Morphological integration and the evolution of knuckle-walking

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ABSTRACT

The evolution of knuckle-walking has profound implications for our understanding of the emergence of bipedalism. The modern debate surrounding its evolution is concerned with whether or not it is homologous in chimpanzees and gorillas. Here, this problem is approached using the methods of morphological integration to test hypotheses of patterns and magnitudes of integration in the third manual ray and capitate. If knuckle-walking morphologies are highly integrated and evolve in a correlated bundle (i.e., comprising a functional complex), it seems reasonable that they could have been recruited independently relatively easily in gorillas and chimpanzees, thus increasing the likelihood of homoplasy. If, however, there is no evidence for a knuckle-walking complex, then it seems less likely that chimpanzees and gorillas would have evolved knuckle-walking independently. Results indicate that chimpanzees and gorillas are not characterized by high magnitudes of integration or unique patterns of integration that distinguish them from non-knuckle-walking taxa. This does not support the hypothesis of a knuckle-walking complex, nor does it support the contention that knuckle-walking could have been easily evolved independently in chimpanzees and gorillas. Implications for trait analysis and the evolution of bipedalism are discussed, as are recent analyses supporting the independent origins of knuckle-walking.

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Introduction

The debate surrounding the evolution of knuckle-walking has a long history and its inception predates the discovery of an early fossil hominin (Dart, 1925). Although W. K. Gregory and D. J. Morton agreed in general about the evolution of orthogrady in apes, their views on the evolution of bipedalism were not congruent. While Gregory (1916:334) proposed that the terrestrial locomotion of gorillas and chimpanzees is a "peculiar method of taking strides with the forearms, in a semi-erect posture" and "forms a necessary prelude to fully erect bipedal progression," Morton (1926:158) rejected the view "that the terrestrial semi-erect posture of the great apes represents an approach toward the upright posture of man," instead arguing that "there is nothing homologous in their respective terrestrial postures." This early disagreement marks the beginning of a long debate over the role of knuckle-walking in human evolution (see Richmond et al., 2001; Crompton et al., 2008 and sources therein). Currently, the debate is concerned with whether knuckle-walking is homologous in chimpanzees and gorillas, having evolved only once in the common ancestor of hominines (gorillas, chimpanzees, and humans) or whether it has evolved multiple times independently (Dainton and Macho, 1999;

Inouye, 2002; Inouye and Shea, 2004; Orr, 2005; Williams, 2006; Filler, 2007; Kivell and Schmitt, 2009; Lovejoy et al., 2009).

The possibility that knuckle-walking may have evolved independently in gorillas and chimpanzees has been offered as an alternative to the homologous origin of knuckle-walking for some time (e.g., Pilbeam, 1970; de Bonis, 1983; Boaz, 1988), but it was not explicitly supported by morphological data until Dainton and Macho (1999), in a study of the ontogeny and allometry of chimpanzee and gorilla wrist bones, concluded that the parallel evolution of knuckle-walking was more parsimonious than a single origin. Recently, Kivell and Schmitt (2009) came to the same conclusion based on a similar study of wrist bones. Lovejoy et al. (2009) have most recently expressed support for the independent evolution of knuckle-walking based on their interpretation of the forearm of *Ardipithecus ramidus*.

If knuckle-walking is homologous, then the last common ancestor of not only hominines, but also that of humans and chimpanzees, was a knuckle-walker. This evolutionary history would place the emergence of bipedalism in the context of a knuckle-walking background. Alternatively, if knuckle-walking evolved independently in the chimpanzee and gorilla clades, then it is likely that bipedalism was preceded by some other type of locomotor mode. This issue is fundamental to our understanding of the evolution of bipedal locomotion. In order to attempt to explain

why bipedalism evolved in the first place, we need to understand the evolutionary sequence of events that preceded it.

Several researchers have discussed a "complex" of knuckle-walking morphologies in the chimpanzee and gorilla wrist and hand (Tuttle and Basmajian, 1974; Tuttle, 1975; Corruccini, 1978; Ciochon, 1983; Tuttle and Watts, 1985; Andrews, 1987; Andrews and Martin, 1987; Begun, 1992; Inouye, 1994, 2002; Tuttle et al., 1999; Corruccini and McHenry, 2001; Orr, 2005; Williams, 2006). Andrews and Martin (1987) have even claimed that features related to knuckle-walking are identical in chimpanzees and gorillas. Similarly, according to Begun (1992):1932), knuckle-walking specializations "are all functionally correlated, always occurring together, and may be more legitimately considered as a single complex trait." That traits related to knuckle-walking might interact as a functional module and evolve in a correlated bundle suggests that they could have been relatively easily recruited and evolved independently in gorillas and chimpanzees. McCollum (1999) made a similar argument in support of the independent evolution of "robust" craniofacial morphologies in *Paranthropus boisei* and *Paranthropus robustus*. Using principles of growth remodeling and craniofacial morphogenesis, she argued that features that had been considered homologous in the robust australopithecines were in fact "merely developmental by-products" resulting from parallel adaptations to heavy chewing in two separate lineages (McCollum, 1999:304). This argument implies that morphological complexes can be readily recruited and easily evolved, increasing the likelihood of homoplasy in trait complexes (Lockwood and Fleagle, 1999; Lockwood, 2007).

The hypothesis of the existence of a knuckle-walking complex (i.e., strong correlations among knuckle-walking traits and shared patterns of integration among knuckle-walkers) is testable using the methods of morphological integration (Olson and Miller, 1958; Cheverud et al., 1989; Porto et al., 2009). Natural selection is expected to favor the co-inheritance of morphological elements that perform common functions or developmental processes, selecting for the genetic integration of such traits. In this way, functional and developmental integration lead to genetic integration, which in turn leads to evolutionary morphological integration, "the coordinate evolution of elements contained within functional complexes" (Marroig and Cheverud, 2001:2576). Traits of a functional complex, therefore, should be highly integrated and evolve higher correlations among themselves than with unrelated traits, particularly in regions of the body where function plays a major role (i.e., locomotion). In addition, taxa characterized by a common morphological complex should share similar patterns of integration to the exclusion of other taxa. Here, I employ correlation analyses in order to determine if it is likely that chimpanzees and gorillas evolved knuckle-walking independently. The existence of a knuckle-walking morphological complex in these taxa could have allowed for the independent recruitment of knuckle-walking in response to similar selection pressures (i.e., a tradeoff between efficient terrestrial locomotion and the maintenance of long fingers for climbing). Alternatively, if a discernable knuckle-walking complex does not exist, then knuckle-walking behavior would likely have been more difficult to evolve independently, supporting the homology of knuckle-walking.

Materials and methods

To test the hypothesis that a knuckle-walking complex characterizes the extant knuckle-walkers, linear morphological data were collected from the hand and wrist of 345 hominid (great ape) specimens of the following species: humans (*Homo sapiens*, $n = 88$), chimpanzees (*Pan troglodytes*, $n = 78$), bonobos (*Pan paniscus*, $n = 17$), eastern gorillas (*Gorilla beringei*, $n = 34$), western gorillas

(*Gorilla gorilla*, $n = 86$), and orangutans (*Pongo pygmaeus*, $n = 42$). Cheverud (1988) and Ackermann (2009) have shown that relatively large sample sizes are required for studies of morphological integration. Ackermann (2009) calculated correlations between covariance matrices constructed from various sample sizes and from a "true" matrix constructed with a sample size of 250. Her results indicate that at least 40 specimens from each taxon are required to reliably produce correlations of 0.90 or higher (with an average correlation of about 0.96). In this study, the sample size of orangutans ($n = 42$) is above this threshold and those of humans ($n = 88$), chimpanzees ($n = 76$), and western gorillas ($n = 86$) are well above it.

Fourteen linear distances of the capitate and third manual ray (third metacarpal and its associated proximal and intermediate phalanges) were measured from adult, museum specimens to the nearest hundredth of a millimeter using a digital sliding caliper (Mitutoyo Absoulte Digimatic, Tokyo). These measurements were chosen based on their purported functional role in knuckle-walking in chimpanzees and gorillas (Table 1, Fig. 1). The third ray is centrally located and both chimpanzees and gorillas exert large forces on it during knuckle-walking throughout ontogeny (Matarazzo, 2008; Wunderlich and Jungers, 2009). The capitate has been identified as the "most obviously modified [carpal] bone" in hominines (Richmond et al., 2001:93; see also Aiello and Dean, 2002). For this reason, and because of its association with the base of the third ray, the capitate was also selected for analysis in this study.

Because variation due to sexual dimorphism can obscure inter-trait correlations (de Oliveira et al., 2009), a difference of means sex adjustment is applied to taxa in which differences between sexes are significant, as determined by canonical variates analysis. Specimens whose sex is unknown are classified as either male or female if they can be confidently allocated to one sex or the other using discriminate function analysis. In only two cases was this not possible, and two chimpanzees were excluded from analysis for this reason. In addition, when subgeneric differences are significant, these taxa are treated as separate groups for analysis. In this way, spurious correlations due to variation between subgroups are minimized and the number of taxa examined is maximized. Bonobos and eastern gorillas were treated as separate groups, but were excluded from further analysis because their correlation matrices produce negative eigenvalues (i.e., they are non-positive definite), presumably due to low sample size and missing data. Detailed analyses, therefore, were conducted only on humans ($n = 88$; hereafter *Homo*), chimpanzees ($n = 76$; hereafter *Pan*), western gorillas ($n = 86$; hereafter *Gorilla*), and orangutans ($n = 42$; hereafter *Pongo*).

If a knuckle-walking complex exists, we should reasonably expect to find: 1) high correlations between traits within that functional complex, and 2) similar patterns of integration shared among knuckle-walking taxa. Correlations among traits are quantified in a correlation matrix, where a trait's correlation with itself is one (along the diagonal) and the off-diagonal elements represent correlations among the traits used to construct the matrix. The magnitude of integration (MI) is measured in two ways: 1) as the variance of eigenvalues (Cheverud et al., 1989; Pavlicev et al., 2009), and 2) as the average squared Pearson product−moment correlation coefficients among inter-trait (off-diagonal) elements (de Oliveira et al., 2009). Both of these methods require standardization procedures. In the first case, the variance of eigenvalues is standardized by the number of traits and the maximum eigenvalue, following Pavlicev et al. (2009), yielding the standardized variance of eigenvalues (VE). For the second method, because correlations are not normally distributed, raw Pearson correlations are normalized using a Fisher's Z-transformation (Van Valen, 1965).