floor. For all subjects, movements were elicited by means of food rewards. At the end of each recording session the electrodes were removed and the subject was returned to its home cage. There were no adverse effects following any of the EMG recording sessions.

Results

Fig. 2 displays species' averages of the most consistent patterns of recruitment for the three humeral retractors during walking for all taxa included in the analysis. Also included in Fig. 2 is the phasic activity[†] of the humeral retractors during slow walking in the opossum *Didephis virginiana* as a representative of a nonprimate mammal [data from Jenkins and Weijs (Jenkins and Weijs, 1979)] for comparison. Activity levels in the primates are generally low to modest, reflecting a limited contribution by these three muscles to quadrupedal walking. In the opossum, the pectoralis is active through most of support phase (Jenkins and Weijs, 1979). Among primates, however, similar support phase activity is only observed in New World monkeys and chimpanzee outside-hand step cycles. Three of the four prosimian species also display a small burst of activity just after midsupport, but the most broadly shared pattern of recruitment for caudal pectoralis in primates is activity toward the end of swing phase that continues only until just after hand touchdown. For many of the primate species this is the only notable activity in this muscle.

As with pectoralis, latissimus dorsi in the opossum is active through much of support phase (Jenkins and Weijs, 1979). However, only the brown lemurs and the howler monkey exhibit support phase activity in latissimus dorsi, and in both cases it is at very low levels. In fact, activity levels for latissimus are low for all of the primate taxa. Some activity is observed toward the end of swing phase in all the anthropoids except the howler monkey, and in the chimpanzees and patas monkey it continues until after hand touchdown. However, none of the prosimian species exhibit this terminal swing-phase recruitment of latissimus. Ring-tail and red-ruffed lemurs both display small latissimus bursts at the support/swing transition, a pattern of recruitment that also occurs in patas and vervet monkeys in addition to their terminal swing latissimus activity. Red-belly lemurs display no notable recruitment of latissimus during walking.

Teres major activity at the support/swing transition was observed in the opossum (Jenkins and Weijs, 1979) [in contrast to the support phase recruitment that has been reported for dogs (Tokuriki, 1973a) and cats (English, 1978a; English, 1978b)], and a similar pattern of activity is seen in the Old World monkeys, spider monkeys, and the red-belly and red-ruffed lemurs. In chimpanzees, however, teres major was active at the end of swing phase. For the ring-tail and brown lemurs and the howler monkey, teres major was inactive during walking.

In sum, no primate appears to use either teres major or latissimus dorsi to help pull the trunk over the supporting forelimb during quadrupedal locomotion. Only caudal pectoralis major displays any noteworthy support phase

recruitment that could be interpreted as contributing to forward impulse; however, this activity is mainly confined to New World monkeys and chimpanzees when the hand is outside the overstriding hindlimb. Activity in teres major at the support/swing transition is similar to what has been reported for opossums (Jenkins and Weijs, 1979), but again this only occurs in some primate species. Indeed, comparisons across these ten primate species yield a somewhat mixed signal in regards to commonality of recruitment patterns. All share a pattern of circum-touchdown activity in caudal pectoralis major that was previously reported in chimpanzees (Larson and Stern, 1987) and vervet monkeys (Larson and Stern, 1989). However, this touchdown activity continues for much of support phase in the New World monkeys but not the Old World monkeys. Prosimians show yet a different pattern, with a small burst of activity in pectoralis about three quarters of the way into support phase. Latissimus dorsi and teres major are similar in the sense that they both can be active at the support/swing transition, the swing/support transition, or both, but similarities among species seem less clearly associated with taxonomic divisions. The swing/support activity in latissimus observed in Old World monkeys and chimpanzees is also seen in woolly monkeys, but not the other two New World monkey species. However, the Old World monkeys also display support/swing transition activity in both latissimus and teres major that is not seen in the chimpanzee, but is observed in some of the prosimians. It would appear, therefore, that additional factors beyond motor programming are influencing the patterns of muscle recruitment in these primate taxa. It should be emphasized that the activity data in Fig. 2 are only for the most consistent patterns of muscle recruitment averaged across all individuals of a species. To further explore the variability in patterns of muscle use in primates, Figs 3–9 present muscle recruitment profiles for each individual of each species.

Fig. 3 displays the muscle activity patterns for the brown and red-belly lemurs, both species of the genus *Eulemur*. While caudal pectoralis major is active at the swing/support transition in all individuals, this activity begins earlier in brown lemur #3 and the two red-belly lemurs. In addition, only brown lemur #3 and red-belly lemur #2 display a consistent pectoralis burst after midsupport. Such activity is only variably present in the other red-belly lemur, and one of the other two brown lemurs; the third brown lemur showed no notable post-midsupport activity in pectoralis. Two of the three brown lemurs display low-level support and swing activity in latissimus dorsi during walking, while the muscle is silent in the third brown lemur. The latissimus activity in the red-belly lemurs is so low as to be trivial. The three brown lemurs exhibit a similar tiny burst of teres major activity at the very beginning of support phase of walking, but the red-belly lemurs recruit teres major at the support/swing transition, one at an amplitude of about 20% of the maximum burst.

The ring-tail lemurs (Fig. 4) and red-ruffed lemurs (Fig. 5) also display individual variation in muscle recruitment patterns. While two of the three ring-tail lemurs exhibit caudal pectoralis

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[†]In their analysis of muscle recruitment in the opossum, Jenkins and Weijs (Jenkins and Weijs, 1979) did not quantify the EMG interference patterns, but instead used grades of 'none', 'slight' and 'strong', as well as timing and consistency to compare EMG across individuals. The recruitment patterns for the opossum included in Fig. 2 reproduce what they report as strong and consistent (occurring in at least 66% of the observations) activity, and have been arbitrarily set to 30% of maximum.

Fig. 2. Humeral retractor recruitment during quadrupedal walking across all taxa. Shaded areas represent the most consistent patterns of muscle use, that is, activity occurring 75% or more of the time in the samples of step cycles. Magnitudes of RMS values are shown as a percentage of the maximum level of activity observed during a recording session, with 100% of the maximum burst equal to the top of the *y*-axis. Step-cycle lengths have all been equalized for ease of comparisons. Each support phase begins with hand touchdown and ends with hand lift-off. Each swing phase begins with hand lift-off and ends with hand touchdown. Where there are multiple subjects for a single species, individual activity profiles were first scaled to their maximum bursts, and then the scaled RMS values were averaged to portray the species-specific profile. Colors refer to taxonomic groups: red, lemur species; blue, New World monkeys; orange, Old World monkeys; green, ape (chimpanzee). Lemurs are prosimians, a group that retains more primitive primate features; the other three groups are anthropoids or more advanced primates. *Opossum data is reproduced from Jenkins and Weijs (Jenkins and Weijs, 1979) for comparison.
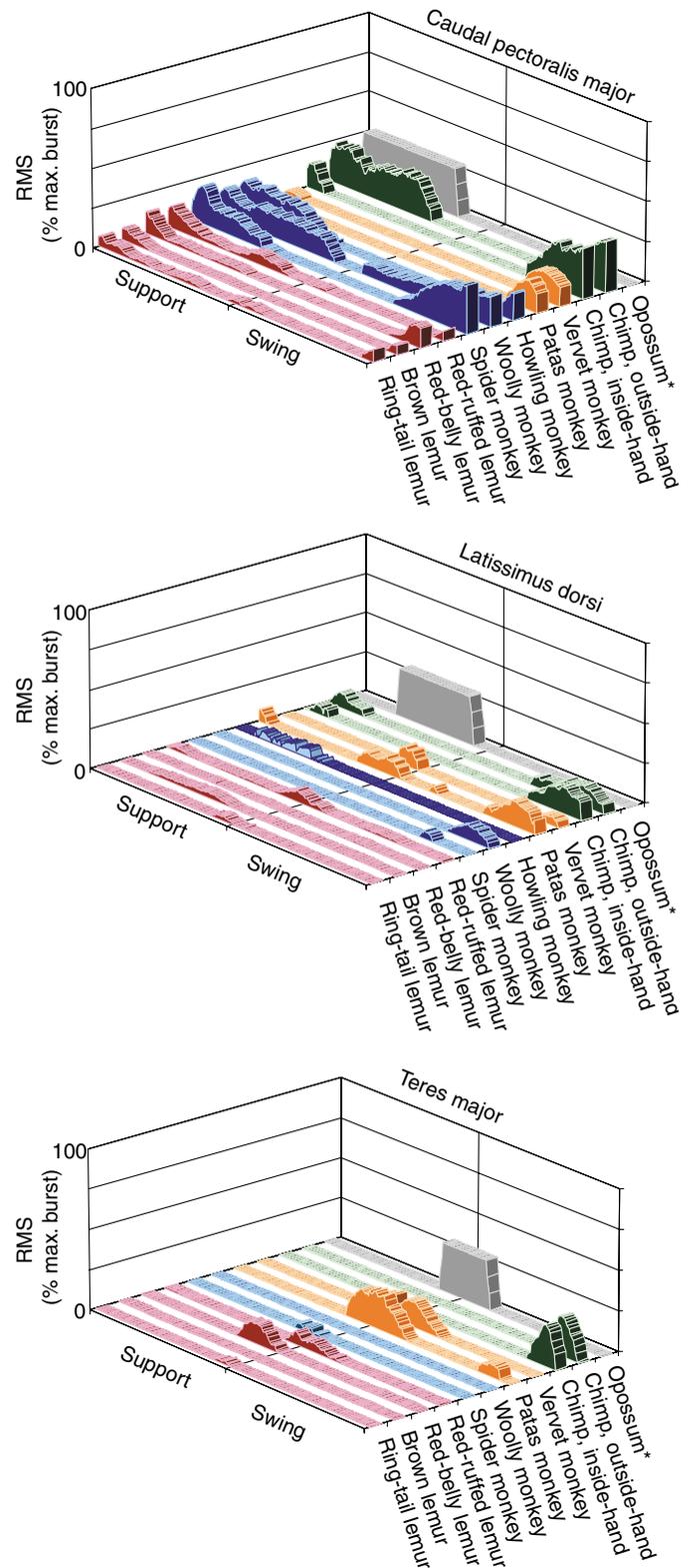
major activity at the swing/support transition, the third does not, and only one of the three displays continued support phase recruitment of pectoralis. The red-ruffed lemurs, on the other hand, display very similar patterns of pectoralis use during walking. For latissimus dorsi, two of the three individuals in both species show activity at the support/swing transition, while the third subject for both species displayed very low-level support phase activity. Support/swing transition activity in teres major was observed consistently in two of the three ring-tail lemurs, but only intermittently in the third, while in the red-ruffed lemurs, a small support/swing burst in teres was seen frequently in one individual, occasionally in a second, but not at all in a third.

Among New World monkeys (Fig. 6, Fig. 7), we only have multiple samples of caudal pectoralis major activity for spider monkeys. While both individuals display late swing to early support phase activity during walking, in one the support phase activity continues until midsupport but in the other it ends a little after touchdown. In the first, the pectoralis swing phase activity begins before midswing but not until the final third of swing in the second. For the other two New World monkey species, for which we had pectoralis data for only single subjects, the howler monkey resembled the first spider monkey in support phase recruitment of pectoralis, but displayed much less swing phase activity. The woolly monkey exhibited pectoralis activity through much more of the step cycle than did any of the other primate species examined here. Two of the three spider monkeys did not use latissimus dorsi at all during walking, and the third displayed a late swing phase burst, before the swing/support transition. The two woolly monkeys also showed late swing phase activity in latissimus. In one individual this activity sometimes continued into early support phase, but not in the other. The howler monkey, like some of the lemurs, displayed very low-level support phase activity in latissimus.

The patterns of recruitment of the humeral retractors are generally similar across the Old World monkeys (Fig. 8). All three vervet monkeys and the patas monkey recruit caudal

pectoralis major most consistently at the end of swing phase. In one of the vervets, however, this activity consistently continued into early support phase and did so occasionally in a second but not at all in the third. Late swing phase activity
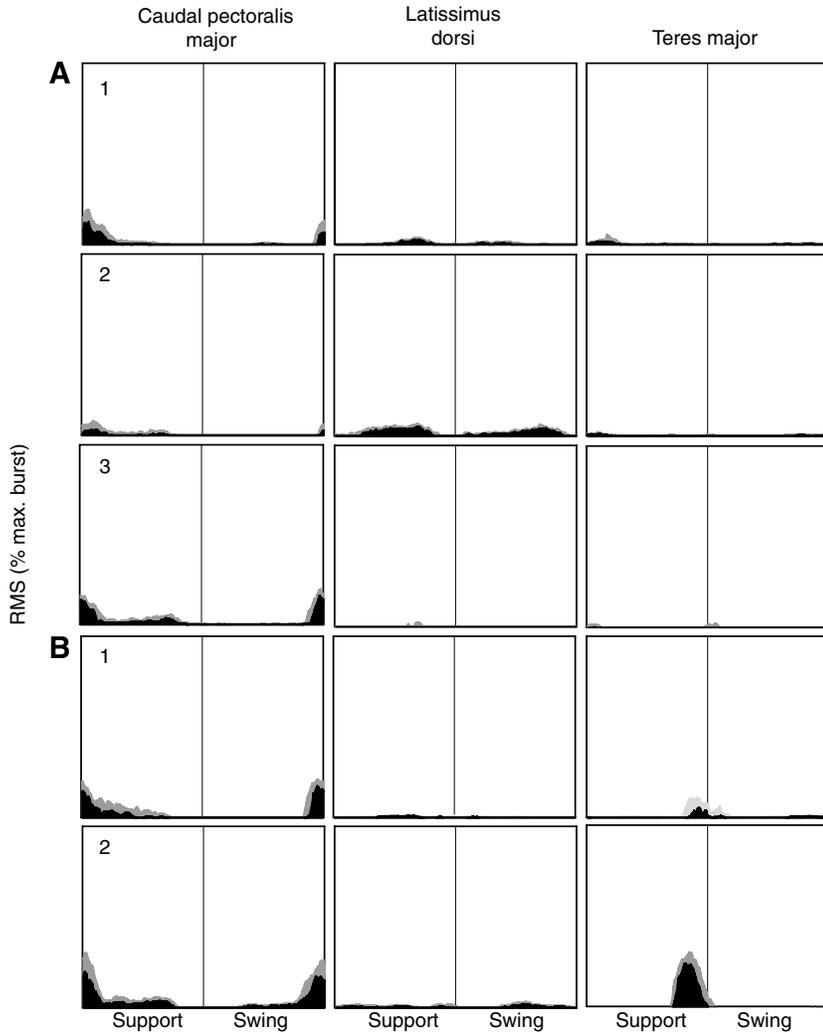
Fig. 3. Humeral retractor muscle recruitment profiles for individual brown lemur (A1–3) and red-belly lemur (B1,2) subjects. As in Fig. 2, step-cycle lengths have all been equalized for ease of comparisons. Each support phase begins with hand touchdown and ends with hand lift-off. Each swing phase begins with hand lift-off and ends with hand touchdown. The magnitude of the RMS values are shown as a percentage of the maximum level of activity observed during a recording session, with 100% of the maximum burst equal to the top of the box along the y-axis. Blackened areas represent the most consistent activity, occurring in 75% or more of the step cycles, and the gray shaded areas represent more variable activity occurring at least 50% of the time.
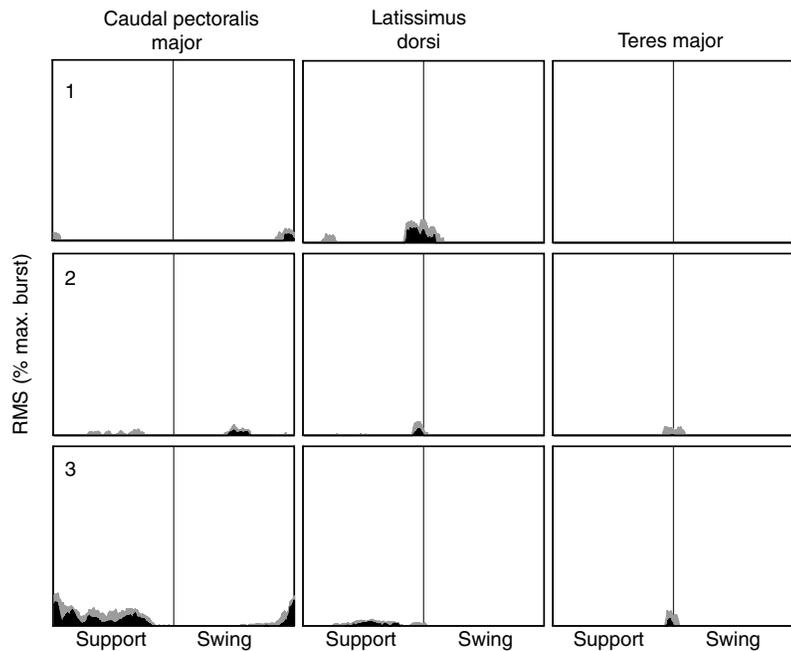

Fig. 4. Humeral retractor muscle recruitment profiles for individual ring-tail lemur subjects (1–3). See Fig. 3 caption for further explanation.

in latissimus dorsi was also observed in all four Old World monkeys, although it only occurred consistently in one of the vervets and the patas monkey. The three vervets and patas
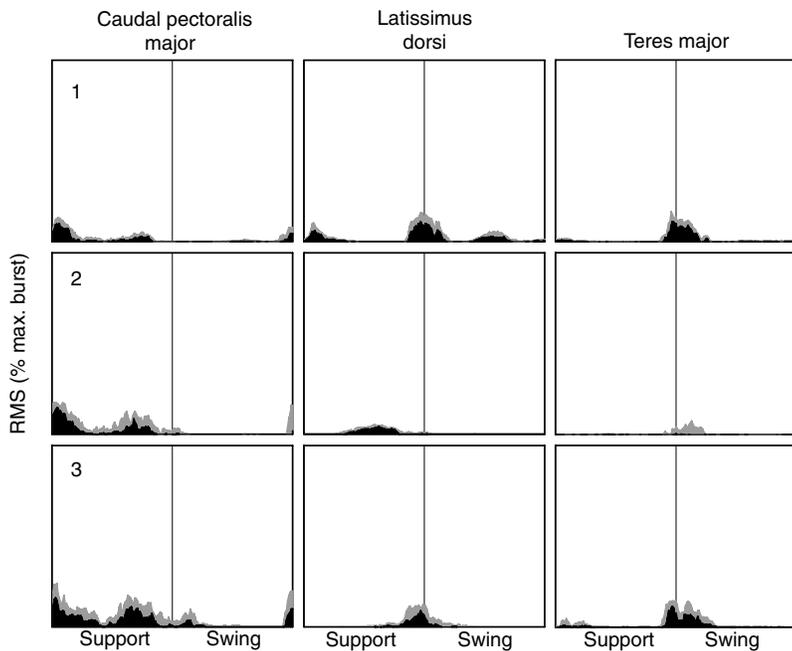

Fig. 5. Humeral retractor muscle recruitment profiles for individual red-ruffed lemur subjects (1–3). See Fig. 3 caption for further explanation.
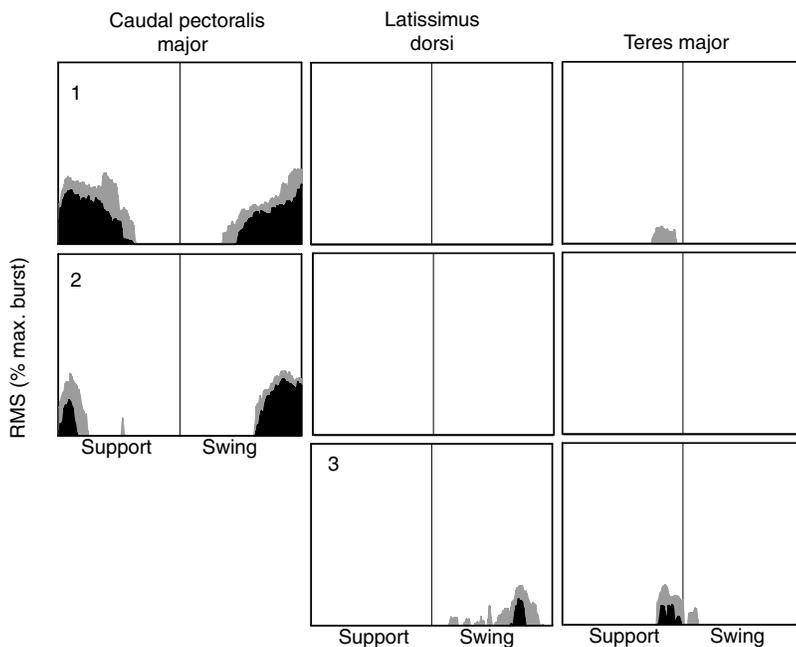

Fig. 6. Humeral retractor muscle recruitment profiles for individual spider monkey subjects (1–3). There were no successful recordings of caudal pectoralis major activity during walking for spider monkey #3. See Fig. 3 caption for further explanation.

monkey were also similar in displaying teres major activity at the support/swing transition, and two of the three vervets and patas also recruit latissimus dorsi at the end of swing phase.

However, for vervet monkey #1 the support/swing activity in teres major was more variable, and it did not use latissimus at the end of support phase.

While chimpanzee #1 readily switched between outside-hand and inside-hand steps during all EMG recording sessions, chimpanzee #2 did not, and we were only able to collect samples of both types of steps in both individuals for latissimus dorsi and teres major (Fig. 9). As it turned out, there was little difference in the patterns of recruitment between inside and outside hands for these two muscles. Chimpanzee #1 exhibits a clear difference in caudal pectoralis major activity between outside-hand and inside-hand steps. For outside-hand steps, the muscle is active for most of support phase, but its activity is frequently confined to the beginning of support phase of inside-hand steps. The recruitment of caudal pectoralis major in Chimpanzee #2, which only walked with inside-hand steps during the pectoralis major recording session, is similar to the inside-hand steps of Chimpanzee #1 except that the muscle is more consistently actively until about midsupport in Chimpanzeee #2. For teres major, both chimpanzees display the virtually identical pattern of terminal swing phase activity. However, there is some variation in latissimus activity between the two individuals. Although both recruit latissimus at the end of swing phase, this activity is more substantial and of longer duration in chimpanzee #1 compared to chimpanzee #2.

Discussion

Based on the patterns of muscle use observed in the ten taxa examined here, it does not appear that the humeral retractors make any substantial contribution to forward impulse during quadrupedal locomotion in primates. This stands in contrast to what has been reported for various nonprimate mammals. Only caudal pectoralis major is recruited at more than a low level during support phase, and even this occurs only in some species. This confirms the earlier postulation, based on more limited data, that primates are a significant counter-example to the hypothesis that neuromuscular programming has been conserved across all tetrapods (Goslow et al., 1989; Peters and Goslow, 1983; Jenkins and Goslow, 1983). In addition, the variation in muscle use observed across these ten primate species refutes the proposal that primates display a unique pattern of
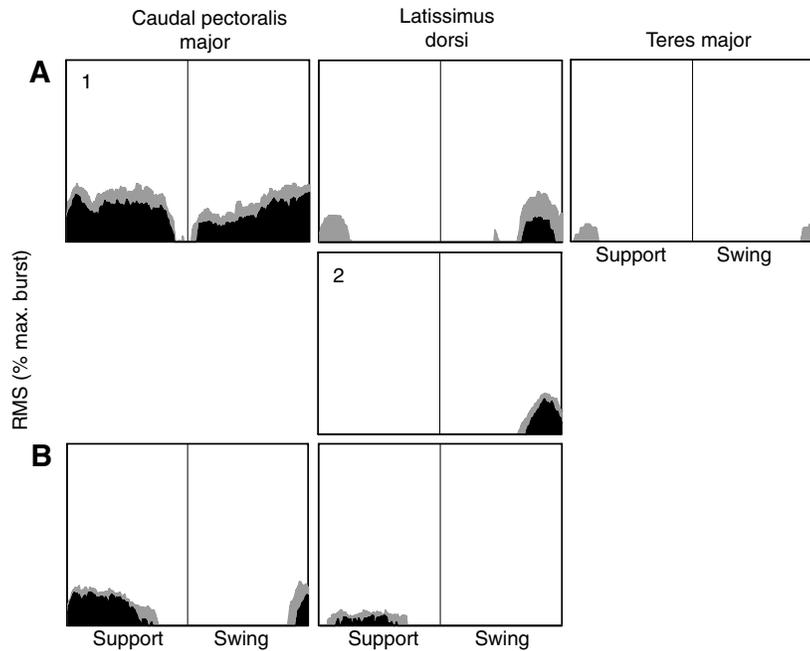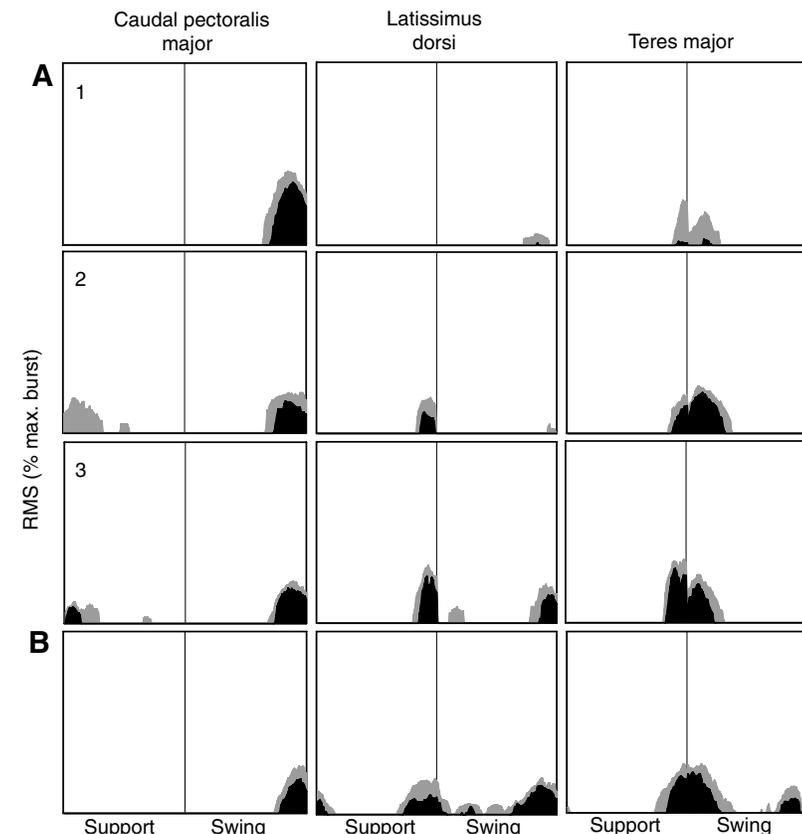
Fig. 7. Humeral retractor muscle recruitment profiles for individual woolly monkey subjects (A,1,2) and the howler monkey (B). The only humeral retractor recording available for woolly monkey #2 was for latissimus dorsi. There was no successful recording of teres major activity for the howler monkey. See Fig. 3 caption for further explanation.

neuromuscular conservation of their own (Vilensky and Larson, 1989; Larson and Stern, 1989). Indeed, individuals of the same species sometimes exhibit differences in their patterns of muscle use, suggesting that activity patterns can vary with individual differences in limb posture and motion. Unfortunately, documentation of these individual differences in limb kinematics is beyond the scope of this study. However, these results suggest that neural control of locomotion is a flexible system that is subject to evolutionary change and individual variation in the same way as musculoskeletal morphology.

Despite this variability, it is possible to make some generalizations about humeral retractor use in primates. Caudal pectoralis major appears to stand out compared to the other muscles in displaying modest levels of recruitment during support phase in New World monkeys, red-ruffed lemurs and chimpanzees. Noting that the pectoralis recruitment in chimpanzees occurs during outside-hand support phases when the shoulder is somewhat abducted, but not during inside-hand support phases when the forelimb is more nearly vertical, we concluded (Larson and Stern, 1987) that pectoralis major acts mainly as an adductor during chimpanzee knuckle-walking to prevent increasing abduction at the shoulder. The fact that New World monkeys tend to walk with more abducted forelimbs (Grand, 1968; Cant, 1986; Schmitt, 1994) than most other quadrupedal primates suggests that their recruitment of caudal pectoralis major during support phase may be serving a similar purpose. In addition, the step cycles documented here for the New World monkey and prosimian species were all derived from walking along a horizontal branch. When primates walk on branches, they typically exert a medially directed force to the substrate, whereas on the ground the transverse component of their applied forces is usually directed laterally (Schmitt, 2003; Carlson et al., 2005). It seems likely that the pectoralis activity that occurs during support phase in New World monkeys and prosimians contributes to this adductory force.

Other than this support phase recruitment of pectoralis, the three humeral retractors are most commonly active at either the swing/support or support/swing transition, or sometimes both. Late swing phase recruitment of pectoralis

Fig. 8. Humeral retractor muscle recruitment profiles for individual vervet monkey subjects (A1–3) and for the patas monkey (B). See Fig. 3 caption for further explanation.

major, latissimus dorsi and teres major observed in many of the anthropoid species is not seen in cats (English, 1978a; English, 1978b), opossums (Jenkins and Weijs, 1979) or dogs (Goslow et al., 1981; Nomura et al., 1966; Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974). We interpreted such late swing phase activity in chimpanzee and vervet monkey humeral retractors as a means of slowing down the swinging forelimb in preparation for hand touchdown (Larson and Stern, 1987; Larson and Stern, 1989), and we suggest they are playing the same role in the other anthropoid species. However, none of the four prosimian species display late swing phase activity in latissimus dorsi or teres major, and the swing phase activity in pectoralis major is so near to the end of the phase to suggest that it contributes little to slowing down the swinging limb and is only related to hand positioning. It is unclear why the prosimians do not need to actively slow down their forelimbs toward the end of swing phase. Perhaps their smaller size and relatively shorter forelimbs (low intermembral indices) result in sufficiently different inertial properties for their forelimbs that swing phase can be terminated through a different mechanism.

Support/swing transition activity in teres major was seen in the Old World monkeys, spider monkeys, and many of the prosimians, and some of those species also recruited latissimus dorsi at the same time. Similar activity in teres major in the opossum was interpreted as acting to retract the humerus as the forelimb is lifted off the ground in preparation for swing phase

(Jenkins and Weijs, 1979), and it seems likely that teres and latissimus are playing similar roles in these primate species.

Conclusions

The anthropoid and prosimian primate taxa examined here are similar to each other and different from those nonprimate mammals that have been studied in not recruiting their large humeral retractors to pull the trunk over the supporting forelimb to help propel the body forward during quadrupedal walking. This absence of a contribution to propulsion by the humeral retractors can therefore be added to the list of characteristics that distinguish the form of quadrupedalism exhibited by primates from that of other mammals (see Vilensky, 1987; Vilensky, 1989; Larson, 1998; Schmitt and Lemelin, 2002). In a previous study, we considered two possible explanations for why primates do not use their humeral retractors to create forward impulse during walking (Larson and Stern, 1989). One possibility is that the absence of propulsive activity in the humeral retractors is part of a greater degree of functional differentiation between for fore- and hindlimbs that characterizes primates. Force plate studies have shown that the primate hindlimb bears a greater proportion of the responsibility for support and propulsion than in other mammals (Kimura et al., 1979; Kimura, 1985; Demes et al., 1994). This difference has been related to the manipulative role of the forelimb in primates, and the concomitant demand for greater limb mobility resulting in a reduced ability to withstand high disruptive locomotor forces. A second possibility is that the absence of propulsive activity in the humeral retractors is a byproduct of changes in spinal circuitry that is claimed to have occurred in primates in association with greater cortical control of forelimb movements (Vilensky and Larson, 1989). According to this proposal (Vilensky and Larson, 1989), increasing use of the forelimb for exploration and manipulation was brought about through evolutionary changes shifting direct control of the forelimb from spinal pattern generators to the cerebrum, thereby permitting greater flexibility and versatility in forelimb use. We speculated
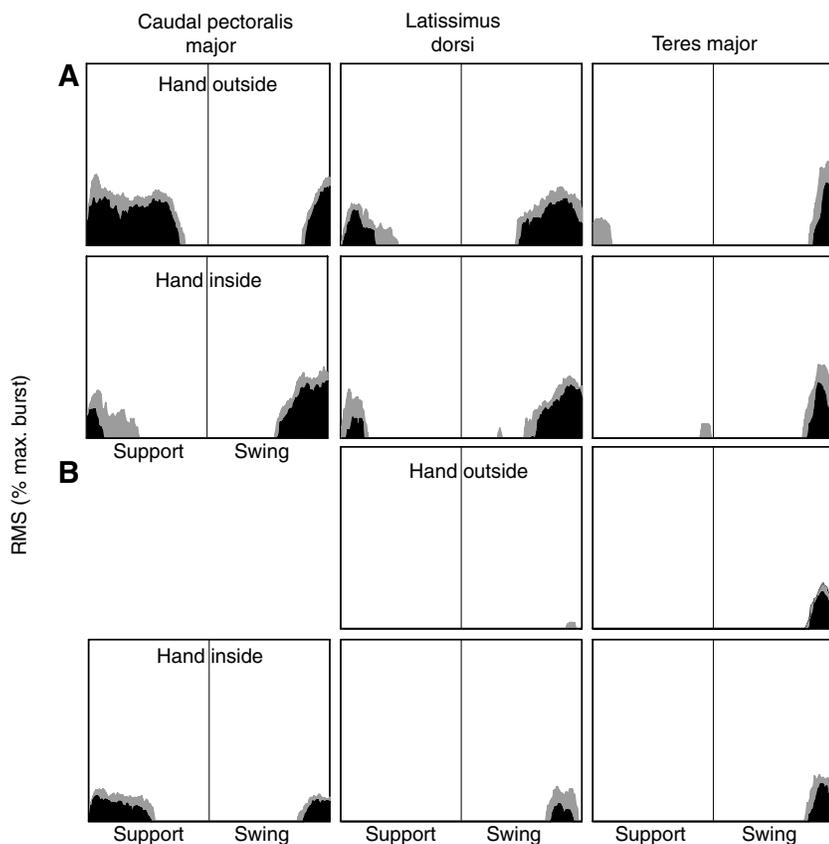

Fig. 9. Humeral retractor muscle recruitment profiles for individual chimpanzee subjects (A, chimpanzee #1; B, chimpanzee #2). Because of differences in forelimb posture between step-cycles when the overstriding hindlimb stepped inside the ipsilateral hand and ones where the foot landed outside the ipsilateral hand, outside-hand and inside-hand step-cycles were digitized separately [see (Larson and Stern, 1987) for additional details and explanations]. For caudal pectoralis major recordings, only samples of inside-hand steps were available for chimpanzee #2. See Fig. 3 caption for further explanation.

(Larson and Stern, 1989) that while the lack of propulsive activity in primate humeral retractors did not have an obvious functional relationship to these proposed changes in neural control mechanisms, the similarity in humeral retractor activity patterns in primate species with such different morphologies as the chimpanzee and vervet monkey could be a reflection of such rearrangements in spinal and cortical circuitry. However, EMG data reported here for a larger sample of primate species do not indicate uniformity in muscle use despite differences in morphology across primates. On the contrary, patterns of muscle recruitment appear to be species-specific and to some degree even individualistic, probably related to differences in kinematics and limb inertial properties between species and individuals. Therefore, while the EMG data presented here does not refute the basic premise (Vilensky and Larson, 1989) that alterations of neural control mechanisms have led to more direct cortical control of the forelimb, it suggests that the distinctive patterns of humeral retractor recruitment in primates are not simply a byproduct of rearrangements in spinal circuitry. In addition, since we documented EMG patterns for only one behavior and a limited set of muscles, these data do not directly address the question as to whether or not a common set of muscle synergies is encoded within the spinal cord of primates, a possibility raised by more recent views of central nervous system control of limb movements (e.g. Saltiel et al., 2001; d'Avella et al., 2003; d'Avella and Bizzi, 2005; Ting and Macpherson, 2005).

As to why primates do not use their humeral retractors to help propel them forward during walking, as we concluded in a previous study (Larson and Stern, 1989), the proposed explanations relating to functional differentiation between fore- and hindlimbs and to changes in neural control mechanisms are not really in conflict. Emphasis on the evolutionary development of grasping and manipulative abilities brought about changes in the primate forelimb to enhance its mobility and versatility. These changes included alteration of musculoskeletal morphology to enhance the range of motion at forelimb joints as well as changes in neurological mechanisms controlling this motion. This combination of factors led to the greater degree of functional differentiation between the fore- and hindlimbs, including mechanisms to reduce stress on the forelimb during quadrupedal locomotion.

Finally, the observation that muscle activity patterns can vary between individuals of a single species may lead one to question whether studies such as this one, which typically report EMG data for only a small number of subjects, can ever be viewed as accurately representing a species-specific profile of muscle use. For the muscles and particular locomotor behavior examined here, we believe this individual variability is in fact part of the species profile of muscle use. Caudal pectoralis major, latissimus dorsi and teres major are all recruited at low levels and play correspondingly minor roles during quadrupedal walking in primates. These relatively small contributions of muscle force are apparently only variably needed in many cases depending on slight differences in limb posture or motion. However, in behaviors that require high

levels of force production in the humeral retractors, such as climbing or hoisting, this individual variability disappears and patterns of muscle use become very consistent and predictable.

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