

RESEARCH ARTICLE

Electromyography of wrist and finger flexor muscles in olive baboons (*Papio anubis*)

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SUMMARY

Some non-human primates use digitigrade hand postures when walking slowly on the ground. As a component of an extended limb, a digitigrade posture can help minimize wrist joint moments thereby requiring little force production directly from wrist flexors (and/or from the assistance of finger flexors) to maintain limb posture. As a consequence, less active muscle volume would be required from these anti-gravity muscles and overall metabolic costs associated with locomotion could be reduced. To investigate whether the use of digitigrade hand postures during walking in primates entails minimal use of anti-gravity muscles, this study examined electromyography (EMG) patterns in both the wrist and finger flexor muscles in facultatively digitigrade olive baboons (*Papio anubis*) across a range of speeds. The results demonstrate that baboons can adopt a digitigrade hand posture when standing and moving at slow speeds without requiring substantial EMG activity from distal anti-gravity muscles. Higher speed locomotion, however, entails increasing EMG activity and is accompanied by a dynamic shift to a more palmigrade-like limb posture. Thus, the ability to adopt a digitigrade hand posture by monkeys is an adaptation for ground living, but it was never co-opted for fast locomotion. Rather, digitigrady in primates appears to be related to energetic efficiency for walking long distances.

Key words: EMG, hand, digitigrade, palmigrade, terrestrial, locomotion, primate.

INTRODUCTION

Most ground-dwelling mammals assume an extended digitigrade limb posture during locomotion, with only the phalanges and distal ends of the metapodials in contact with the substrate during stance, and the more proximal elements of the autopodia (e.g. wrist, ankle) elevated off the ground. It is generally accepted that digitigrady is a postural adaptation for cursoriality (i.e. fast locomotion) on terrestrial substrates (Howell, 1944; Gambaryan, 1974). Specifically, by increasing effective limb length, digitigrady can contribute to a longer step length and thereby increase stride length (Brown and Yalden, 1973; Hildebrand and Goslow, 2001). Longer stride length in turn may permit animals to move at faster speeds and/or allow them to move fast more economically by reducing the need for increased stride frequency (e.g. Heglund and Taylor, 1988; Maes et al., 2008). Serving as a component of an overall longer and extended limb, digitigrady can also help align distal limb joints more closely to the ground reaction force (GRF) vector, thus reducing the length of the GRF load arm and ultimately distal joint moments (Fig. 1) (Gray, 1944). As a consequence, the demands on anti-gravity muscles to maintain limb posture are reduced (Biewener, 1989; Biewener, 1990). As GRFs increase with speed (Rubin and Lanyon, 1982; Biewener, 1983; Biewener and Taylor, 1986; Demes et al., 1994), the energetic savings achieved *via* this reduction in joint moments are particularly beneficial to animals that run fast.

Obligate digitigrade mammals are able to maintain their erect distal limb postures at both slow and fast speeds because of anatomical adaptations that increase stability and limit the range of motion in distal limb joints (e.g. Yalden, 1970). In contrast, some facultative digitigrade mammals like non-human primates have more mobility at their distal limb joints (e.g. Yalden, 1972), allowing them to change between digitigrade and plantigrade postures. Contrary to predictions based on the association of digitigrady with

cursoriality, experimental studies have shown that (semi-) terrestrial monkeys (e.g. baboons) adopt digitigrade hand postures only during slow walking, and use less digitigrade or more ‘palmigrade’-like hand postures (i.e. the forepaw equivalent to plantigrade hindfoot postures) when running and using asymmetrical gaits (Patel, 2009; Patel, 2010a; Patel and Polk, 2010; Patel and Wunderlich, 2010). These primates transition to palmigrady at faster speeds because of the inability of their mobile distal forelimb joints to passively resist extension moments at the wrist joint while experiencing higher GRFs – effectively forced palmigrady (Patel, 2009; Patel, 2010a). Whether forced or not, palmigrady at faster speeds when GRFs are higher is beneficial in distributing those higher forces over a larger contact area and thereby dynamically moderating the stresses acting on relatively fragile hand bones and accompanying soft tissues (Patel, 2010b; Patel and Wunderlich, 2010). If this explains why terrestrial primates use palmigrade-like postures at faster speeds, why then do they use digitigrade postures at slower speeds?

In general, primates are not typically regarded as cursors (Brown and Yalden, 1973; Alexander and Maloiy, 1984; Preuschoft and Günther, 1994; Larson, 1998), and field studies on digitigrade monkeys have shown that fast locomotion only accounts for a small percentage of their total locomotor time budgets (Rose, 1974; Rose, 1977; Isbell et al., 1998). Rather, these terrestrial primates typically move at walking speeds over considerable distances, allowing them to attain relatively long day ranges (Isbell et al., 1998). Walking efficiency, then, may have a major influence on daily energy requirements (e.g. Janis and Wilhelm, 1993; Isbell et al., 1998; Reilly et al., 2007). Digitigrady may improve walking efficiency in non-human primates by increasing functional forelimb length, allowing them to take fewer but absolutely longer strides to travel a given distance (Patel, 2009). In addition, as the generation of muscular force is a large contributor to active metabolism (e.g. Kram and

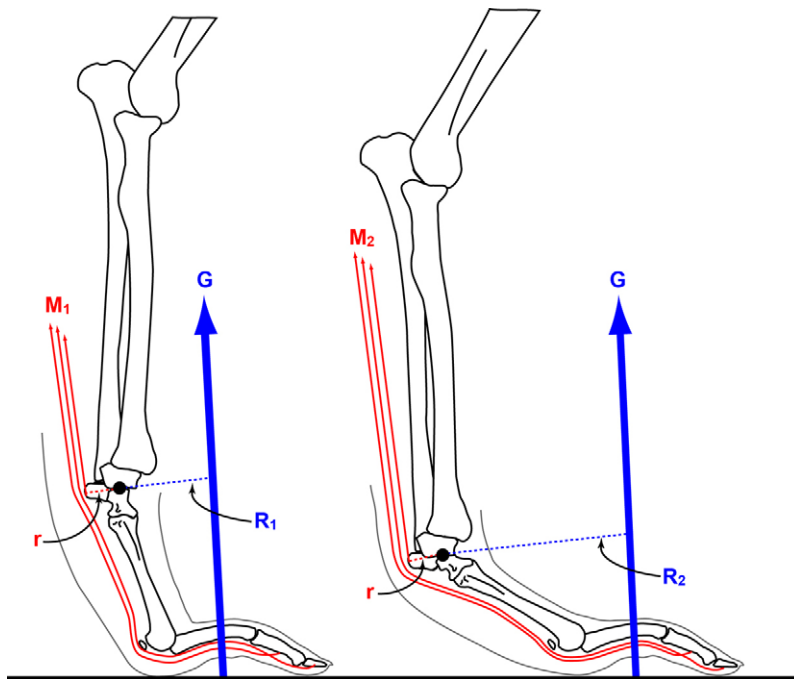


Fig. 1. Schematic illustrations of digitigrade (left) and 'palmigrade'-like (right) quadrupedal primate hands. An extension moment at the wrist joint (black circle) is created by the ground reaction force vector (G), which is at a distance R from the center of the wrist joint. A flexion moment produced by muscle force (M) from the wrist flexors (and assisted by the finger flexors), acting at a distance r from the center of the wrist joint, helps balance the extension moment. R_1 is shorter in the digitigrade hand, and consequently M_1 is smaller. In contrast, M_2 is larger when adopting a palmigrade-like hand because R_2 is longer. With $M_1 < M_2$, a digitigrade hand posture should be more energetically efficient.

Taylor, 1990), any amount of energy saving that can be gained by reducing muscle recruitment while walking would also be advantageous for these animals. As outlined above, one potential benefit of digitigrady is the reduction of moments at distal limb joints through better alignment of the limb with the GRF vector. Although the magnitude of the GRF is not high at slow walking speeds, utilization of digitigrady in this circumstance would nonetheless minimize wrist and ankle joint moments, resulting in very low demands on anti-gravity muscles to maintain limb posture (Fig. 1) and, by extension, reduce overall metabolic costs. Thus, digitigrady in primates may be a means for reducing locomotor costs during slow locomotion (Patel, 2010a).

Calculated wrist joint moments in primates are indeed lower during digitigrade walking than when these animals run with a more palmigrade-like hand posture (Patel, 2010b). However, this could be due mainly to the higher GRF magnitudes at faster speeds; a moment equals the product of the GRF magnitude and its load arm length about the center of a joint. If digitigrady is truly related to increased locomotor efficiency when walking, these primates should also display lower activation of the wrist flexors when walking compared with running. Additionally, because the finger flexor muscles have tendons crossing the volar side of the wrist joint, they too should be recruited more when running in order to assist the wrist flexors in balancing extension moments at this joint (Fig. 1). Electromyography (EMG) patterns for finger flexor muscles in rhesus macaques reported by Courtine and colleagues (Courtine et al., 2005) offer some support for this proposal in that higher levels of EMG activity were observed in both the m. flexor digitorum superficialis and m. flexor digitorum profundus in one individual when it moved fast and used what appears to be a less digitigrade hand posture. However, the fact that similar EMG activity patterns were not observed in their second experimental subject (Courtine et al., 2005), and that there are currently no published EMG data from the flexors of the wrist joint in any other digitigrade monkey, leaves this issue unresolved.

In this study, we investigated the relationship between digitigrade hand postures and use of anti-gravity muscles during walking,

running and galloping in (semi-) terrestrial, facultatively digitigrade olive baboons. Using telemetered EMG from the wrist and finger flexor muscles, four questions were addressed. (1) What is the typical recruitment profile of each muscle during a step cycle of quadrupedal locomotion? (2) Do speed and the use of different hand postures influence muscle activity patterns? (3) Is the use of a digitigrade hand posture at slow speeds in baboons associated with reduced activation of these anti-gravity muscles? (4) Is the use of a palmigrade hand posture at fast speeds associated with increased activation of these same muscles?

MATERIALS AND METHODS

Two adult olive baboons [*Papio anubis* (Lessen 1827)] were the animal subjects for this study. The male subject weighed 28 kg and the female weighed 23.5 kg at the time of the experiments. The animals were housed separately in large chain-link cages where they were permitted to freely move on the ground and on simulated 'arboreal' supports between experiments. All experiments were conducted at the Stony Brook University Primate Locomotion Laboratory (Stony Brook, NY, USA) and the Stony Brook University's Institutional Animal Care and Use Committee (IACUC) approved all protocols.

EMG data collection focused on the primary flexors of the wrist and fingers: m. flexor carpi radialis (FCR), m. flexor carpi ulnaris (FCU), m. palmaris longus (PL), m. flexor digitorum superficialis (FDS) and m. flexor digitorum profundus (FDP). For the finger flexors, no specific bundle of fascicles acting on any specific digit was targeted. In some experiments, data were also obtained from the wrist and finger extensor muscles [m. extensor carpi radialis longus (ECRL), m. extensor carpi ulnaris (ECU) and m. extensor digitorum communis (EDC)] to help clarify the contributions of the flexor muscles to joint moments. Prior to EMG experiments, detailed dissections were carried out on a male baboon cadaver to determine the best approach to insert EMG electrodes in the focal muscles. For those muscles lying just under the skin, it was relatively easy to identify the middle of their muscle bellies for electrode placement. For FDP, two possible insertion routes were

taken: (1) directly through the main belly of FDS, or (2) from a medial approach between FDS and FCU. Even though the latter method was preferred, there were no obvious differences in our EMG data related to the route of electrode insertion. Information on the number of recording sessions and step cycles for each muscle is presented in Table 1. We were most successful at recording data from FCR, FDS and FDP, but obtained only limited data samples from the remaining muscles.

Electrode construction and insertion follow previous protocols (Larson and Stern, 2007; Larson and Stern, 2009). Bipolar fine-wire electrodes (50 μ m) were threaded through a 25 gauge hypodermic needle and inserted into the bellies of focal muscles while the subjects were under isoflurane anesthesia. As the needle was removed the bent tip of the electrode remained inside the muscle; manipulation of the animal's hands and forearms while the needle was in place ensured that the electrode was in a stable position. Each focal muscle was back-stimulated through the electrode with a small (200–500 μ A) sinusoidal current (50 Hz) to ensure proper placement and to verify the action of the muscles (in isolation). These back-stimulation experiments produced expected findings: FCR, FCU and PL all flexed the wrist. Additionally, FCR caused radial deviation and FCU caused ulnar deviation at the wrist. FDS and FDP both flexed the wrist, metacarpophalangeal (MP) and proximal interphalangeal (PIP) joints. FDP also flexed the distal interphalangeal (DIP) joints. After the back-stimulation experiments, the free ends of the electrode wires were connected to a 112 g, 4-channel, Bio-Sentry Telemetry FM telemetry transmitter, which was then attached to a non-restrictive harness and shirt worn by the subjects (e.g. Larson and Stern, 2007).

Subjects were placed in a large enclosure (7.3 m long \times 3.7 m wide \times 2.7 m high) surrounded by chain-link fencing. Following recovery from anesthesia the subjects were allowed to move freely on the floor (coated with an epoxy resin) or use a large horizontally positioned tree trunk (5.3 m in length by 15 cm in diameter) suspended from the ceiling approximately 1 m above the floor. The tree trunk served as the 'arboreal' support for our experiments. Movements were elicited by food rewards. The subjects used both symmetric (e.g. walks, runs, ambles) and asymmetric (canter, gallop) gaits, and nearly all symmetric gaits followed a diagonal sequence/diagonal couplet footfall pattern. The analyzed trials (i.e. step cycles) were grouped into the following categories: (a) branch walking at slow speeds (branch slow); (b) ground walking at slow speeds (ground slow); (c) ground walking/running at fast speeds (ground fast); and (d) ground galloping at fast speeds (ground gallop). [In this manuscript, we use the term 'gallop' loosely to

include all asymmetrical gaits that a primate might use, including both true gallops and canters (e.g. Hildebrand, 1985).] In all the gallop trials, the forelimb of interest was always the leading limb. Because actual moving speed was not measured during the recording sessions, 'slow' versus 'fast' step cycles were identified based on forelimb stance phase duration. Specifically, faster trials were those with stance durations of <20 video fields, whereas slower trials had stance phases lasting >30 video fields (video recorded at 60 Hz; see below). As seen in prior studies (Patel, 2009; Patel, 2010a), this dichotomy in speed selection corresponded well with the hand posture used by both animals: digitigrade postures were used when moving slowly and palmigrade-like postures were used when moving more quickly. One important point that must be noted is that the behavioral preferences of the subjects coupled with variable success in EMG recording resulted in unequal samples of step cycles analyzed for each muscle and for each behavior (Table 1). Specifically, slow steps on both the ground and the elevated tree trunk outnumber those from fast trials. Finally, EMG data were also collected when the animals were standing quietly in a digitigrade hand posture on both the ground and the tree trunk for comparison with the locomotion data. At the end of each recording session the electrodes and harness were removed and the subject was returned to its home cage.

The technique of collecting telemetered EMG data together with simultaneous video recording used here follows previous studies (e.g. Boyer et al., 2007; Larson and Stern, 2007; Larson and Stern, 2009; Kingston et al., 2010). Briefly, using a Panasonic 5100HS color video camera with an electronic high-speed shutter, analog video of the subject's behavior was recorded at 60 Hz on Fuji SVHS ST-120 videotapes using a Panasonic AG-5210 VCR. Simultaneous EMG signals were detected by an FM receiver that sends demodulated EMG output to a National Instruments SCXI-1000 A–D converter (Austin, TX, USA), whose signal is acquired at 2700 Hz using National Instruments LabView v. 5.01 software installed on a PC computer. The LabView virtual instrument displays the EMG signals on a computer monitor and simulates a 4-channel storage oscilloscope with sweeps of 2 s in duration; each sweep is given its own unique file name and contains the raw EMG data. This file name is also displayed on the computer monitor, as is a counter that is set to 0 when each sweep begins and reaches 120 when the sweep ends (thereby giving an indication of time as the sweep counter changes in intervals of 1/60 s). The digital computer image (containing the 4-channel oscilloscope, sweep counter and file name) was superimposed and recorded onto the aforementioned video image of the moving subjects using a

Table 1. Summary of experiments and number of step cycles

	Experiments	Hand posture	FDP	FDS	FCR	FCU	PL	EDC	ECRL	ECU
Animal										
Male	3		4	4	2	0	0	0	0	0
Female	5		4	3	3	1	2	1	2	2
Total	8		8	7	5	1	2	1	2	2
Behavior										
Branch slow		Digitigrade	137	132	106	34	34	34	49	43
Ground slow		Digitigrade	142	105	82	25	17	25	32	27
Ground fast		Palmigrade-like	0	13	8	2	0	0	0	0
Ground gallop		Palmigrade-like	26	4	3	0	0	0	0	0

FDP, m. flexor digitorum profundus; FDS, m. flexor digitorum superficialis; FCR, m. flexor carpi radialis; FCU, m. flexor carpi ulnaris; PL, m. palmaris longus; EDC, m. extensor digitorum communis; ECRL, m. extensor carpi radialis longus; ECU, m. extensor carpi ulnaris.

Values in the top section of the table are number of recording sessions with successful electrode placement. Note that some muscles were sampled more than once in an experiment (e.g. FDS and FDP in the male subject). Values in the bottom section of the table are number of step cycles.

See text for definitions of behavior/speed categories.

Panasonic WJ 45P special-effects generator (Fig. 2). The superimposed video images allow the precise determination of the relationship between muscle activity and the subject's movements.

Using a Panasonic AG-7350 VCR that enables field-by-field playback of the superimposed video recordings at 60 fields s^{-1} , the file name and counter number corresponding to specific behaviors, step cycles and kinematic events of interest were noted. This information was entered manually into a text file, which served as input for a Fortran program 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 (r.m.s.; at intervals of 1.85 ms, using a time constant of 41.85 ms) of the EMG data for all samples of stance and swing phase. A second Fortran program reads all the sample files containing the r.m.s. information for any specified phase, equalizes all samples with regard to phase duration, and calculates at 1% intervals an average distribution of the r.m.s. The 'average activity' profiles for a muscle over a step cycle were used to compare activity patterns across muscles and behaviors. In figures illustrating r.m.s. EMG activity (Figs 3–5), the amplitude of muscle activity during locomotion is shown as the level of the r.m.s. relative to the 'maximum burst' r.m.s. 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. Typically, four or five such examples were collected and quantified, and the average of the highest r.m.s. values was used to scale the r.m.s. values observed during locomotion. Not surprisingly, climbing the chain-link fence, turning on the ground, jumping or trying to maintain balance on the horizontal tree trunk were among the behaviors most frequently eliciting maximum activity levels for the wrist and finger flexors. Because the focus of this study was mainly on recognizing major differences in amplitude during different quadrupedal behaviors, no attempt was made to statistically compare r.m.s. values across individuals, muscles or behaviors.

RESULTS

Examples of raw EMG data superimposed on the video of our animal subjects standing and walking slowly are illustrated in Fig. 2. Fig. 3 displays the average r.m.s. EMG profiles for all muscles during the

four locomotor behaviors of interest: branch slow, ground slow, ground fast and ground gallop. The median value of the r.m.s. EMG activity during stance phase for each muscle and each locomotor behavior is presented in Fig. 4.

As demonstrated by the raw EMG data, there is no significant activity in the finger flexors (FDS and FDP), FCR or PL when baboons stand still with an extended digitigrade posture (Fig. 2A; Table 2). There is some continuous, but very low-level activity in FCU during standing (Fig. 2B). In contrast, during quadrupedal locomotion there are observable levels of EMG activity in all muscles, although the amplitude is often low compared with the maximum bursts witnessed during activities such as climbing and jumping (Fig. 2C,D).

When walking slowly either on the ground or on the tree trunk, the baboons used a stereotypical, extended digitigrade hand posture during stance phase (Fig. 2C,D). Although the tree trunk was elevated and circular in cross-section, the r.m.s. EMG profiles for the wrist and finger flexor muscles in the two forms of slow speed walking are quite similar (Fig. 3). The three wrist flexors (FCR, FCU and PL) display low to modest activity for approximately the first three-quarters of stance phase of slow locomotion, with FCR and PL exhibiting a small additional burst at lift-off. Of the two finger flexors, FDS displays low level activity through most of the stance phase of slow walking, while FDP exhibits only minor activity very early during stance.

When walking fast and running or during galloping, both baboons adopted a less digitigrade (i.e. more palmigrade-like) hand posture. Although our data are incomplete, it is clear that the relative EMG amplitude in the flexor muscles was much higher during stance phase of fast locomotion with decreased digitigrade compared with standing and slow walking with an extended digitigrade posture (Figs 3 and 4, Table 2). Moreover, muscle activity levels were higher when using an asymmetrical gait than when using fast symmetrical gaits, corresponding to generally higher GRFs observed in primates when using gaits such as the gallop or canter (e.g. Demes et al., 1994; Carlson and Demes, 2010; Patel and Wunderlich, 2010). Increased activity in FCR, FDP and FDS is most pronounced during the early to middle part of stance phase when the vertical component of GRFs is typically highest (Schmitt, 1999) (Fig. 3). Particularly noteworthy is the rise of r.m.s. EMG activity in FDP from <5% of



Fig. 2. Still images of raw electromyography (EMG) traces superimposed on video of the experimental subjects. The white circles surround the hand of interest. (A) Male baboon standing with a digitigrade hand posture. EMG traces reveal minimal activity in m. flexor carpi radialis (FCR), m. flexor digitorum superficialis (FDS) and m. flexor digitorum profundus (FDP). (B) Female baboon standing with a digitigrade hand posture; the hand is also ulnarly deviated. EMG traces show consistent low-level activity in m. flexor carpi ulnaris (FCU) and m. extensor carpi ulnaris (ECU), but no activity in m. extensor carpi radialis longus (ECRL) and m. extensor digitorum communis (EDC). (C) Male baboon walking slowly with a digitigrade hand posture; image is taken at forelimb mid-stance. There is increased EMG activity in FCR, but only minimal activity in FDS and FDP. (D) Female baboon walking slowly with a digitigrade hand; image is taken at forelimb mid-stance. There is moderate EMG activity in FCU and ECU, but no activity in ECRL and EDC. In A and C, there are no data for the first EMG trace.

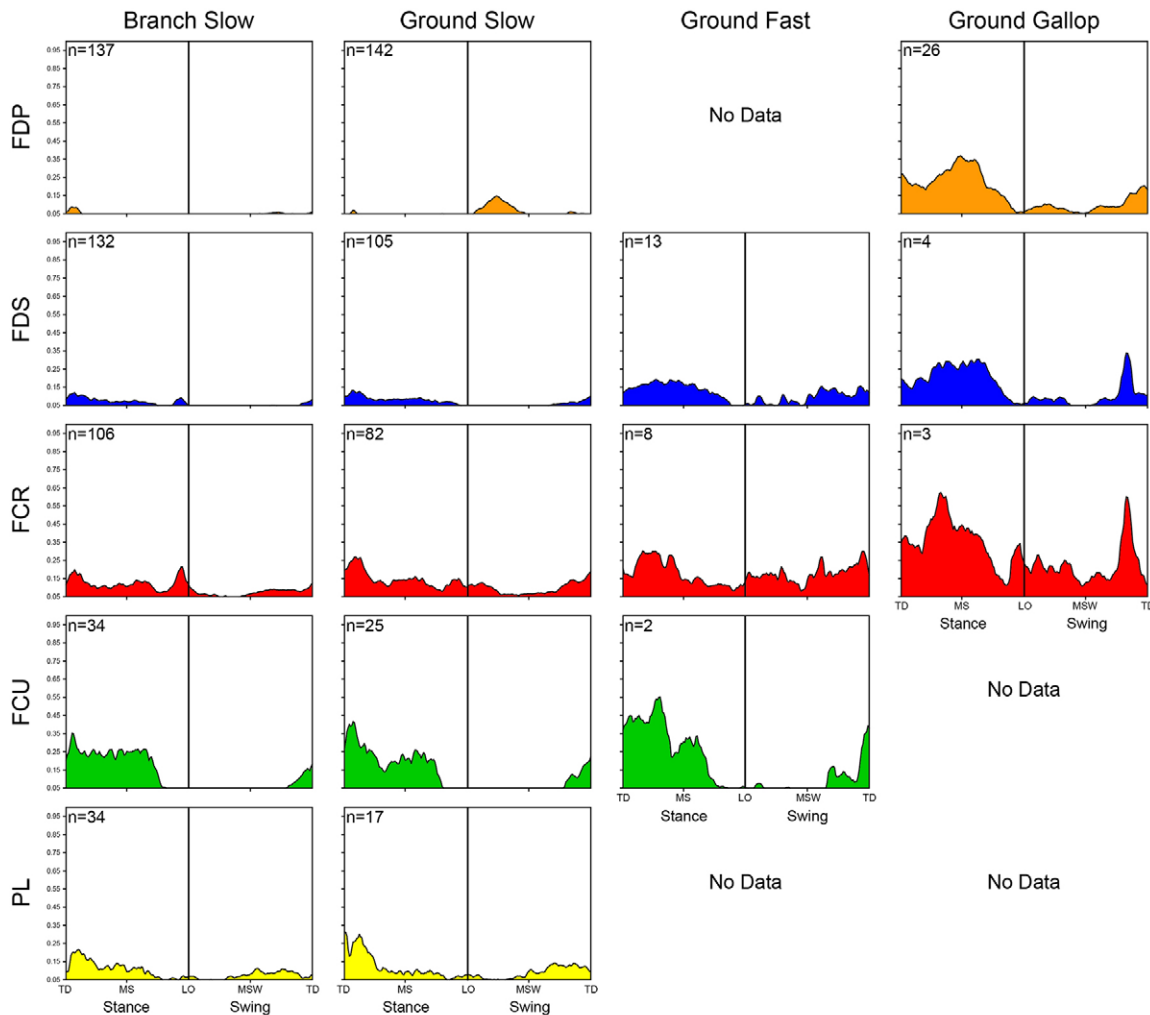


Fig. 3. Results of our quantified root mean square (r.m.s.) EMG activity profiles for each of our focal muscles (FDP, FDS, FCR, FCU and PL, *m. palmaris longus*) in our four locomotor behavior categories (from left to right): branch walking at slow speeds with a digitigrade hand posture; ground walking at slow speeds with a digitigrade hand posture; ground walking/running at fast speeds with a palmigrade hand posture; and ground galloping (or other asymmetrical gait) with a palmigrade hand posture. The shaded areas in these profiles represent the average pattern of muscle use across all step cycles. The magnitudes of the r.m.s. 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. Following Boyer et al. (Boyer et al., 2007), only r.m.s. values greater than 5% of maximum burst were considered to be meaningful and only these are displayed in our profile plots. Across the x-axis, step cycle duration for both stance and swing phases have been equalized for ease of comparison. Each stance phase begins with hand touchdown (TD) and ends with hand lift-off (LO). Each swing phase begins with hand LO and ends with hand TD. MS refers to mid-stance and MSW refers to mid-swing. Where there are multiple experiments for a single muscle (as in most cases), activity profiles for each experiment were first scaled to their maximum bursts, and then the scaled r.m.s. values were averaged to portray muscle-specific profiles. The number of step cycles for each muscle in each behavior is indicated on the top left of each EMG profile.

the observed maximum activity during slow walking to ~20–30% of the observed maximum activity during galloping. Similarly, the median stance phase value of r.m.s. EMG activity in FCR increased to >35% of the observed maximum activity during galloping. Although less dramatic, there are also observable increases in median r.m.s. EMG amplitude in both FCU and FDS during faster locomotion (Fig. 4).

DISCUSSION

Like many terrestrial mammals, baboons and other large-bodied (semi-) terrestrial monkeys (e.g. geladas, mandrills, macaques and patas monkeys) adopt a digitigrade hand posture when standing still and moving slowly. When walking, digitigrady increases the functional length of the forelimb, which allows these primates to take absolutely longer strides (Patel, 2009). As a component of an

overall longer and straighter forelimb, digitigrady also helps align the GRF vector closer to the center of the wrist joint, thereby reducing the extension moments about this joint (Fig. 1) (Patel, 2010a). Coupled with already relatively low GRFs during standing and slow locomotion, absolutely lower extension moments should reduce the need for significant force production from anti-gravity muscles to balance these moments and maintain a straighter distal limb posture (Fig. 1) (Gray, 1944; Biewener, 1989; Polk, 2002). The anti-gravity muscles that can produce flexion moments at the wrist primarily include the wrist flexors (PL, FCR and FCU), but these muscles may also be assisted by the finger flexors (FDS and FDP). The invasive nature of methods for measuring actual muscle force makes it difficult to directly document the magnitude of muscle force in non-human primates. But, as general patterns of force magnitude can be inferred from muscle recruitment patterns if proper

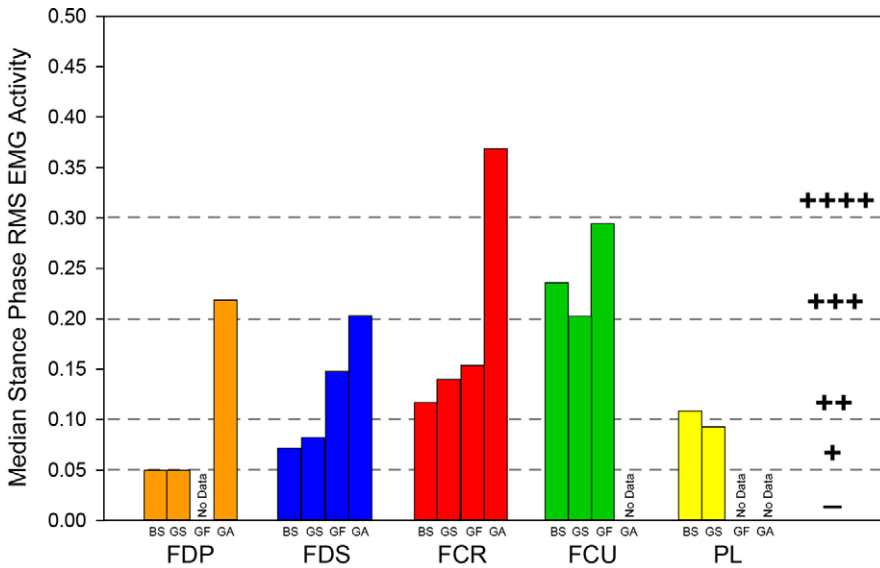


Fig. 4. The median value of average r.m.s. EMG values during stance phase for each of our focal muscles (FDP, FDS, FCR, FCU and PL) in our focal locomotor behavior categories: branch walking at slow speeds with a digitigrade hand posture (BS); ground walking at slow speeds with a digitigrade hand posture (GS); ground walking/running at fast speeds with a palmigrade hand posture (GF); and ground galloping (i.e. using an asymmetrical gait) with a palmigrade hand posture (GA). The dashed horizontal line represents levels of 'meaningful' activity: 5%, 10%, 20% and 30%. Symbols on the right side of the graph represents qualitative characterizations of r.m.s. EMG activity levels: -, activity less than 5% of maximum burst; +, activity between 5% and 10% of maximum burst; ++, activity between 10% and 20% of maximum burst; +++, activity between 20% and 30% of maximum burst; +++++, activity >30% of maximum burst. See also Table 2.

caution is exercised [see Roberts and Gabaldón (Roberts and Gabaldón, 2008) and references therein], we have used EMG to test the hypothesis that baboons require relatively little muscle force to maintain a more digitigrade posture when standing or moving slow.

No meaningful muscle activity was observed in FCR, PL or the finger flexors when baboons stood on an extended digitigrade hand. Although FCU is active during standing, the amplitude of the activity is quite low. These findings support the hypothesis that flexor muscle force production can be minimized by the use of a digitigrade hand posture, and indicate that the osseoligamentous configuration of the baboon radiocarpal and midcarpal joints, coupled with passive tension in muscles, is sufficient to resist the low extension moments about the wrist during standing postures (Tuttle, 1970; Yalden, 1972; Susman and Stern, 1979). Similar joint-stabilizing mechanisms are found in the wrist of other habitually digitigrade mammals such as felids and canids (Yalden, 1970).

In general, EMG amplitudes are relatively higher in all flexor muscles during quadrupedal locomotion than when standing still. Thus, despite the osseoligamentous features that baboons and other terrestrial monkeys have to enhance distal forelimb joint stability, there is enough mobility in their hands and wrists to require some muscle force to maintain a digitigrade posture during slow locomotion. Though the muscle activity levels are higher during slow walking than when standing, the median r.m.s. EMG values during stance phase of slow locomotion are still below 15% of their respective maximum burst activity in all muscles except FCU, and are less than 25% of FCU maximum burst activity.

Unlike other habitually digitigrade mammals, monkeys do not maintain a stereotypical digitigrade hand posture when moving at faster speeds. When running and galloping on the ground, their hands dynamically assume a palmigrade-like posture. The change to a palmigrade-like hand posture increases contact area, which probably attenuates peak pressure at the metacarpal heads to some degree (Patel, 2010b; Patel and Wunderlich, 2010). However, it appears that the center of pressure does not substantially translate proximally even though a larger portion of the thenar and hypothenar regions of the hand make contact with substrate [see fig. 2 in Patel and Wunderlich (Patel and Wunderlich, 2010)]. Patel and colleagues (Patel, 2009; Patel, 2010a; Patel and Polk, 2010) argue that the inherent mobility in the configuration of the distal limb joints of monkeys essentially makes passive resistance to the larger extension moments resulting from higher GRFs at higher speeds impossible. To the degree that EMG amplitude reflects relative muscle force (see Roberts and Gabaldón, 2008), the EMG patterns observed here indicate that this shift to a palmigrade-like hand posture is also accompanied by increased muscular force from the wrist and finger flexors. This potentially higher force could be acting to resist these high extension moments thereby helping to regulate the rate at which the wrist joint collapses into more dorsiflexed postures (e.g. Goslow et al., 1973). Alternatively, or in addition, these muscles could be acting as dynamic elastic bodies absorbing energy as the wrist (and MP) joints yield, to be recovered as elastic recoil later in stance phase (e.g. Roberts et al., 1997).

Table 2. Qualitative 'grades' of median r.m.s. EMG activity during standing and stance phase of quadrupedal locomotion

Muscle	Standing	Branch slow	Ground slow	Ground fast	Ground gallop
FDP	-	-	-	No data	+++
FDS	-	+	+	++	+++
FCR	-	++	++	++	++++
FCU	+	+++	+++	+++	No data
PL	-	++	+	No data	No data

Symbols in the table: -, activity less than 5% of maximum burst; +, activity between 5% and 10% of maximum burst; ++, activity between 10% and 20% of maximum burst; +++, activity between 20% and 30% of maximum burst; +++++, activity >30% of maximum burst. See Fig. 3 for more details.

See text for definitions of behavior/speed categories.

FDP, m. flexor digitorum profundus; FDS, m. flexor digitorum superficialis; FCR, m. flexor carpi radialis; FCU, m. flexor carpi ulnaris; PL, m. palmaris longus; r.m.s., root mean square.

Stance phase activity in distal forelimb anti-gravity muscles has also been observed in other mammalian quadrupeds. Tokuriki (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974) reports continuous EMG activity in FDP and FCU, although not in FCR, during quadrupedal locomotion in dogs. The activity in both FDP and FCU increases in trotting compared with walking, and FDP shows an even more dramatic increase in galloping compared with trotting. English (English, 1978) recorded EMG activity from these same muscles as well as PL in walking, trotting and galloping cats. Unfortunately, he only reports sample traces of raw EMG data, but his figures suggest a notable increase in EMG amplitude in PL, which is large in cats, in trotting compared with walking, although with a decrease again during galloping. FDP appears to increase in amplitude slightly from walking to trotting to galloping, but changes in activity levels for the wrist flexors (FCR and FCU) are not apparent.

English (English, 1978) relates the activity he observed in the cat's distal forelimb flexors to resisting lengthening during stance phase, to allow stretch of elastic components of the muscles to store mechanical energy. He suggests that the pennate fascicle architecture of these muscles and their long tendons make them especially suitable for this function. While a similar interpretation is possible for the roles of FCR, FCU, PL, FDS and FDP during faster locomotion in baboons, they, like other quadrupedal primates, have long muscle fascicle lengths and relatively short tendons, unlike most cursorial digitigrade mammals (Alexander, 1993). Although this configuration does not make the use of spring mechanics impossible, the large volume of muscle that must be activated to resist stretch and the limited elastic tissue available for energy storage suggest that any energetic savings *via* this mechanism will be small (see also Reilly et al., 2007).

The above discussion focused on the recruitment of baboon distal forelimb anti-gravity muscles related to hand posture and locomotor speed. In the course of this study, we observed several additional interesting aspects of the activity patterns of baboon wrist and finger flexors during stance that merit further discussion. Unlike the other muscles examined, FCU displays low but continuous levels of activity during quiet standing, and moderate levels of activity even during slow walking (Fig. 3). In addition to its role in wrist flexion, FCU acts as an adductor (i.e. an ulnar deviator) of the wrist joint. Lemelin and Schmitt (Lemelin and Schmitt, 1998) [*contra* Preuschoft et al. (Preuschoft et al., 1993)] report that baboons and other (semi-) terrestrial primates often place their hands in an adducted orientation as the hand touches down on the substrate, and/or will actively deviate their hands in an ulnar direction to some degree during stance phase when walking on both arboreal and terrestrial substrates. The distinctive recruitment of FCU could be related to this tendency for ulnar deviated hand postures. This interpretation is supported by the observation that ECU has a similar recruitment profile to FCU (Fig. 5). In humans, ECU is almost a pure ulnar deviator when the forearm is pronated (Stern, 1997), and the same might be true of ECU in quadrupedal primates that walk with a pronated forearm. Alternatively, or additionally, the flexion and extension components of FCU and ECU, respectively, can cancel each other out when recruited simultaneously, resulting in more or less pure ulnar deviation during stance phase. The other extensor muscles (EDC, ECRL) are not recruited in a similar fashion (Fig. 5), further suggesting that the activity in ECU is unrelated to extension. Tokuriki (Tokuriki, 1973a) similarly observed that digitigrade dogs make contact with the ground with an ulnarly deviated manus, and that both their FCU and ECU are active prior to forelimb touchdown and during the first half of stance. In our

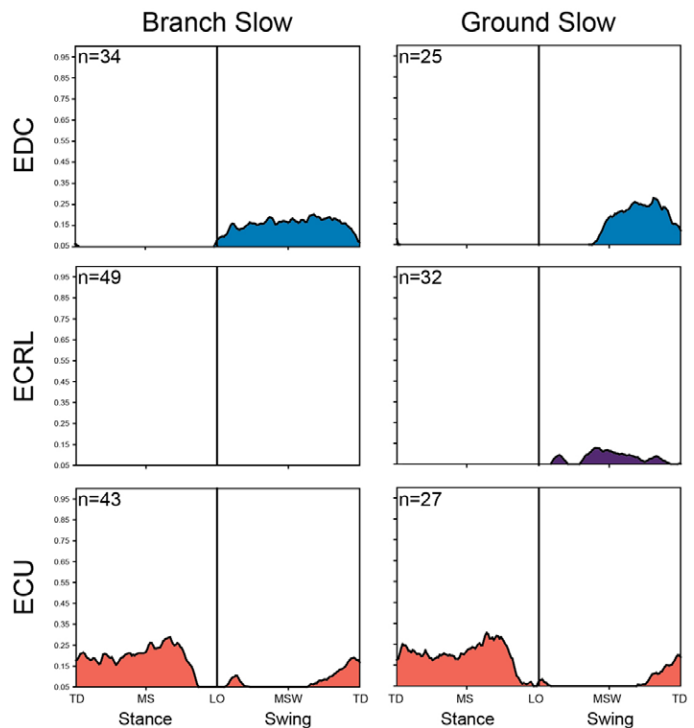


Fig. 5. Results of our quantified r.m.s. EMG activity profiles for EDC, ECRL and ECU during branch walking at slow speeds with a digitigrade hand posture and ground walking at slow speeds with a digitigrade hand posture. The shaded areas in these profiles represent the average pattern of muscle use across all step cycles. The magnitude of the r.m.s. values is 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. Following Boyer et al. (Boyer et al., 2007), only r.m.s. values greater than 5% of maximum burst were considered to be meaningful and only these are displayed in our profile plots. Across the x-axis, step cycle lengths have been equalized for ease of comparison. Each stance phase begins with hand touchdown (TD) and ends with hand lift-off (LO). Each swing phase begins with hand LO and ends with hand TD. MS refers to mid-stance and MSW refers to mid-swing. Where there are multiple experiments for a single muscle (as in most cases), activity profiles for each experiment were first scaled to their maximum bursts, and then the scaled r.m.s. values were averaged to portray muscle-specific profiles. The number of step cycles for each muscle in each behavior is indicated on the top left of each EMG profile.

baboons, the median r.m.s. EMG levels for FCU during the stance phase of branch walking are actually slightly higher than during slow ground locomotion (Figs 3 and 4), which also supports Lemelin and Schmitt's observation that ulnar deviation is greater when baboons use arboreal supports with circular cross-sections (Lemelin and Schmitt, 1998).

Another noteworthy pattern is the difference in EMG activity profiles between FDS and FDP during slow locomotion. While FDP is essentially inactive, FDS shows continuous low-levels of recruitment throughout stance phase on both the ground and the arboreal support. This activity may aid in maintaining a slightly flexed PIP joint during forelimb support as has been observed in digitigrade baboons and patas monkeys (Fig. 1) (Richmond, 1998; Patel and Wunderlich, 2010). Although terrestrial monkeys already have relatively short fingers compared with their palm lengths (Midlo, 1934; Napier and Napier, 1967; Etter, 1973; Patel et al., 2009; Patel and Wunderlich, 2010), flexion of the PIP joints will make them even shorter. Functionally shorter digits may improve

maneuverability in primates when on the ground, and help minimize potentially high bending moments in finger bones during quadrupedal locomotion (Nieschalk and Demes, 1993; Richmond, 1998), which may be particularly important during terrestrial locomotion when GRFs are higher (Schmitt, 1999). The minimal to no recruitment of FDP during most of stance phase is probably the result of several factors. First, the morphology of the DIP joints in primates significantly limits extension, thus reducing dependence on FDP to prevent hyperextension. Second, the sustained activity in FDS that helps to flex the PIP joints may be sufficient to resist any extension moments at the MP joints, thereby limiting any further need to recruit FDP (see also Rolian et al., 2009).

CONCLUSION

The goals of this study were to: (1) investigate when wrist and finger flexor muscles are recruited during the step cycle of quadrupedal locomotion in facultatively digitigrade baboons and determine whether muscle activity patterns differ across speeds and when using different hand postures (i.e. across a digitigrade–palmigrade gradient), and (2) test the hypothesis that locomotion with a digitigrade hand posture at slow speeds is more efficient, in the sense of requiring less active muscle volume, than when using a palmigrade hand posture at fast speeds. The results demonstrate that baboons can adopt a digitigrade hand posture when standing and moving at slow speeds without requiring substantial contributions from distal anti-gravity muscles. Higher speed locomotion, however, likely entails increasing levels of muscle force output and is accompanied by a dynamic shift to a more palmigrade-like limb posture. Although adopting a palmigrade-like posture could be an example of limb yield for the purpose of stretching tendons and storing elastic strain energy, the configuration of primate forelimb muscles (e.g. Alexander, 1993) suggests that this energy-saving mechanism may have limited effectiveness in primates. Accordingly, the fact that adopting a digitigrade hand posture increases the functional length of the forelimb, thereby contributing to absolutely longer stride lengths (Patel, 2009), and is associated with reduced active muscle volume (this study) supports the proposal that digitigrady in (semi-) terrestrial primates such as baboons may be accompanied by lower locomotor costs and thus increased efficiency during long distance travel and foraging. The significantly higher levels of flexor muscle recruitment during fast locomotion with a palmigrade-like hand posture suggest that it is much more energetically costly. Additional EMG data from the wrist and finger flexors of habitually palmigrade primates, as well as oxygen consumption data, would be useful in further testing this hypothesis. Although it has been well documented in a variety of animals that the cost of locomotion is higher during running and galloping than during walking (e.g. Taylor et al., 1982; Hoyt et al., 2006), the fact that it is associated with a transition from digitigrady to palmigrady in baboons and other (semi-) terrestrial monkeys may make the increment in cost more dramatic, which might help explain, in part, why such monkeys run infrequently. In our view, the ability to adopt a digitigrade hand posture by monkeys is indeed an adaptation for ground living, but it was never co-opted for fast locomotion. It is instead related to locomotor efficiency to maintain posture and walk over long distances. Interestingly, studies in other obligate digitigrade and unguligrade mammals have drawn similar conclusions (Janis and Wilhelm, 1993; Reilly et al., 2007).

LIST OF ABBREVIATIONS

DIP	distal interphalangeal joint
ECRL	m. extensor carpi radialis longus

ECU	m. extensor carpi ulnaris
EDC	m. extensor digitorum communis
EMG	electromyography
FCR	m. flexor carpi radialis
FCU	m. flexor carpi ulnaris
FDP	m. flexor digitorum profundus
FDS	m. flexor digitorum superficialis
GRF	ground reaction force
MP	metacarpophalangeal joint
PIP	proximal interphalangeal joint
PL	m. palmaris longus
r.m.s.	root mean square

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