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Hallucal grasping in *Nycticebus coucang*: further implications for the functional significance of a large peroneal process

Amanda K. Kingston[a,*], Doug M. Boyer[b], Biren A. Patel[b], Susan G. Larson[b], Jack T. Stern Jr.[b]

[a] *Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, New York 11794, USA*
[b] *Department of Anatomical Sciences, Stony Brook University Medical Center, Stony Brook, New York 11794, USA*

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ABSTRACT

Euprimate grasping feet are characterized by a suite of morphological traits, including an enlarged peroneal process on the base of the first metatarsal, which serves as the insertion site of the peroneus longus muscle. In prosimians, a large process has typically been associated with a powerful hallucal grasp via the contraction of the peroneus longus to adduct the hallux. Recent electromyography (EMG) studies have documented that peroneus longus does not contribute substantially to hallucal grasping in lemurids (Boyer et al., 2007). However, non-lemurid prosimians have a I-V opposable grasp complex that is morphologically different and phylogenetically more primitive than the I-II adductor grasp complex of the lemurids previously studied. Therefore, it is possible that peroneus longus did function during grasping in early euprimates, but lost this function in large-bodied lemurids. The present study tests the hypothesis that a large peroneal process is related to powerful grasping ability in primates displaying the more primitive I-V grasp complex. We use EMG to evaluate the recruitment of peroneus longus, other crural muscles, and adductor hallucis in static and locomotor grasping activities of the slow loris (*Nycticebus coucang*). Results show that peroneus longus is active during grasping behaviors that require the subject to actively resist inversion of the foot, and likely contributes to a hallucal grasp in these activities. Peroneus longus activity level does not differ between grasping and power grasping activities, nor does it differ between grasping and non-grasping locomotor modes. Conversely, the digital flexors and hallucal adductor are recruited at higher levels during power grasping and grasping locomotor modes. Consequently, we reject the hypothesis that an enlarged peroneal process represents an adaptation specifically to enhance the power of the I-V grasp, but accept that the muscle likely plays a role in adducting the hallux during grasping behaviors that require stabilization of the ankle, and suggest that further work is necessary to determine if this role is sufficient to drive selection for a large peroneal process.

Introduction

The base of the prosimian first metatarsal presents a hypertrophied peroneal process, the function of which has been contested (Walker, 1974; Conroy, 1976; Gebo, 1985, 1986, 1987, 1988, 2004; Szalay and Dagosto, 1988; Bloch and Boyer, 2002; Boyer et al., 2007; Gebo et al., 2008). This process serves as the insertion site for the tendon of the peroneus longus muscle, which has been hypothesized to adduct the hallux in addition to its commonly recognized role as an evertor of the foot (Lewis, 1972; Conroy, 1976; Gebo, 1985, 1987, 1993). These actions have been experimentally confirmed by electromyography (EMG) in two lemur species (Boyer et al., 2007).

Adduction of the hallux has been thought to play an important role in hallucal grasping by effectively pinching the substrate between the first and second digits, thus adding additional power to the grasping force generated during flexion of the digits (Cartmill, 1985; Szalay and Dagosto, 1988; Gebo, 1993; Lemelin, 1999; Boyer et al., 2007). Such speculations have lead to the hypothesis that a hypertrophied peroneal process enables powerful grasping by increasing the lever arm of the peroneus longus muscle (and thereby increasing its mechanical advantage) and/or by increasing its attachment area (Walker, 1974; Szalay and Dagosto, 1988; Gebo and Dagosto, 1988). This hypothesis has, in turn, been invoked to divide species into groups of “powerful” or “non-powerful” grasping ability (Gebo, 2004).

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* Corresponding author. Tel.: +1-651-341-6921; fax: +1-631-444-3947.
E-mail address: Kingston.amanda@gmail.com (A.K. Kingston).

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In contrast to this hypothesis, a recent electromyography (EMG) study has indicated that peroneus longus does not contribute significantly to grasping behaviors in lemurid prosimians (Boyer et al., 2007). Boyer et al. (2007) found peroneus longus to be relatively inactive when grasping during both static (i.e., postural) and dynamic (i.e., locomotion) activities. Accordingly, these findings call into question the plausibility of a real functional link between peroneal process size and improved hallucal grasping ability.

Boyer et al. (2007) acknowledged that lemurids possess a derived foot morphology compared to non-lemurid primates. Specifically, most lemuriformes possess what Gebo (1985) described as a I-II adductor grasp, which is characterized by (1) a continuous, oblique articular surface across the second through fifth tarsometatarsal joints, which orients the metatarsals in an arch, (2) a lateral plantar facet on the second metatarsal, which deviates laterally from vertical and is confluent with the tarsometatarsal joint, and (3) a relatively large adductor hallucis muscle with fused transverse and oblique heads. The obliquely oriented second metatarsal lateral plantar facet prevents the third metatarsal from lying in line with the second metatarsal, forcing the third metatarsal dorsally. The continuous tarsometarsal joint allows the fourth and fifth metatarsals to shift their proximal articulations dorsally to meet the elevated third metatarsal. This arrangement of metatarsals results in an arrangement of the foot wherein the third through fifth metatarsals lie in a plane oblique to that created by the first and second metatarsals (Gebo, 1985). This oblique foot arrangement, in conjunction with a relatively larger adductor hallucis muscle, was interpreted by Gebo (1985) to be a mechanically advantageous adaptation for vertically clinging primates with large body sizes; the relatively larger adductor hallucis muscle could supply the additional force needed to generate a secure grasp around a vertical substrate.

A second, more phylogenetically primitive mechanism described by Gebo (1985) as the “I-V opposable grasp” is found in cheirogaleids, lorisids, *Daubentonia*, tarsiids, and adapids. The first digit opposes the fifth digit around the substrate, with all four lateral digits contributing to force production during grasping. Species possessing the I-V grasp have feet that are characterized by (1) a discontinuous joint surface at the tarsometatarsal joints, where the ectocuneiform sits slightly more distal than the cuboid, (2) a vertically oriented lateral plantar facet on the second metatarsal, and (3) relatively more massive intrinsic musculature for flexing and opposing the first and fifth digit. The vertically oriented lateral plantar process and discontinuous tarsometatarsal joint surface allow all five digits to lie in the same horizontal plane (Gebo, 1985). This grasp is possessed largely by small-bodied primates, and has been interpreted by Gebo (1985) to be less powerful than the more derived I-II adductor grasp.

To evaluate whether or not the patterns of muscle recruitment observed by Boyer et al. (2007) reflect a general pattern of muscle use for all prosimians, or are specific for those that have the I-II grasp complex, we have undertaken a similar EMG analysis on the slow loris, *Nycticebus coucang*. Although the foot of the slow loris displays certain derived characteristics, such as a hallux that is deviated 90 degrees from digits two through five, volar pads that are expanded to increase surface contact area, and a second, clawed digit that is reduced in length (Grand, 1967; Dykyj, 1980), the slow loris retains the phylogenetically primitive I-V opposable grasp and has an enlarged peroneal process. The I-V grasp is evidenced not only by the osteological characters discussed previously, but also in the muscular contributions to, and use of, the second digit in grasping; the second digit receives the smallest of the five flexor tendons and, because of its diminutive length, rarely lies in direct opposition to the hallux during grasping activities (Grand, 1967; Dykyj, 1980).

In the present study, the hypothesized link between an enlarged peroneal process and powerful grasping ability was tested in two ways. First, involvement of peroneus longus in general grasping activities through adduction of the hallux was explored. If an enlarged peroneal process reflects the importance of peroneus longus for grasping, it should be actively recruited during all ordinary grasping activities. Second, a specific link to powerful grasping was tested; use of an enlarged peroneal process to categorize taxa into groups with “powerful” or “non-powerful” grasps requires evidence that peroneus longus is responsible for increased grasp strength during power grasping behaviors. Demonstration of increasing levels of peroneus longus EMG activity from non-grasping behaviors to ordinary grasping to powerful grasping would support such an interpretation.

Grasping activities were defined as those in which the hallux was observed to (1) forcefully oppose the lateral digits around a substrate, and (2) adduct to pinch the substrate between the first and second digits. Grasping behaviors were subdivided into a set of ordinary grasps involved in static positional behaviors, grasps involved in dynamic positional behaviors (i.e., locomotion), and power-grasping behaviors, which required that the grasp be maintained against a larger antagonistic force than generated by normal locomotor or static positional behaviors. Non-grasping activities were defined as those that did not require the forceful opposition or adduction of the hallux and the lateral digits (such as standing or walking across the top of a cylindrical substrate, the circumference of which was more than two or three times the circumference of a substrate that the subject could grasp with the tips of the hallucal digit just touching those of the lateral digits).

Materials and methods

Experimental subjects

Two adult female *Nycticebus coucang* individuals were studied. Both animals were on loan from the Duke Lemur Center and were temporarily housed in the Stony Brook University Primate Locomotion Laboratory. Body-weights for these subjects are provided in Table 1. The Animal Care and Use Committees of Stony Brook University and Duke University approved all experimental protocols.

Focal muscles

The experimental procedures of Boyer et al. (2007) were followed closely to facilitate comparison of results. These procedures are detailed here for the reader’s convenience.

Because the role of peroneus longus in grasping activities was of primary interest, this known evertor of the foot was observed along with muscles used in grasping activities in other taxa: flexor digitorum tibialis, flexor digitorum fibularis, and adductor hallucis. Peroneus brevis, an evertor of the foot that does not adduct the hallux, was observed to reveal which activities require eversion (or the prevention of inversion) of the foot, with or without grasping. Figure. 1 illustrates the positions of the focal muscles in the leg and foot.

Table 1
Number of experiments conducted for each muscle and subject.

Subject (Mass)	Total	PL	PB	FDT	FDF	AH
Female 1 (0.9 kg)	5	5	5	5	2	4
Female 2 (1.15 kg)	2	2	2	1	0	2
Total	7	7	7	6	2	6

PL: peroneus longus, PB: peroneus brevis, FDT: flexor digitorum tibialis, FDF: flexor digitorum fibularis, AH: adductor hallucis