SHAPE MEETS FUNCTION: STRUCTURAL MODELS IN PRIMATOLOGY

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Locomotor performance, morphology and environment: An integrative approach to primate locomotion

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Summary - Understanding the evolutionary processes leading to the various locomotor adaptations of primates requires a functional linking of locomotor behaviour with morphological features. However, the currently available data on primate locomotion are often not sufficient to validate theories on the evolutionary history of primate locomotion, especially regarding the emergence of habitual bipedalism in the lineage of early humans. In addition to studies of kinetics and muscle activity that require sophisticated equipment in a laboratory, it is crucial to obtain kinematic data from relatively many untrained subjects which locomote freely in large, semi-natural enclosures. In this paper, studies of vertical climbing in several primate genera are summarised. Gait parameters such as cycle duration, duty factor, stride length and speed are used to determine the influence of body size (through an intraspecific comparison of age/sex classes), the influence of the environment (through an intraspecific comparison of animals moving on different substrates or living in different habitats) and the influence of morphology (through an interspecific comparison with other primate species) on the locomotor performance of living primates.

Keywords – Kinematics, vertical climbing, Ateles fusciceps, Gorilla gorilla, Lagothrix lagotricha, Pan paniscus, Pongo abelii, Hylobates lar, Nomascus gabriellae, Nomascus leucogenys, Symphalangus syndactylus.

Introduction

Understanding the evolutionary processes leading to the various locomotor adaptations of primates requires a functional linking of locomotor performance with morphological features. However, the currently available data on primate locomotion are often not sufficient to validate theories on the evolutionary history of primate locomotion, especially regarding the emergence of habitual bipedalism in the lineage of early humans (Gebo, 1996).

In addition to studies of kinetics and muscle activity that require sophisticated equipment in a laboratory (reviewed in Schmitt, 2003), it is crucial to obtain kinematic data from relatively many untrained subjects which locomote freely in large, semi-natural enclosures. The more complex the acquisition of data, the smaller the number of subjects included in a study will become. To assess whether those few subjects locomote in a way typical for their species, it is therefore necessary to compare the basic gait parameters with a larger kinematic database containing a representative sample of intraspecific variation.

In a comparative study of vertical climbing kinematics in primates, we have collected spatio-temporal gait parameters such as gait patterns, stride length, frequency, duty factor and speed, as well as intersegmental joint angles in three dimensions, for more than 50 individuals of bonobos, gorillas, orang-utans, gibbons, spider and woolly monkeys climbing on vertical ropes or poles. In this paper, the results of those studies are summarised. In addition, different factors that influence the locomotor performance are isolated and their consequences for interspecific comparisons are discussed. Ultimately, we are interested in the influence of morphology on locomotion, which will allow us to draw conclu-
sions about the locomotor habits of our past relatives from fossilized primate remains. To this aim, the influence of differences in body size and environment are analyzed separately while keeping the other factors constant.

Subjects and methods

More than 12 rehabilitant or wild orang-utans from Sumatra, as well as 39 hominoid individuals in the zoos of Zürich, Mulhouse, Jersey, Apenheul Primate Park and Brookfield Zoo, Chicago, were videotaped with up to four digital video cameras (50 frames per second) during vertical climbing on ropes, lianas, poles or trees. The following parameters were analyzed: footfall patterns, cycle frequency, relative duration of the support phase (duty factor), stride length, speed, intersegmental angles of shoulder, elbow, hip and ankle joints, and the distance of the body centre of gravity from the substrate. Parameters were normalised using lower leg length as a determinant of body size following Aerts et al. (2000). A detailed description of the study subjects and methods can be found in (Isler & Thorpe, 2003; Isler, 2004, 2005).

Differences between captive, rehabilitant and wild individuals were analyzed in Sumatran orang-utans (Pongo pygmaeus abelii). Climbing on different substrates was analyzed in spider monkeys (Ateles fusciceps robustus), woolly monkeys (Lagothrix lagotricha) and rehabilitant orang-utans. Differences in body size within a species can be attributed to sexual dimorphism as in gorillas (Gorilla gorilla gorilla) or woolly monkeys, or to ontogenetic growth studied in infant bonobos (Pan paniscus), juvenile gorillas and juvenile orang-utans. Unfortunately, intraspecific variation in body size between sex and age groups is often accompanied by variation in morphological characteristics such as limb length ratios or distribution of mass within or between body segments (Isler et al., submitted). These two factors cannot be separated. Further, there are other factors that may influence locomotor performance, such as motivation, hidden illness or pathology, or individual disposition.

Interindividual variation can only be assessed if enough individuals of the same sex/age group locomoting on the same substrates are included in a study. In the present analysis, this was possible for juvenile gorillas, adult female orang-utans, and, to a limited extent, adults of both sexes in bonobos and crested gibbons (Nomascus gabriellae and N. leucogenys). Finally, interspecific comparisons were conducted between spider and woolly monkeys, gibbons (Hylobates lar) and siamangs (Symphalangus syndactylus), gorillas and bonobos, orang-utans vs. African apes, and gibbons vs. great apes.

Results and discussion

The following results were found (summarized from Isler, 2002b, a, 2003; Isler & Thorpe, 2003 Isler, 2004, 2005; and unpublished data):

Gait parameters of spider monkeys climbing on vertical ropes, vertical thin trees or oblique ropes do not differ significantly. Gibbons climbing on vertical ropes or on nearly vertical bamboo poles show very similar gait parameters. On the other hand, differences between flexed-elbow climbing on small-diameter substrates and extended-elbow vertical climbing on large-diameter substrates are pronounced: spider monkeys climbing on large-diameter tree trunk take shorter strides, at a higher frequency and with a lower duty factor than when climbing on small-diameter substrates (Fig. 1). However, the two types of climbing differ less in orang-utans than in spider monkeys. Spider monkeys exhibit adaptations to suspensory locomotion and are convergent to hominoids in many morphological traits, although their arms are not as elongated as in orang-utans. Thus, the observed differences between orang-utans and spider monkeys suggest that climbing on a large-diameter vertical substrate may indeed be of adaptive significance for the evolution of elongated arms, as biomechanical considerations suggest (e.g. Cartmill, 1974; Stern et al., 1977; Fleagle et al., 1981; Preuschoft, 1990).

Captive, rehabilitant and wild orang-utans show very similar gait parameters during flexed-elbow vertical climbing (Fig. 2). Captives climb faster,
supposedly because they have an intimate knowledge of the substrates used for climbing, whereas in the Sumatran rainforest seemingly robust substrates may break under the animal body weight. Thus it is beneficial for wild individuals to move cautiously.

A large sexual dimorphism in body size and especially in body weight has profound influences on the locomotor performance. Climbing is disproportionately more energetically demanding for heavier individuals (Taylor et al., 1972). The adult male gorilla climbs with shorter strides at an equivalent speed than the adult female or the juvenile gorillas. The range of motion of the major limb joints is greatly reduced in this individual. In woolly monkeys, which also exhibit a large sexual size dimorphism, differences between adult males and females are less pronounced than in gorillas.

The effects of age-related differences in body size are more difficult to detect since they are accompanied by differences in the expertise of locomotion. While the climbing style of infant bonobos is clearly not mature, showing in unstable gait patterns and highly variable gait parameters, juvenile apes are mostly equally or more adept in climbing than adults. Juvenile orang-utans and gorillas climbed more easily than adults, showing in a higher cycle frequency, lower duty factor and a larger distance between the body centre of gravity from the substrate. In the wild, juvenile apes are often more arboreal than adults (Doran, 1992; Hunt, 1994; Remis, 1995; Doran, 1997). Due to metabolic differences and the allometric relationship of muscle dimensions to body weight, climbing is energetically relatively more expensive for larger animals (Taylor et al., 1972; Cartmill, 1974). Thus, juveniles are expected to climb more easily than adult animals of the same species, which is corroborated by the observed differences in gait parameters during flexed-elbow vertical climbing.

Interindividual differences between three juvenile gorillas of almost exactly the same age were found to be negligible. On the other hand, differences between adult female orang-utans are

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Fig. 1 - Climbing on different substrates: Least-squares regression of relative stride length versus normalised speed during flexed-elbow vertical climbing on ropes and thin trees (circles) and extended-elbow vertical climbing on large-diameter trees (crosses) of Ateles fusciceps robustus in Apenheul Primate Park, NL.
sometimes large, presumably caused by individual disposition and character. The most affected parameter is climbing speed, whereas differences in speed modulation or duty factor are small. In adult bonobos, males and females climbed very differently, although sexual size dimorphism is small. A reason for this is currently unknown.

If all these intraspecific factors influencing climbing performance are taken into consideration, it becomes obvious that evolutionary conclusions from locomotor studies on laboratory primates must be treated with utmost caution. Nevertheless, it is now possible to obtain valid interspecific distinctions in climbing kinematics, which are larger than previously assumed (Hunt, 1991, 1992). Adult male gorillas, infant bonobos, as well as subjects engaging in extended-elbow vertical climbing were all excluded from this analysis.

Even if all parameters are normalised with body size, gibbons climb faster, with a higher cycle frequency, longer strides and a lower duty factor than siamangs. The acrobatic gibbons climb more easily than the great apes, at higher speed and taking relatively long strides. The arms take much longer strides than the legs, resulting in completely irregular footfall patterns that change continuously. Gibbons never walk quadrupedally on the ground or on horizontal branches, and thus they seem also to lack a quadrupedal limb coordination during climbing. It would be interesting to investigate whether this is innate or lost during gibbon infancy. Further, gibbons abduct the arm more and the thigh less during climbing than any of the great apes. The postcranial morphology of gibbons is mainly adapted for brachiation (Andrews & Groves, 1976), which influences their climbing style considerably.

Orang-utans are the largest extant canopy-dwelling animals (Delgado and van Schaik, 2000). To minimise the risk of breaking substrates, they move slowly and cautiously. For orthograde scrambling and bridging, their limb joints are highly mobile (Morbeck & Zihlman, 1988; Tuttle & Cortright, 1988). The high mobility of the orang-utan limbs is reflected in the kinematics of vertical climbing. Orang-utans climb slowly, with very long strides at a very low frequency. Compared to gorillas and bonobos, they take longer strides at an equivalent speed (Fig. 3). The range of motion of the major limb joints in adult

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Fig. 2 - Climbing in different habitats: Least-squares regression of relative stride length versus normalised speed during vertical climbing in adult female orang-utans (Pongo abelii) in Jersey Zoo (circles) and in Bukit Lawang, Sumatra (crosses).
orang-utans is larger than in African apes, although the hip is not more extended. Compared to orang-utans, the morphology and the locomotor behaviour of bonobos and gorillas is relatively similar. Both exhibit knuckle-walking on horizontal substrates, and are also well adapted for suspension and climbing. However, gorillas and bonobos are not geometrically similar animals of different body size, as comparative data among the African apes reveal a complicated mix of differences in chest girth, shoulder height, scapular positioning and thoracic shape (e.g. Schultz, 1930; Shea, 1981; Jungers and Susman, 1984; Shea, 1984). Shea (1981) noted that, as the African apes increase in body size, they become relatively shorter, more stout and barrel-chested. He suggested that the reorganisation of these body proportions may be the result of selection to maintain functional equivalence at different body sizes. If this were correct, we would expect basic similarities of climbing kinematics between gorillas and bonobos. Indeed, most gait parameters and joint angles during vertical climbing were found to be very similar in the two species of African apes studied. Nevertheless, the climbing of bonobos is more diverse in speed and gait patterns compared to gorillas. More variable footfall patterns are combined with a larger range of speed and stride lengths (cf. Fig. 3). Speed modulation also differs slightly between gorillas and bonobos. To increase speed, gorillas tend to increase stride length less and frequency more than adult bonobos do. It seems that the light-weight bonobos can afford to have long legs and use them in a multitude of climbing styles, whereas the heavier gorillas remain close to an energetically optimal relationship of kinematics, stride length and speed. In a hypothetical light-weighed ancestral hominoid, a corresponding flexibility could have opened ways to new locomotor behaviours such as frequent or habitual bipedalism.

Maximum limb extension seems to be more similar between Ateles and the hominoids than between Ateles and Macaca (Hirasaki et al., 1999; Hirasaki et al., 1993; Hirasaki & Matano, 1996; Hirasaki et al., 2000). Maximum protraction of the shoulder, however, is more pronounced in gibbons and orang-utans, and maximum hip extension is larger in adult great apes than in spider monkeys. If, as Hirasaki and colleagues (2000) conclude, the type of vertical

![Fig. 3 - Climbing with different morphologies: Least-squares regression of relative stride length versus normalised speed during vertical climbing in Pongo abelii (circles) compared to African apes (Gorilla gorilla: crosses, Pan paniscus: squares).](image-url)
climbing of the spider monkeys is more preadaptive to bipedal walking than that of macaques, this applies equally or even more to the hominoid type of vertical climbing.

In conclusion, the results presented here corroborate the findings of Hirasaki et al. (2000), that there are different types of vertical climbing which are not all equally preadaptive for bipedalism. Moreover, even the climbing styles of the different hominoid species differ considerably. Body weight and limb lengths clearly influence the kinematics of vertical climbing, but they are not sufficient to explain the interspecific differences found. Locomotor specialisations of some species, e.g., brachiation in gibbons or slow scrambling in orang-utans, can also be recognised in the vertical climbing performance.

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