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Functional integrative analysis of the human hip joint: The three-dimensional orientation of the acetabulum and its relation with the orientation of the femoral neck

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ABSTRACT

In humans, the hip joint occupies a central place in the locomotor system, as it plays an important role in body support and the transmission of the forces between the trunk and lower limbs. The study of the three-dimensional biomechanics of this joint has important implications for documenting the morphological changes associated with the acquisition of a habitual bipedal gait in humans. Functional integration at any joint has important implications in joint stability and performance. The aim of the study was to evaluate the functional integration at the human hip joint. Both the level of concordance between the three-dimensional axes of the acetabulum and the femoral neck in a bipedal posture, and patterns of covariation between these two axes were analysed.

First, inter-individual variations were quantified and significant differences in the three-dimensional orientations of both the acetabulum and the femoral neck were detected. On a sample of 57 individuals, significant patterns of covariation were identified, however, the level of concordance between the axes of both the acetabulum and the femoral neck in a bipedal posture was lower than could be expected for a key joint such as the hip. Patterns of covariation were explored regarding the complex three-dimensional biomechanics of the full pelvic-femoral complex. Finally, we suggest that the lower degree of concordance observed at the human hip joint in a bipedal posture might be partly due to the phylogenetic history of the human species.

Introduction

Although numerous primates use bipedalism in their locomotor repertoire, the species *Homo sapiens* is characterized by a habitual and permanent bipedal gait and posture. Compared with quadrupeds, the human permanent bipedal posture entails an important decrease of the base of support and a rise of the body's center of mass, two disadvantages in a biomechanical static point of view. In response to the new biomechanical constraints imposed by the erect posture, the skeleton of our ancestors was adaptively modified over the course of evolution, optimizing the functional performances of the locomotor system. In the literature, human synapomorphies that could be functionally involved in bipedal gait and posture have been identified, including morphological traits of the hip (e.g., Zihlman and Hunter, 1972; Lovejoy et al., 1973; McHenry, 1975; Berge and Ponge, 1983; Stern and Susman, 1983; Tardieu, 1983, 1999; Berge et al., 1984; Asfaw, 1985; Berge and Kazmierczak, 1986; Lovejoy, 1988, 2005a, b; Abitbol, 1989, 1995; Ruff, 1994, 1998; MacLatchy and Bossert, 1996; Macchiarelli et al., 1999; Marchal, 2000; Haüsler, 2002). The hip joint, a diarthrosis, which articulates the acetabular region with the proximal femur, occupies a central place in the locomotor skeleton. It plays an important role in body support and the transmission of the forces between the trunk and lower limbs. Consequently, the hip joint is of main importance to the study of human evolution in that additional data could be provided to document and better understand bipedal acquisition in the human lineage.

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Numerous authors have used the biomechanical approach for the study of the evolution of the human hip joint (e.g., Ruff, 1991, 1995, 1998; MacLatchy, 1996; MacLatchy and Bossert, 1996; Lovejoy, 2005b). Anthropological and medical studies have together contributed to identify the strong relationships between both micro- and macro-architectures of the two opposing articulating components of the hip joint and its weight-bearing function, as it is now surveyed. Rather than being a simple part of a sphere, the acetabular socket presents a complex structure, which optimizes its functional performance. First, the general horseshoe-shaped structure of the facies lunata optimizes the stress distribution along the contact surface, refocusing the peak constraints in the center of the surface rather than close to its edge (Daniel et al., 2005). Moreover, this surface was described as an arched dome (Bullough et al., 1968, 1973; Goodfellow and Mitsou, 1977), which makes possible deformations under high loads, resulting in an increase of the sphericity and a more homogeneous distribution of the forces along the total contact surface (Dalstra and Huiskes, 1995). Under high loads, for example during the one-legged stance of walking, the acetabular roof, composed not of hyaline cartilage but of fibrocartilage (Day et al., 1975), comes in contact with the femoral head (Greenwald and Haynes, 1972; Day et al., 1975; Mizrahi et al., 1981) and the horns of the facies lunata connect with the femoral head (Teinturier et al., 1984; Lazennec et al., 1997). The incongruity between the acetabular roof and the femoral head may be important to ensure the circulation of synovial fluid needed for the nutrition and lubrication of the cartilage (Greenwald and O'Connor, 1971). Moreover, differences between humans and great apes have been identified in the size of the acetabular socket, thus also in the size of the femoral head. While an isometric relation was described between the femoral head size and body mass in non-human hominoids (Ruff and Runestad, 1992; Ruff, 1998), humans demonstrate a larger femoral head size for their body size (Corruccini and McHenry, 1978; Ruff, 1988; Rafferty, 1998). This is likely due to the fact that during the one-legged stance, the body mass is supported by only one limb increasing the reaction force received by each foot while the body weight is shared with two or three legs during quadrupedal gait. Concerning the femur, the femoral neck demonstrates also a complex architecture in accordance with its biomechanical role. A strong asymmetric cross-sectional distribution of the cortical bone along the femoral neck has been observed in humans (Lovejoy, 1988, 2005b; Ohman et al., 1997). Although this character is not a distinctive human feature, as it was observed in other primate species (Rafferty, 1998; Matsumura et al., 2010), a strong relationship between asymmetric cortex and locomotor behaviour has been demonstrated. Concerning humans, biomechanical models showed that both forces induced by the body weight and forces induced by abductor muscles, which act to prevent pelvic drop (Pauwels, 1935; Inman, 1947; McLeish and Charnley, 1970), result in a gradient of compressive constraints running from low intensity at the superior part to high intensity at the superior part (Pauwels, 1980; Lovejoy, 1988, 2005b). This gradient may partly explain the asymmetric growth of the femoral neck cortex. Moreover, the trabecular bone is organized along three major trabecular systems (medial, trochanteric and arcuate), which reveal the lines of principal stresses induced by the erect posture and bipedal gait (Inman, 1947; Heimkes et al., 1993; Ryan and Krovitz, 2006; Skuban et al., 2009).

Biomechanical analyses can reveal the functional relevance of a structure by identifying the links between particular morphological traits and constraints imposed by functions they ensure. Evolutionary changes identified using this morphofunctional approach result from direct selection pressure related to the functions ensured by the structure. However, in addition to the direct selection, evolution depends on the morphological integration as well (Lande and Arnold, 1983; Arnold, 1992; Cheverud, 1996). Indeed, morphological traits are not independent of each other and patterns of covariation between traits have consequences on the evolvability of a structure (Lande and Arnold, 1983; Cheverud, 1996), i.e., its ability to evolve (Hansen and Houle, 2004, 2008). Because of this integration, direct selection on a specific character may lead to associated responses in other characters. In some cases, change in character due to associated response could have a negative effect on the complete fitness, limiting change in the initial selective character. This results in stabilizing selection, which explains the relatively low rate of evolution compared with global evolutionary models (Lynch, 1990; Hansen and Houle, 2004; Estes and Arnold, 2007; Uyeda et al., 2011). Consequently, we can easily understand that morphological integration can lead to evolutionary changes that could be different than those expected based on biomechanical models. Thus, integrative analyses are of importance for the study of evolution. An example illustrating the significance of integrative analyses in understanding evolution are the recent studies on morphological integration of the pelvis in primates. These studies demonstrated that evolution of the human pelvic girdle was facilitated by reduced levels of integration between the ilium and ischiopubic modules (Grabowski et al., 2011; Grabowski, 2012; Lewton, 2012).

Morphological integration is partly due to genetic integration. Genetic integration corresponds to traits that are inherited together (Cheverud, 1996). This association between inherited traits can be caused by genes that have pleiotropic effects on multiple elements (Lande, 1980), or by linkage disequilibrium where several genes that affect different traits are inherited together (Falconer, 1989). These two mechanisms resulting in genetic integration are expressed during development, which partly explains developmental integration. Developmental integration is not only directed by genetic integration but also by both direct interactions between several morphological elements during their development and/or non-genetic common external sources (e.g., biomechanical constraints, pollution, maternal hormone). Consequently, research regarding hip joint development, using studies on humans but also of other animals such as rodents, birds or amphibians, has provided useful information to understand morphological integration. It is currently demonstrated that all of the constituents of the hip joint (e.g., bone, cartilage, capsule, ligaments, synovial fluid) evolve from a single mesenchymal mass, which derives entirely from lateral mesoderm (Chevallier, 1977; Clavert, 1987; Uhthoff and Carey, 1990; Lee and Eberson, 2006; Malashichev et al., 2008; Pomikal and Streicher, 2010). At the third week after fertilization in humans, a hint of the hindlimb is observed as a limb bud. Ablation experiments of this limb bud in very early chicken embryos lead to an abnormal development of the pelvic elements, illustrating that the presence of the hindlimb bud is required for pelvis formation at a very early stage of development (Spurling, 1923; Malashichev et al., 2005). In a normal atherogenesis, all main components of the human joint are in place at the sixth week but the articular cavity is absent. This very early interactive development between the acetabulum and the femoral head is characteristic of the 'primary joint' morphogenesis (Francis-West et al., 1999). The articular cavity in the human hip joint appears around the eighth week by cell death (Spitz and Duboule, 2001; Mariani and Martin, 2003). The complete achievement of the articular cavity is dependant on the limb movements, as experiments using artificial immobilization in embryos have demonstrated the critical role of muscular loading in joint formation (Hall, 1972; Hall and Herring, 1990; Pitsillides, 2006). Throughout growth, the normal development of both the acetabular socket and the femoral head depends greatly upon the interactions between these two opposing components (Le Damany, 1903b; Harrison, 1961; Lee and Eberson, 2006). Abnormal placement or growth of one of these two components induces a pathological growth of the other one.