Integrative experimental and morphological study of the metacarpal and metatarsal bones of the Japanese macaque (*Macaca fuscata*)

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**Abstract** Primate hands and feet are versatile and offer an opportunity to examine how morphology reflects compromises among different functions in daily activities. In this study, we investigated the diaphyseal robusticity of metacarpals (MCs) and metatarsals (MTs) and discussed their correlation with locomotor and other behaviors in the semiterrestrial Japanese macaque (*Macaca fuscata*). The objectives of this study were to determine (1) whether more robust MCs and MTs experience higher forces during terrestrial locomotion than less robust bones; and (2) whether MT3, which is suggested to be the functional axis of the foot in Japanese macaques, is more robust than MT2, MT4, and MT5. Computed tomography of MCs1–5 and MTs1–5 was performed in 10 monkeys. As a measure of bone robusticity, the buckling strength of each MT and MC was calculated as $J/L^2$ where $J$ is the polar second moment of area and $L$ is the bone length. Hand and foot pressure were recorded using plantar pressure measurement systems while two monkeys moved on a flat floor over a range of speeds (0.72–2.56 m/s). The relationship between the bone robusticity and the load applied to the bones during terrestrial locomotion was analyzed. Our results did not support the two predictions. There was no positive correlation between diaphyseal robusticity and the peak force in both male and female Japanese macaques. There was no clear difference in bone robusticity among MTs2–5 in both males and females. These results suggest that the relation between MC and MT robusticity and mechanical loading during locomotion is not as straightforward as might be expected, possibly due to the complex multifunctionality of primate hands and feet. Additional integrative studies that similarly incorporate morphological and experimental approaches are expected to provide useful insights into macaque hand and foot morphology.

**Key words:** Foot, hand, locomotion, manipulation

**Introduction**

Primate hands and feet are versatile; they are used to support primate body weight and to apply propulsive, braking, and mediolateral forces to the substrate during motion, to change speed and direction (Rossignol et al., 2006; Musienko et al., 2012). Primates also have grasping feet with an opposable big toe, used to maintain balance on narrow branches during arboreal locomotion (Cartmill, 1974; Higurashi et al., 2010). The primate hand displays dextrous finger movements when manipulating small food items and grooming (Heffner and Masterton, 1983; Fragaszy, 1998); during these activities, a variety of hand postures are used (Christel, 1993; Murata et al., 2000) and movements of the opposable thumb are of great importance (Napier, 1993). These similarities and differences in the use of primate hands and feet offer an excellent opportunity to examine how morphology reflects compromises among different functions.

This study investigated the diaphyseal robusticity of the metacarpals (MCs) and metatarsals (MTs) and discussed their correlation with locomotor and other behaviors in the semiterrestrial Japanese macaque (*Macaca fuscata*). In particular, we attempted to relate bone robusticity with mechanical loading during terrestrial quadrupedism, which is a primary mode of locomotion for Japanese macaques (Chatani, 2003), and with the functional or leverage axis of the foot (Morton, 1922, 1924). An explanation for the morphological adaptation of bone to the mechanical environment throughout the lifetime is the general concept of bone functional adaptation (Ruff et al., 2006). This model states that, for example, a bone responds to increased strain by depositing more bone tissue, although other competing factors, including phylogeny and age, can influence bone response to loading. We compared adult bones located in similar anatomical regions in a single species to control for phylogenetic and age effects. Bones of nonhuman primates are subjected to large loads during locomotion. However, the relation between bone morphology and mechanical loading during locomotion is not always straightforward (Demes et
al., 1998, 2001; Morimoto et al., 2011) and requires further investigation. Demes et al. (1998, 2001) indicated that the macaque ulna and tibia are not reinforced in the plane of bending during functional activities. Morimoto et al. (2011) showed that average femoral morphology is largely similar in wild and zoo chimpanzees although captive individuals clearly differ from wild ones in the frequency of each locomotor behaviors, including bipedal and quadrupedal locomotion, climbing, leaping, and suspensory behavior (Jensvold et al., 2001). Although measuring strain in vivo during activity by implanting strain gauges into the bone is a useful approach to this problem (Demes et al., 1998, 2001; Lieberman et al., 2004), it is invasive and not always feasible.

With regard to primate hand and foot skeletal elements, MCs and MTs are suitable bone models to investigate the relation between bone morphology and mechanical loading during locomotion. MCs and MTs differ in length, thickness, and cross-sectional shape (Fleagle, 2013). It follows that these bones also differ in diaphyseal robusticity because the strength of a structure depends on its length and the geometric properties of its cross-section, all other properties being equal (Case et al., 1999). Furthermore, the distal articular surfaces (heads) of MCs and MTs have been shown to make direct contact with the substrate during locomotion in some primates, including Japanese macaques (Higurashi et al., 2010, 2018; Hirasaki et al., 2010), white-handed gibbons (Vereecke et al., 2005), chimpanzees (Wunderlich and Ischner, 2017), bonobos (Vereecke et al., 2003), and humans (Pataky and Goulermas, 2008; Stolwijk et al., 2013). Accordingly, the pressure, or force per unit area, exerted on these bones can be measured non-invasively through the use of plantar pressure measurement systems. MT robusticity may also be related to the functional axis of the foot. Some research suggests that Japanese macaques have the functional axis on MT3, which has been suggested as the functional axis of the foot in Japanese macaques, is more robust than MT2, MT4, and MT5.

**Materials and Methods**

**Metacarpal and metatarsal robusticity**

The skeletal objects of study were the ipsilateral MCs1–5 and MTs1–5 of 10 Japanese macaques (Table 1). Attempts were made to measure the bones from the right side. The sample included five males and five females, all of whom were captive animals. No pathological signs were observed. The sex, age at death, and body mass at death were obtained from museum records. L was measured from the midpoint of the proximal articular facet to the midpoint of the distal articular facet using digital calipers (Figure 1A). All specimens were housed at the Primate Research Institute, Kyoto University.

Bones were imaged on a helical computed tomography (CT) scanner (Asteion™ PREMIUM 4 Edition; Toshiba Medical Systems, Tochigi, Japan) at the Primate Research Institute, Kyoto University. Scans of the full length of the bone were performed at a slice thickness of 0.5 mm, tube voltage of 120 kV, and tube current of 200 mA. Before scanning, each specimen was placed on the scanner table and oriented such that cross-sections were orthogonal to the long axis of the diaphysis (Figure 2A). CT images were reconstructed as a matrix of 512 × 512 pixels. The reconstructed field of view was adjusted according to the cross-sectional area of the bone specimen, and pixel sizes ranged from 0.019 to 0.125 mm. For cross-sectional images of the midshaft (Figure 2B), J was quantified using the ImageJ plugin MomentMacroJ version 1.4 (www.hopkinsmedicine.org/fae/mmacro.html; Figure 1B). The midshaft was taken as 50% of the maximum length. Buckling strength of the bone was normalized as follows:

\[ J = \frac{L}{E \times I} \]

where \( J \) is the polar second moment of area and \( L \) is the bone length (Biewener, 1992; Currey, 2003; Cowgill, 2010). \( J \) is a cross-sectional geometric property that represents the general bending rigidity of the bone in all planes of a section (Lieberman et al., 2004; Stock and Shaw, 2007). Furthermore, because \( J \) and \( L \) are expected to vary with body size, it is necessary to control for this variable. Therefore, we used \( J/(L^2 \times mg) \) as a measure of bone robusticity where \( m \) is body mass and \( g \) is gravitational acceleration (≈9.81 m/s²).

This work represents a comprehensive study of the functional morphology of MCs and MTs in Japanese macaques. To our knowledge, no data have been published on the J values of MCs and MTs in this species. Some studies have reported hand and foot pressure during locomotion in Japanese macaques (Higurashi et al., 2010, 2018; Hirasaki et al., 2010), but detailed data on individual hand regions have not been reported. Although the design of this study did not allow us to reveal cause-and-effect relationships between morphological features and behaviors, understanding their correlations will facilitate more plausible interpretations of macaque hand and foot morphology. The specific aims of this study were twofold. We investigated whether more robust MCs and MTs experience higher force during terrestrial locomotion than less robust bones. We also explored whether MT3, which has been suggested as the functional axis of the foot in Japanese macaques, is more robust than MT2, MT4, and MT5.

**Table 1. Metacarpal and metatarsal specimens used in this study**

| Catalog No. | Sex | Age at death (years) | Body mass at death (kg) |
|-------------|-----|----------------------|-------------------------|
| 2177        | M   | 17                   | 10.9                    |
| 3466        | F   | 9                    | 6.9                     |
| 3719        | F   | 15                   | 6.4                     |
| 4067        | F   | 9                    | 7.3                     |
| 4334        | M   | 13                   | 13.4                    |
| 4379        | F   | 10                   | 6.5                     |
| 6554        | F   | 15                   | 5.0                     |
| 6560        | M   | 12                   | 10.6                    |
| 6925        | M   | 14                   | 11.1                    |
| 7664        | M   | 20                   | 9.2                     |

* Mean ± SD.
 normalized buckling load $= \frac{J}{L^2 \times m \times g} \times 10^6$.

The accuracy of the medical CT images was tested by comparing the raw $J$ values of MCs1–5 and MTs1–5 of specimen #6554, the smallest individual in this study, as determined by medical CT and peripheral quantitative CT (pQCT). The latter has been shown to have a spatial resolution sufficient for evaluating the geometric properties of small bones of small animals, including mice and rats (Jämsä et al., 1998; Schmidt et al., 2003). The bones of specimen #6554 were scanned using a pQCT scanner (XCT Research SA+; Stratec Medizintechnik, Pforzheim, Germany) at the Evolutionary Morphology Section, Primate Research Institute, Kyoto University using procedures similar to those used in medical CT. The pQCT scans were performed at a voxel size of 0.06 mm, tube voltage of 50.4 kV, and tube current of 0.454 mA. The threshold for the cortical bone in the pQCT images was set at 500 mg/cm$^3$, and $J$ was calculated using MomentMacroJ version 1.4 software. The differences between medical CT and pQCT were slight compared with those between bones (Table 2). These results show that medical CT achieves a satisfactory spatial resolution that provides accurate information on the geometric properties of macaque MCs and MTs.

**Table 2. Comparisons of the polar second moment of area ($J$) determined by medical computed tomography (CT) and peripheral quantitative CT (pQCT) for specimen #6554**

| Bone | Medical CT | pQCT |
|------|------------|------|
| MC1  | 6.4        | 5.9  |
| MC2  | 9.9        | 10.1 |
| MC3  | 15.9       | 16.3 |
| MC4  | 13.0       | 12.9 |
| MC5  | 7.5        | 6.8  |
| MT1  | 23.3       | 22.6 |
| MT2  | 18.2       | 19.2 |
| MT3  | 35.3       | 33.6 |
| MT4  | 19.7       | 19.6 |
| MT5  | 14.9       | 15.3 |

MC, metacarpal; MT, metatarsal.

**Figure 2.** (A) Three-dimensional virtual surface model of a first metatarsal, illustrating the midshaft (50%) location, at which the polar second moment of area was calculated. The midshaft location was calculated from the maximum length. The virtual surface model was created using a DAVID 3D Scanner (DAVID Vision Systems, Koblenz, Land Rheinland-Pfalz, Germany). (B) Examples of midshaft cross-sectional CT images of the first metacarpal (MC1) and first metatarsal (MT1). The pixel size was 0.033 mm.

**Figure 1.** (A) Mean metacarpal and metatarsal lengths ($L$) of male and female Japanese macaques. $L$ was taken as the distance from the midpoint of the proximal articular facet to the midpoint of the distal articular facet. Error bars represent one standard deviation of the mean. (B) Mean polar second moment of area ($J$) for the metacarpals and metatarsals of male and female Japanese macaques. $J$ provides an estimate of the torsional and (twice) average bending rigidity of the bone.
a flat 6-m-long concrete floor (Figure 3; Higurashi et al., 2010, 2018). Without prompting by leash, the monkeys were either allowed to select their own preferred speeds or incentivized to move faster using food rewards. Because the hand-pressure records were originally obtained for another study (Higurashi et al., 2018), only foot pressure was recorded, at 120 Hz using a 220 mm × 240 mm pressure mat (BIG-MAT quarter; Nitta, Osaka, Japan) at the midpoint of the path. The pressure mat quantified normal forces with an array of 5 mm × 5 mm sensing elements (Figure 4). Forces were standardized by dividing the force by (mg). Locomotion was videotaped in the lateral view at 60 frames/s using one or two digital video cameras to assess speed. Each monkey performed locomotor trials continuously for 25 min each day. Trials were discarded if hand and foot contact with the pressure mat was only partial. We obtained 47 hand-pressure and 30 foot-pressure records from 54 strides of monkey A and 33 hand-pressure and 32 foot-pressure records from 50 strides of monkey B.

Dynamic pressure data analysis was performed using MATLAB R2015a software (MathWorks, Natick, USA). We defined three hand or foot regions for this analysis: MC/MT1, MC/MT2–3, and MC/MT4–5. In all pressure records, the thenar pad and interdigital pads were readily identifiable (Figure 4). The thenar pad is the region where the heads of MC/MT1 are located, and the interdigital pads are the area where the heads of MC/MT2–5 are located. However, currently available plantar pressure measurement systems may not have sufficient spatial resolution to accurately distinguish forces acting on individual MCs2–5 and MTs2–5 of small to medium-sized primates. Accordingly, we divided this area into MC/MT2–3 and MC/MT4–5 following methods used in pedobarographic studies of chimpanzees (Wunderlich and Ischinger, 2017) and Japanese macaques (Hirasaki et al., 2010). The peak force over a stride cycle

Figure 3. Experimental setup for hand-pressure and foot-pressure measurements. Monkeys were trained to travel in a straight path, as denoted by a dashed line. A pressure mat was located at the midway point of the path.

Figure 4. (A) The palmar surface of the hand and plantar surface of the foot of a Japanese macaque. The images were taken using a GT-8700F flatbed scanner (EPSON, Nagano, Japan). Dashed curves denote boundary lines between adjacent interdigital pads. MC1, first metacarpal; MCs2–5, second to fifth metacarpals; MT1, first metatarsal; MTs2–5, second to fifth metatarsals. (B) Representative peak pressure patterns under the hand and foot during terrestrial locomotion. When analyzing the dynamic pressure data, we divided the interdigital pads into two regions: MC/MT2–3 and MC/MT4–5.
was calculated for each sensing element within a region, and the maximum value was used to determine the peak force on the region. Speed was calculated as the average velocity of easily identifiable body landmarks, including the base of the tail and the external auditory meatus, in one stride, as defined by two successive touchdowns of the same limb (Figure 3). Coordinates of these landmarks were determined using Frame-DIAS V software (DKH, Tokyo, Japan).

Statistical analyses
Data for males and females were analyzed separately to prevent differences in male and female behavior from affecting the results. Chatani (2003) found that males were more terrestrial than females in a free-ranging group at the Tsubaki Wild Monkey Park, Shirahama, Wakayama, Japan; her results suggested that preferred positional behaviors differed between male and female Japanese macaques. Statistical analyses were performed using OriginPro 2017 software (LightStone, Tokyo, Japan) at a significance level of $\alpha = 0.05$. Significant differences in peak force among hand and foot regions were evaluated using one-way ANOVA and post-hoc multiple comparisons. The relation between the bone robusticity and the peak force applied to the bones during terrestrial locomotion was analyzed by Pearson’s correlation coefficient.

Results
We obtained pressure data over a range of speeds (monkey A: 0.72–2.56 m/s; monkey B: 0.76–1.35 m/s). The mean ± SD speed was 1.23 ± 0.60 m/s in monkey A and 1.07 ± 0.13 m/s in monkey B. Most steps were diagonal sequence gaits (Hildebrand, 1967). A gallop, which is the fastest quadrupedal gait, was not observed. One-way ANOVA revealed that different hand and foot regions experienced significantly different magnitudes of peak force during terrestrial locomotion in all monkeys (Figure 5 and Table 3). Post-hoc multiple comparisons revealed common patterns among individuals. In all monkeys, MC2–3 and MC4–5 experienced significantly higher peak force than MC1, MT1, MT2–3, and MT4–5. In turn, MT1, MT2–3, and MT4–5 experienced significantly higher peak force than MC1. Thus, MC1 was the region that experienced the lowest peak force during terrestrial locomotion. Some individual differences were observed. MC4–5 experienced significantly higher peak force than MC2–3 in monkey A, whereas there was no significant difference between these regions in monkey B. No significant differences were observed among MT1, MT2–3, and MT4–5 in monkey A, whereas MT2–3

Table 3. Results of one-way analysis of variance (ANOVA) and post-hoc tests comparing peak force during terrestrial locomotion across six anatomical regions

| Individual | ANOVA results | $P$ value obtained from post-hoc multiple comparisons |
|------------|---------------|----------------------------------------------------|
|            | $F(5225) = 52.716$ | MC1 | MC2–3 | MC4–5 | MT1 | MT2–3 | MT4–5 |
| Monkey A   | $P < 0.001$   | $<0.001$ | $<0.001$ | 0.001 | $<0.001$ | 0.014 |
|            | $F(5189) = 32.955$ | MC2–3 | 0.002 | $<0.001$ | $<0.001$ | $<0.001$ |
|            | $<0.001$ | $<0.001$ | 0.001 | $<0.001$ | $<0.001$ | $<0.001$ |
|            | $<0.001$ | $<0.001$ | 0.026 | $<0.001$ | 0.005 | 0.009 |
|            | $NS$ | $NS$ | $NS$ | $NS$ | $NS$ | $NS$ |

NS, not significant; MC, metacarpal; MT, metatarsal.
and MT4–5 experienced significantly higher peak force than MT1 in monkey B.

There was no positive correlation between diaphyseal robusticity and the peak force applied to the bone in both male ($r = -0.291, df = 8, P = 0.415$) and female Japanese macaques ($r = -0.605, df = 8, P = 0.064$; Figure 5). Because the standard deviation was large, there was no clear difference in bone robusticity among MTs2–5 in both males and females.

**Discussion**

We investigated the diaphyseal robusticity of MCs and MTs and the forces applied to these bones during terrestrial locomotion in Japanese macaques to explore how their morphology reflects compromises among different functions in the daily activities of primates. In this section, we discuss how MC and MT robusticity correlates with locomotor and other behaviors, including terrestrial locomotion. Unlike many other studies that have simply explored the adaptive influence of ‘locomotor behaviors’ in general, our study is unique in that we attempted to directly relate bone morphology with biomechanical data. The results of this study do not support our two predictions. There was no positive correlation between diaphyseal robusticity and the peak force applied to the bone during terrestrial locomotion. There was no clear difference in bone robusticity among MTs2–5.

We observed that MCs2–5 experienced significantly higher peak forces than MTs2–5, but there was no positive correlation between robusticity and load applied. A possible explanation for this discrepancy is that the peak force imposed by terrestrial locomotion at the speeds analyzed in this study (0.72–2.56 m/s) is rather low compared with the buckling strength of MCs2–5 and MTs2–5, and thus does not correlate well with their diaphyseal robusticity. As a result of the low speed range, we did not observe galloping. MCs2–5 may experience relatively high peak pressures because, at low speeds, the hand is more digitigrade and the contact area is smaller (Higurashi et al., 2018). At high speeds, Japanese macaques change hand posture to increase contact area under the palm and possibly to mitigate stresses on the hand skeleton (Higurashi et al., 2018). The macaque foot is semiflattened at low speeds, and the calcaneus never contacts the substrate (Hirasaki et al., 2010), but there has been no study indicating an increase of contact area under the foot with increasing speed, as with the hand. Therefore, it is likely that the relative magnitude of the force applied to hand and foot regions varies depending on locomotion speed, when the full speed range of Japanese macaques in their natural habitat is considered. This speculation needs to be confirmed by investigating hand and foot pressure during high-speed galloping in Japanese macaques.

Given the peak force experienced during terrestrial locomotion, MC1 and MT1 appear to be overly robust (Figure 5). We acknowledge that bone morphology may be related to other modes of locomotion. Monkeys perform halluxal grasping to maintain lateral stability while moving on a narrow arboreal substrate, by pinching the substrate between the big toe and the other pedal digits (Higurashi et al., 2010). This foot use probably results in heavy loads being applied to MT1 during arboreal locomotion. The association between MT1 robustness and halluxal grasping was also indicated by an experimental study using a mouse model, in which laboratory mice reared in arboreal habitats developed more robust MT1 than those reared in terrestrial habitats (Byron et al., 2015). The robustness of MC1 may be partly associated with grasping by the thumb during arboreal locomotion, as with MT1. Hands are also used for manipulation and social interaction. To our knowledge, there has been no report of preferential use of the foot over the hand for food item manipulation or grooming in Japanese macaques. Therefore, it is likely that MC1 morphology reflects compromises between powerful grasping during arboreal locomotion and the control of dexterous finger movement. However, MC1 of humans is more robust than that of non-human primates, despite the advanced manual dexterity of humans (Marzke, 2013). This apparent contradiction may be explained by the fact that the human hand experiences high mechanical stresses during stone tool production and use (Key and Dunmore, 2015; Williams-Hatala et al., 2018).

A limitation of this study was the use of discrete samples to obtain bone morphology and dynamic pressure data. Because the living environments of each animal can lead to individual differences in bone morphology (Carlson and Judex, 2007; Byron et al., 2015), intra-individual comparisons would be preferable. We observed considerable individual variation in diaphyseal robusticity among MCs and MTs in Japanese macaques. Perhaps this result should be unsurprising, because individual variation in diaphyseal robusticity among MTs has also been reported in humans, chimpanzees, bonobos, and gorillas (Patel et al., 2018).

In summary, the results of this study suggest that the relationship between MC and MT robusticity and mechanical loading during locomotion is not as straightforward as might be expected, possibly due to the complex multifunctionality of primate hands and feet. Our results add to those of integrative studies incorporating morphological and experimental approaches in the field of functional morphology (Demes et al., 2001; Fernández et al., 2016; Fabre et al., 2018; Wilson et al., 2018). Although collecting comparable data across all possible behaviors is practically impossible, this relatively rare type of research is expected to overcome our lack of knowledge about the quantifiable relationship between bone morphology and mechanical loading during daily activities and offer valuable insights into primate hand and foot morphology.

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