Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion

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Abstract

It has long been thought that quadrupedal primates successfully occupy arboreal environments, in part, by relying on their grasping feet to control balance and propulsion, which frees their hands to test unstable branches and forage. If this interlimb decoupling of function is real, there should be discernible differences in forelimb versus hind limb musculoskeletal control, specifically in how manual and pedal digital flexor muscles are recruited to grasp during arboreal

locomotion. New electromyography data from extrinsic flexor muscles in red ruffed lemurs (*Varecia rubra*) walking on a simulated arboreal substrate reveal that toe flexors are activated at relatively higher levels and for longer durations than finger flexors during stance phase. This demonstrates that the extremities of primates indeed have different functional roles during arboreal locomotion, with the feet emphasizing maintenance of secure grips. When this dichotomous muscle activity pattern between the forelimbs and hind limbs is coupled with other features of primate quadrupedal locomotion, including greater hind limb weight support and the use of diagonal-sequence footfall patterns, a complex suite of biomechanical characters emerges in primates that allow for the co-option of hands toward non-locomotor roles. Early selection for limb functional differentiation in primates probably aided the evolution of fine manipulation capabilities in the hands of bipedal humans.

Keywords

grasping hands, grasping feet, digital flexors, electromyography, *Varecia*, arboreal locomotion

Introduction

The early 20th century anatomist Wood Jones (1916) hypothesized that in ground-dwelling quadrupedal animals, the forelimbs and hind limbs are equally responsible for controlling balance and propulsion during locomotion, whereas in arboreal quadrupedal primates, these functions are accomplished mainly by the hind limbs and their grasping feet. He referred to this as the “emancipation of the forelimbs” in primates. Cartmill (1972) later expounded that by relying on their hind limbs and grasping feet for support and propulsive forces, in particular the big toe (hallux), primates free their hands for other critical tasks of arboreal living such as

reaching out for and testing unstable branches, and facilitating foraging on thin terminal branches. Wood Jones, Cartmill, and others have argued that this functional differentiation between the forelimbs and hind limbs likely appeared early in primate evolution and served as the basis for the eventual evolution of more specialized locomotor behaviors seen in living primate taxa including vertical leaping in strepsirrhines, forelimb suspension in hominoids, and bipedalism in humans (Wood Jones, 1916; Napier, 1967; Cartmill, 1972; Rollinson and Martin, 1981; Martin, 1990; Schmitt, 2003; Cartmill et al., 2007).

Laboratory-based studies have provided empirical evidence for the atypical features of primate quadrupedalism and, in particular, for the distinct functional roles that the forelimbs and hind limbs play during arboreal locomotion (Larson, 1998; Schmitt, 2003). During above-branch pronograde locomotion, primates typically support more of their body mass on their hind limbs (Kimura et al., 1979; Demes et al., 1994; Schmitt and Hanna, 2004; Franz et al., 2005; Carlson and Demes, 2010), while in non-primate quadrupeds, body mass is supported more uniformly across the limbs or more on the forelimbs than the hind limbs (Kimura et al., 1979; Demes et al., 1994). Additionally, primate quadrupeds are highly unusual in their habitual use of diagonal-sequence symmetrical gaits, in which each foot touchdown is followed by the contact of the diagonally opposite hand (Muybridge, 1887; Hildebrand, 1967; Rollinson and Martin, 1981; Larson, 1998; Cartmill et al., 2002, 2007; Shapiro et al., 2014). This may be due, in part, to an increase in the duration of the contact time of the foot relative to the hand (Cartmill et al., 2002). In an arboreal environment, this gait pattern can potentially ensure that a foot is placed in a protracted position under the animal's center of mass on a tested branch at the moment when the contralateral hand strikes down on an untested substrate, while at the same time the contralateral foot continues to maintain a tight grip for increased stability (Cartmill et al., 2002,

2007; Fig. 1).

Electrophysiological experiments of the primary sensorimotor cortex in pronograde monkeys have shown that the point-to-point mirroring of shape and function (i.e., somatotopic representation) of the five toes is fused, and thus all digits likely function as a unit during arboreal locomotion (Hashimoto et al., 2013). In contrast, neural mapping of the fingers shows that the five digits are independent of each other, and they are therefore better suited for finer dexterity and manipulation than the toes. Complementing this, the gross morphology of various non-human primates reveals that the tendons of extrinsic digital flexor muscles of the hands have independent insertions and likewise control of different distal joints, whereas the homologous tendons in the foot often fuse together before inserting and thereby act on the same joints to produce motion (Hartman and Straus, 1971; Lewis, 1989). Additionally, relative weights of total leg and foot muscles are generally greater than total forearm and hand muscles in many primates (Tuttle, 1972).

Despite the evidence suggesting limb functional differentiation during locomotion, coupled with somatosensory and gross morphological differences between the hand and foot in primates, a critical issue remains open to question: are the muscles responsible for grasping recruited differently during arboreal quadrupedal locomotion? Specifically, do the hind limb digital flexor muscles exhibit higher, more regular, stride-correlated activity during stance than their forelimb counterparts? Rhesus macaques walking on treadmills exhibit some difference in the recruitment patterns of their digital flexor muscles of the forelimb versus hind limb (Courtine et al., 2005); however, treadmill walking cannot provide sufficient insight on the role these muscles play in grasping. For unrestrained arboreal movements, this possibility is only supported by indirect experimental evidence. For example, in common marmosets locomoting on

simulated arboreal supports, hind limb stabilizing muscular torques, estimated from kinematics and force transducer data, are higher than forelimb muscular torques, indicating that the former play a greater role in maintaining lateral stability on branches (Chadwell and Young, 2015). In addition, dynamic palmar/plantar pressure studies of Japanese macaques walking on simulated branches show that peak pressures between digits 1 and 2 of the foot are significantly higher compared to the homologous digits in the hand, thus suggesting that monkeys grasp with their hallux using higher forces than with their pollex (thumb) (Higurashi et al., 2010). The fact that intrinsic muscles controlling the hallux in adduction and flexion are relatively greater in size than those that move the pollex offers additional support for this interpretation (Tuttle, 1972).

In the present study, we investigate this issue further by analyzing the activity patterns of extrinsic toe and finger flexor muscles using telemetered electromyography (EMG) in red ruffed lemurs (*Varecia rubra*) during movement on a simulated arboreal substrate. Ruffed lemurs are an ideal model species because like nearly all extant arboreal primate quadrupeds, they habitually use diagonal-sequence gaits (Cartmill et al., 2002; see also supplemental online material (SOM) Figure S1) and support most of their body mass on their hind limbs (see SOM Table S1). Additionally, studies have demonstrated that *Varecia* primarily uses tiny (< 2.5 cm) and small (2.5-10 cm) branches during locomotion and while foraging (Dagosto, 1994, 1995). This habitat use closely matches the terminal branch environment in which the earliest primates were thought to have evolved. Moreover, evaluation of grasping in this model is relevant for understanding the primitive grasping mechanisms of primates, and possibly their evolution, since ruffed lemurs are more similar to Eocene euprimates (e.g., adapids) than to anthropoids (e.g., macaques) in the structure of their hand and foot grasping complexes, including features related to phalangeal and metapodial proportions, relative pollex and hallux lengths, degree of pollical divergence, and

hallucal grasp types (Gebo, 1985; Hamrick and Alexander, 1996; Kirk et al., 2008; Maiolino et al., 2012; Patel et al., 2012b; Boyer et al., 2013).

Materials and methods

All experimental and analytical procedures have been detailed extensively elsewhere (Boyer et al., 2007) and are only summarized here. All procedures were approved by the IACUC of Stony Brook University and Duke University.

The subjects were three adult female red ruffed lemurs (*Varecia rubra*). EMG recordings were obtained from the extrinsic finger flexors [*flexor digitorum superficialis* (FDS), *flexor digitorum profundus* (FDP)] and the extrinsic toe flexors [*flexor digitorum tibialis* (FDT), *flexor digitorum fibularis* (FDF)]. Although the intrinsic flexors muscles of the hand and foot contribute to overall forces applied by the digits during grasping (Gyambibi and Lemelin, 2013), we focused our study on only the extrinsic muscles rather than intrinsic flexors because the latter are more invasive to sample owing to the fact that electrodes would need to be inserted through the palmar and plantar surfaces and doing so would likely disrupt how the animals use their hands and feet during locomotion. Bipolar fine-wire electrodes (50 μ m) were threaded through a hypodermic needle (25 gauge) and inserted into the middle of muscle bellies while the subject was under anesthesia. Each muscle was back-stimulated with a sinusoidal current (200-500 μ A; 50Hz) to ensure proper electrode placement and verify action of muscles in isolation. Electrodes were connected to a 112 g, 4-channel FM telemetry transmitter (Bio-Sentry Telemetry, Torrance, CA, USA) attached to a non-restrictive harness worn by the subject. Subjects were placed in a large enclosure made of chain-link fence that contained a horizontally positioned pole (length: 4 m; diameter 3.1 cm) elevated ~1.0 m above the floor to simulate an arboreal substrate. A branch

diameter of 3.1 cm is considered to be relatively narrow for an animal the size of *Varecia rubra* (with a species mean of ~3.57 kg; see Goodenberger et al. [2015] and Stevens [2008]), but is considered to be within the range of the most commonly utilized substrate diameters for this species (Dagosto, 1994, 1995). Within the enclosure, subjects were allowed to move freely and only strides using symmetrical gaits (Hildebrand, 1967) without any whole-body aerial phase were studied.

EMG signals were detected by an FM receiver that sent demodulated EMG output to a SCXI-1000 A-D converter (National Instruments, Austin, TX, USA), whose signal was acquired at 2700 Hz with LabView software (National Instruments). Simultaneous video recorded at 60 Hz was superimposed onto digital EMG recordings to determine the relationship between subject behavior and muscle activity. Videos enabled identification of full step cycles and kinematic events including limb touchdown and liftoff. A custom Fortran program read raw EMG data files, identified data points corresponding to touchdown and liftoff, and calculated the root mean square (r.m.s.) of EMG for all samples of stance and swing phase at 1.85 ms intervals using a time constant of 41.85 ms. The r.m.s. EMG values were scaled as a percentage of the maximum r.m.s. EMG observed for each muscle in each experiment, which typically occurred during fence climbing.

Muscle activity was analyzed in two ways. First, another Fortran program read sample files containing r.m.s. EMG information, equalized them with regard to phase duration, and calculated at 1% intervals the weighted average distribution of the r.m.s. EMG over a step cycle for all experiments. From these data, the average activity profiles for each muscle over an entire step cycle were created to qualitatively compare activity patterns across muscles. Second, the duration and peak r.m.s. EMG values for each muscle during stance phase of each analyzed

stride were identified (see SOM for raw data). A mixed-model full factorial designed analysis was performed (to account for pseudo-replication; e.g., Patel et al., 2015) with muscle as the fixed factor and animal subject as the random factor (with experiment date nested within), and this was followed by post-hoc analyses performed using Tukey's honest significant difference (HSD) tests (see also SOM). All statistical analyses were done in JMP Pro v. 10.0 software (SAS Institute, Inc., Cary, NC, USA) with alpha levels set at 0.001.

Results

A total of four recording sessions for the three animal subjects resulted in 80 analyzable strides for each muscle, except FDT for which 69 strides could be evaluated (Table 1). Datasets supporting this article have been uploaded as part of the SOM. All muscles analyzed were active during stance phase but not swing phase, with the highest levels of activity occurring shortly after limb touchdown (Fig. 2). Mixed-model ANOVAs revealed that both duration ($F_{[3,303]} = 150.99, p < 0.001$) and intensity of muscle activity ($F_{[3,303]} = 50.25, p < 0.001$) differed significantly between muscles. Furthermore, post-hoc analyses showed that all muscles differed significantly from each other ($p < 0.001$ for each comparison) and that the toe flexors (FDF, FDT) were active for significantly longer durations and with relatively higher magnitudes than the finger flexors (FDS, FDP) (Table 2; Fig. 3). In the foot, FDF and FDT were activated for, on average (± 1 standard deviation), $89.25 \pm 7.8\%$ and $65.91 \pm 17.3\%$ of the duration of stance phase, respectively. In the hand, durations were lower with FDS and FDP activated for only $53.93 \pm 28.9\%$ and $28.15 \pm 17.5\%$ of stance, respectively. For muscle activation intensity, in the foot, peak activity of FDF and FDT reached $35.21 \pm 12.5\%$ and $28.07 \pm 15.2\%$ of maximum

burst, respectively. In the hand, peak activity of FDS and FDP reached $21.09 \pm 10.3\%$ and $14.46 \pm 6.5\%$ of maximum burst, respectively.

Discussion

Most researchers agree that arboreality shaped the unusual characteristics of primate quadrupedal locomotion (e.g., Wood Jones, 1916; Napier, 1967; Cartmill, 1972; Martin, 1990; Bloch and Boyer, 2002; Schmitt, 2003; Cartmill et al., 2007). To occupy an exclusively arboreal habitat, primates face significant locomotor and sensory challenges. They must navigate a complex three-dimensional environment often composed of flexible substrates oriented in multiple directions, and do so with sufficient stability to allow efficient and safe foraging. In part, prehensile proportions of hands and feet help overcome these challenges. However, observational data (Wood Jones, 1916; Napier, 1967; Cartmill, 1972) supported by indirect empirical biomechanical data derived from analyses of gait, kinematics, kinetics, and hand/foot pressure patterns (Muybridge, 1887; Hildebrand, 1967; Kimura et al., 1979; Rollinson and Martin, 1981; Szalay and Dagosto, 1988; Demes et al., 1994; Larson, 1998; Cartmill et al., 2002; Schmitt, 2003; Schmitt and Hanna, 2004; Franz et al., 2005; Cartmill et al., 2007; Carlson and Demes, 2010; Higurashi et al., 2010; Shapiro et al., 2014; Chadwell and Young, 2015) continue to suggest that it may be hind limb grasping with the feet that plays a more dominant role to maintain stability in an arboreal milieu. In doing so, they would leave the grasping hands available for more manipulative tasks. By investigating motor patterns (i.e., EMG) during relevant dynamic activities (cf. Herrel et al., 2008) such as arboreal locomotion, it is possible to identify whether pedal and manual grasping control differs. Our data on muscle recruitment patterns assessed by telemetered EMG show that the toe flexors are activated at relatively higher

levels and for longer durations than the finger flexors in red ruffed lemurs walking on simulated arboreal branches. These findings imply less reliance on forelimb grasps during quadrupedal locomotion, which creates the potential for directing the hands towards other roles (e.g., Georgopoulos and Grillner, 1989; Hashimoto et al., 2013; Toussaint et al., 2013).

Additional empirical data are needed from other primates and possibly other mammals capable of grasping (e.g., some arboreal marsupials) to confirm the observed differences in neuromuscular control across limb pairs. Nevertheless, previously reported muscle activity patterns appear different in habitually terrestrial mammals (e.g., cats and dogs), which tend to recruit their forelimb digital flexors with the same, if not more, duration and intensity as their hind limb flexors during locomotion (Tokuriki, 1973; English, 1978; Rasmussen et al., 1978). Therefore it remains possible that a greater emphasis on hind limb grasping is a primate-specific phenomena, or at least is stereotypical for arboreal mammals with grasping appendages.

A growing body of literature shows that a difference in the recruitment of synergistic muscles within limbs is common (e.g., O'Donovan et al., 1982; Ahn and Full, 2002; Higham et al., 2008), and this includes the digital flexor muscles (i.e., FDS vs. FDP; FDF vs. FDT). In red ruffed lemurs and baboons, FDS is active for a longer period of time and with relatively higher magnitudes than FDP during stance phase above branches and on the ground (Patel et al., 2012a; this study). In non-human primates, as well as in cats, FDF is more active than FDT (Goslow et al., 1972; O'Donovan et al., 1982; Fleshman et al., 1984; Trank and Smith, 1996; Courtine et al., 2005; Boyer et al., 2007; Patel et al., 2015; this study). The one known exception to this is in slow lorises that use their FDT more than their FDF during powerful pedal grasping bouts (Kingston et al., 2010). This difference may be related to the fact that FDT is the more massive

of the two in slow lorises (Grand, 1977), whereas FDF is relatively larger in other primates (Murie and Mivart, 1872). Irrespective of whether FDF (as in most primates) or FDT (as in slow lorises) is more active, it is clear that one is more dominant in pedal grasping, and it is this muscle that has a more significant role in flexing the hallux, a key adaptation for stability during arboreal locomotion.

The findings presented here agree with previous studies describing the unusual features of primate quadrupedal biomechanics (reviewed in Larson [1998] and Schmitt [2003]), and provide further empirical evidence reinforcing the century-old hypothesis that key hind limb adaptations of the primate neuromusculoskeletal system “emancipate” the forelimbs in their selection potential (Wood Jones, 1916). In addition to generalized quadrupedal locomotion, living primates use other specialized locomotor behaviors including forelimb suspension, hind limb grasp-leaping, quadrumanus bridging, and bipedalism. Each form requires decoupled neuromuscular control and differential use of manual and pedal grasping, or in the case of the latter, a complete independence of the hands from locomotor duties. As proposed by Wood Jones (1916) and his successors, the early neuromusculoskeletal evolution of functional limb differentiation in primates may have allowed for these specialized forms of locomotion to evolve.

Evidence of relatively long manual versus pedal phalanges and of an opposable hallux is present in early Eocene euprimates (Kirk et al., 2008; Maiolino et al., 2012; Boyer et al., 2013). These traits may have evolved as early as the late Paleocene in some closely related primate ancestors (e.g., *Carpolestes*; Hamrick and Alexander, 1996; Bloch and Boyer, 2002). Primate manual phalanges are typically relatively longer than their pedal counterparts (Jungers et al., 2005), which enhances manual prehensility including the ability to manipulate objects such as

food resources (Cartmill, 1972; Lemelin and Grafton, 1998). A relatively long and robust opposable hallux, characteristic of all arboreal primates (Gebo, 1985; Lewis, 1989; Gebo, 2004; Sargis et al., 2007), facilitates balance and stability during stance phase of an arboreal stride when actively wrapped around a branch (Boyer et al., 2007; Kingston et al., 2010; Patel et al., 2015; this study). Given that the hands and feet in our extant lemur model are morphologically similar to those of early euprimates of the Eocene (Hamrick and Alexander, 1996; Maiolino et al., 2012; Boyer et al., 2013), the results presented here lend additional support to the hypothesis (Martin, 1990; Larson, 1998) that the functional differentiation between the forelimbs and hind limbs that distinguishes primate locomotor biomechanics, including differential use of the forelimbs and hind limbs in grasping, likely occurred early in our evolutionary history.

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Author contributions. BAP and DMB designed the study; BAP, DMB, SGL, JTS performed the experiments; IJW analyzed the EMG data; MCG provided essential supporting data; BAP and IJW drafted the manuscript; all authors gave final approval for publication.

References

Ahn, A.N., Full, R.J., 2002. A motor and a brake: two leg extensor muscles acting at the same joint manage energy differently in a running insect. *J. Exp. Biol.* 205, 379-389.

- 275
- 276 Bloch, J.I., Boyer, D.M., 2002. Grasping primate origins. *Science* 298, 1606-1610.
- 277
- 278 Boyer, D.M., Patel B.A., Larson, S.G., Stern, J.T. Jr., 2007. Telemetered electromyography of
- 279 peroneus longus in *Varecia variegata* and *Eulemur rubriventer*: implications for the
- 280 functional significance of a large peroneal process. *J. Hum. Evol.* 53, 119-134.
- 281
- 282 Boyer, D.M., Yapuncich, G.S., Chester, S.G.B., Bloch, J.I., Godinot, M., 2013. Hands of early
- 283 primates. *Yrbk. Phys. Anthropol.* 57, 33-78.
- 284
- 285 Carlson, K.J., Demes, B., 2010. Gait dynamics of *Cebus apella* during quadrupedalism on
- 286 different substrates. *Am. J. Phys. Anthropol.* 142, 273-286.
- 287
- 288 Cartmill, M., 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle, R.H.
- 289 (Ed.), *The Functional and Evolutionary Biology of Primates*. Adline-Atherton, Chicago,
- 290 pp. 97-122.
- 291
- 292 Cartmill, M., Lemelin, P., Schmitt, D., 2002. Support polygons and symmetrical gaits in
- 293 mammals. *Zool. J. Linn. Soc.* 136, 401-420.
- 294
- 295 Cartmill, M., Lemelin, P., Schmitt, D., 2007. Primate gaits and primate origins. In: Ravosa, M.J.,
- 296 Dagosto, M. (Eds), *Primate Origins: Adaptations and Evolution*. Springer, New York, pp.
- 297 403-435.

298
299 Chadwell, B.A., Young, J.W., 2015. Angular momentum and arboreal stability in common
300 marmosets (*Callithrix jacchus*). Am. J. Phys. Anthropol. 156, 565-576.
301
302 Courtine, C., Roy, R.R., Hodgson, J., McKay, H., Raven, J., Zhong, H., Tang, H., Tuszynski,
303 M.H., Edgerton, V.R., 2005. Kinematic and EMG determinants in quadrupedal
304 locomotion of a non-human primate (rhesus). J. Neurophysiol. 93, 3127-3145.
305
306 Dagosto, M., 1994. Testing positional behavior of Malagasy lemurs: a randomization approach.
307 Am. J. Phys. Anthropol. 94, 189-202.
308
309 Dagosto, M., 1995. Seasonal variation in positional behavior of Malagasy lemurs. Int. J.
310 Primatol. 16, 807-833.
311
312 Demes, B., Larson, S.G., Stern, J.T. Jr., Jungers, W.L., Biknevicius, A.R., Schmitt, D., 1994. The
313 kinetics of primate quadrupedalism: hindlimb drive reconsidered. J. Hum. Evol. 26, 353-
314 374.
315
316 English, A., 1978. An electromyographic analysis of forelimb muscles during overground
317 stepping in the cat. J. Exp. Biol. 76, 105-122.
318

- 319 Fleshman, J.W., Lev-Tov, A., Burke, R.E., 1984. Peripheral and central control of flexor
320 digitorum longus and flexor hallucis longus motoneurons: the synaptic basis of functional
321 diversity. *Exp. Brain Res.* 54, 133-149.
- 322
- 323 Franz, T.M., Demes, B., Carlson, K.J., 2005. Gait mechanics of lemurid primates on terrestrial
324 and arboreal substrates. *J. Hum. Evol.* 48, 199-217.
- 325
- 326 Gyambibi, A., Lemelin, P., 2013. Comparative and quantitative myology of the forearm and
327 hand of prosimian primates. *Anat. Rec.* 296, 1196-1206.
- 328
- 329 Gebo, D.L., 1985. The nature of the primate grasping foot. *Am. J. Phys. Anthropol.* 67, 269-277.
- 330
- 331 Gebo, D.L., 2004. A shrew-sized origin for primates. *Yrbk. Phys. Anthropol.* 47, 40-62.
- 332
- 333 Georgopoulos, A.P., Grillner, S., 1989. Visuomotor coordination in reaching and locomotion.
334 *Science* 245, 1209-1210.
- 335
- 336 Goodenberger, K.E., Boyer, D.M., Orr, C.M., Jacobs, R.L., Femiani, J.C., Patel, B.A., 2015.
337 Functional morphology of the hallucal metatarsal with implications for inferring grasping
338 ability in extinct primates. *Am. J. Phys. Anthropol.* 156, 327-348.
- 339
- 340 Goslow, G.E. Jr., Stauffer, E.K., Nemeth, W.C., Stuart, D.G., 1972. Digit flexor muscles in the
341 cat: their action and motor units. *J. Morphol.* 137, 335-342.

342
343 Grand, T.I., 1977. Body weight: its relation to tissue composition, segment distribution, and
344 motor function. I. Interspecific Comparisons. Am. J. Phys. Anthropol. 47, 211-239.
345
346 Hamrick, M.W., Alexander, J.P., 1996. The hand skeleton of *Notharctus tenebrosus* (Primate,
347 Notharctidae) and its significance for the origin of the primate hand. Am. Mus. Novitates
348 3182, 1-20.
349
350 Hartman, C.G., Straus, W.L. Jr., 1971. The Anatomy of the Rhesus Monkey. Hafner, New York.
351
352 Hashimoto, T., Ueno, K., Ogawa, A., Asamizuya, T., Suzuki, C., Cheng, K., Tanaka, M., Taoka,
353 M., Iwamura, Y., Suwa, G., Iriki, A., 2013. Hand before foot? Cortical somatotopy
354 suggests manual dexterity is primitive and evolved independently of bipedalism. Phil.
355 Trans. R. Soc. B. 368, 20120417.
356
357 Herrel, A., Schaerlaeken, V., Ross, C., Meyers, J., Nishikawa, K., Abdala, V., Manzano, A.,
358 Aerts, P., 2008. Electromyography and the evolution of motor control: limitations and
359 insights. Integr. Comp. Biol. 48, 261-271.
360
361 Higham, T.E., Biewener, A.A., Wakeling, J.M., 2008. Functional diversification within and
362 between muscle synergists during locomotion. Biol. Lett. 4, 41-44.
363

- 364 Higurashi, Y., Hirasaki, E., Kumakura, H., 2010. Palmar and plantar pressure while walking on a
 365 horizontal ladder and single pole in *Macaca fuscata*. Int. J. Primatol. 31, 181–190.
 366
- 367 Hildebrand, M., 1967. Symmetrical gaits of primates. Am. J. Phys. Anthropol. 26, 119-130.
 368
- 369 Jungers, W.L., Lemelin, P., Godfrey, L.R., Wunderlich, R.E., Burney, D.A., Simons, E.L.,
 370 Chatrath, P.S., James, H.F., Randria, G.F., 2005. The hands and feet of *Archaeolemur*:
 371 metrical affinities and their functional significance. J. Hum. Evol. 49, 36-55.
 372
- 373 Kimura, T., Okada, M., Ishida, H., 1979. Kinesiological characteristics of primate walking: its
 374 significance in human walking. In: Morbeck, M.E., Preuschoft, H., Gomberg, N. (Eds),
 375 Environment, Behavior and Morphology: Dynamic Interactions in Primates. G. Fischer,
 376 New York, pp. 297-311.
 377
- 378 Kingston, A.K., Boyer, D.M., Patel, B.A., Larson, S.G., Stern, J.T. Jr., 2010. Hallucal grasping
 379 in *Nycticebus coucang*: further implications for the functional significance of a large
 380 peroneal process. J. Hum. Evol. 58, 33-42.
 381
- 382 Kirk, E.C., Lemelin, P., Hamrick, M.W., Boyer, D.M., Bloch, J.I., 2008. Intrinsic hand
 383 proportions of euarchontans and other mammals: implications for the locomotor behavior
 384 of plesiadapiforms. J. Hum. Evol. 55, 278-299.
 385

- 386 Larson, S.G., 1998. Unique aspects of quadrupedal locomotion in non-human primates. In:
 387 Strasser, E., Fleagle, J., Rosenberger, A., McHenry, H. (Eds), Primate Locomotion:
 388 Recent Advances. Plenum Press, New York, pp. 157-173.
 389
- 390 Lemelin, P., Grafton, B.W., 1998. Grasping performance in *Saguinus midas* and the evolution
 391 of hand prehensility in primates. In: Strasser, E., Fleagle, J., Rosenberger, A., McHenry,
 392 H. (Eds), Primate Locomotion: Recent Advances. Plenum Press, New York, pp. 131-144.
 393
- 394 Lewis, O.J., 1989. Functional Morphology of the Evolving Hand and Foot. Clarendon, Oxford.
 395
- 396 Maiolino, S., Boyer, D.M., Bloch, J.I., Gilbert, C.C., Groenke, J., 2012. Evidence for a grooming
 397 claw in a North American adapiform primate: implications for anthropoid origins. PLOS
 398 ONE 7, e29135.
 399
- 400 Martin, R.D., 1990. Primate Origins and Evolution. Princeton University Press, Princeton.
 401
- 402 Murie, J., Mivart, S.G., 1872. On the anatomy of the Lemuroidea. Trans. Zool. Soc. Lond. 7, 1-
 403 113.
 404
- 405 Muybridge, E., 1887. Animal Locomotion. Dover, New York.
 406
- 407 Napier, J.R., 1967. Evolutionary aspects of primate locomotion. Am. J. Phys. Anthropol. 27,
 408 333-342.

409

410 O'Donovan, M.J., Pinter, M.J., Dum, R.P., Burke, R.E., 1982. Actions of FDL and FHL muscles
 411 in intact cats: functional dissociation between anatomical synergists. J. Neurophysiol. 47,
 412 1126-1143

413

414 Patel, B.A., Larson, S.G., Stern, J.T. Jr., 2012a. Electromyography of wrist and finger flexor
 415 muscles in olive baboons (*Papio anubis*). J. Exp. Biol. 215, 115-123.

416

417 Patel, B.A., Seiffert, E.R., Boyer, D.M., Jacobs, R.L., St. Clair, E.M., Simons, E.L., 2012b. New
 418 primate first metatarsals from the Paleogene of Egypt and the origins of the anthropoid
 419 big toe. J. Hum. Evol. 63, 99-120.

420

421 Patel, B.A., Larson, S.G., Stern, J.T. Jr., 2015. Electromyography of crural and pedal muscles in
 422 tufted capuchin monkeys (*Sapajus apella*): implications for hallucal grasping behavior
 423 and first metatarsal morphology in euprimates. Am. J. Phys. Anthropol. 156, 553-564.

424

425 Rasmussen, S., Chan, A.K., Goslow, G.E. Jr., 1978. The cat step cycle: electromyographic
 426 patterns for hindlimb muscles during posture and unrestrained locomotion. J. Morph.
 427 155, 253-270.

428

429 Rollinson, J., Martin, R.D., 1981. Comparative aspects of primate locomotion, with special
 430 reference to arboreal cercopithecines. Symp. Zool. Soc. Lond. 48, 377-427.

431

- 432 Sargis, E.J., Boyer, D.M., Bloch, J.I., Silcox, M.T., 2007. Evolution of pedal grasping in
433 Primates. *J. Hum. Evol.* 53, 103-107.
434
- 435 Schmitt, D., 2003. Insights into the evolution of human bipedalism from experimental studies of
436 humans and other primates. *J. Exp. Biol.* 206, 1437-1448.
437
- 438 Schmitt, D., Hanna, J.B., 2004. Substrate alters forelimb to hindlimb peak force ratios in
439 primates. *J. Hum. Evol.* 46, 237-252.
440
- 441 Shapiro, L.J., Young, J.W., VandeBerg, J.L., 2014. Body size and the small branch niche using
442 marsupial ontogeny to model primate locomotor evolution. *J. Hum. Evol.* 68, 14-31.
443
- 444 Szalay, F.S., Dagosto, M., 1988. Evolution of hallucial grasping in the Primates. *J. Hum. Evol.*
445 17, 1-33.
446
- 447 Tokuriki, M., 1973. Electromyographic and joint-mechanical studies in quadrupedal locomotion.
448 I. Walk. *Jap. J. Vet. Sci.* 35, 433-446.
449
- 450 Toussaint, S., Reghem, E., Chotard, H., Herrel, A., Ross, C.F., Poydebat, E., 2013. Food
451 acquisition on arboreal substrates by the grey mouse lemur: implication for primate
452 grasping evolution. *J. Zool.* 291, 235-242.
453

- 454 Tuttle, R., 1972. Relative mass of the cheiridial muscles in catarrhine primates. In: Tuttle, R.H.
455 (Ed), The Functional and Evolutionary Biology of Primates. Aldine-Atherton, Chicago,
456 pp. 262-291.
457
- 458 Trank, T.V., Smith, J.L., 1996. Adaptive control for backward quadrupedal walking VI.
459 Metatarsophalangeal joint dynamics and motor patterns of digit muscles. J. Neurophysiol.
460 75, 678-694.
461
- 462 Wood Jones, F., 1916. Arboreal Man. Edward Arnold, London.
463

Captions

Table 1. Number of steps sampled for toe flexors (FDF, FDT) and finger flexors (FDS, FDP) in three subjects and across four experiments.

Table 2. Mean, least-squares (LS) mean, and 1 standard error of LS mean values of relative muscle activity duration and peak activity intensity in toe flexors (FDF, FDT) and finger flexors (FDS, FDP). All muscles are significantly different in relative duration and relative peak activity (see also Fig. 3).

Figure 1. Red ruffed lemur walking on a simulated arboreal substrate and wearing a jumpsuit and telemetry transmitter attached to a harness. The subject is using a diagonal-sequence gait in which the right foot touchdown is followed by the contact of the left hand. Stability is maintained by the grasping feet.

Figure 2. Muscle activity determined by EMG in finger flexors (FDS, FDP) and toe flexors (FDF, FDT). (A) Representative raw EMG waves for two consecutive step cycles. Stance phase begins with touchdown (TD) and ends with liftoff (LO). (B) Average distribution of r.m.s. EMG over a step cycle for all experiments. EMG values have been scaled to a percentage of maximum burst. Only r.m.s. EMG values greater than 5% of maximum burst were considered meaningful and only these are illustrated.

485 **Figure 3.** Least squares (LS) means and 1 standard error for relative muscle duration (A) and
486 relative peak activity (B) in toe flexors (FDF, FDT) and finger flexors (FDS, FDP). All muscles
487 are significantly different in relative duration and relative peak activity (see also Table 2).

488

fig 1

A **B**

fig 2

1 **Table 1.**

Subject	Experiment #	FDF	FDT	FDS	FDP
A	1	12	12	13	13
A	2	11	0	9	9
B	1	5	5	5	5
C	1	52	52	53	53
Total Steps:		80	69	80	80

2

3

4 **Table 2.**

Variable	Statistic	FDF	FDT	FDS	FDP
Relative Duration [†]	Mean	89.25	65.91	53.93	28.15
	LS mean	92.05	70.42	56.94	31.16
	1 Std. error	4.756	4.765	4.765	4.899
Relative Peak Activity [*]	Mean	35.21	28.07	21.09	14.46
	LS mean	33.91	26.95	19.84	13.21
	1 Std. error	2.106	2.229	2.114	2.114

5 [†] % of stance phase

6 ^{*} % of maximum burst activity

7