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Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

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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ARTICLE INFO

Article history:

Received 10 May 2012

Accepted 22 December 2013

Available online 03 March 2014

Keywords:

Bipedal gait
Locomotion
Biomechanics
Hip stability
Femur
Hip bone

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.

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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; Häusler, 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 inferior 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; Uthoff 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.

This survey on hip joint morphogenesis demonstrates a high level of developmental integration (Cheverud, 1996; Klingenberg, 2008, 2010) and suggests an important morphological integration between the acetabulum and the proximal part of the femur. The morphological integration of two components involved in the same function can have important functional implications. Functional integration of morphological elements sharing the same function can influence the proper functioning of the structure and thus its performance. Therefore, patterns of functional integration can be selected during evolution, as integration between traits involved in a common biological function can provide an advantage compared with individuals lacking this integration, resulting in better fitness. According to this line of reasoning, patterns of functional integration can lead to genetic integration, which can result in evolutionary integration (Cheverud, 1996). In this study, we have focused on the functional integration of the hip joint. We hypothesize that functional integration between the two neighbouring components was favoured in the course of the evolution of the human hip, resulting in increased joint performance and stability. Like any other joint, the hip joint fulfils two main functions: the transmission of mechanical forces, and the ability (or inability) for specific movements (Ruff and Runestad, 1992). The joint's structure, and in particular its orientation, reflects the need to ensure these two main functions. Therefore, this study focused on the orientations of the acetabulum and the femoral neck. The angles of anteversion and inclination of both the acetabulum and the femoral neck have frequently been used in the literature to infer the orientation of these two structures (e.g., Le Damany, 1903a; Kingsley and Olmsted, 1948; Dunlap et al., 1953; Lewinnek et al., 1978; Murphy et al., 1987; Yoshioka et al., 1987; Murray, 1993; Kim et al., 2000; Lazennec and Saillant, 2004; Lazennec et al., 2004; Tardieu et al., 2006, 2008; Tayton, 2007). However, these parameters quantify the orientation in two dimensions and require anatomical planes of reference to describe the position of the pelvis and the femur. The development of methods allowing quantification of the orientation of both the acetabulum and the femoral neck in three dimensions, and independent of an anatomical reference plane (Bonneau et al., 2012a, b), provides new tools for the study of the morphological integration of the hip joint. Based on these innovative three-dimensional methods, we have tested our hypothesis that the hip joint forms a strong functional unit with a high degree of functional integration between the two neighbouring components. More precisely, we assume that to have an efficient joint the hip geometry needs to demonstrate a close concordance between the three-dimensional orientations of the two functioning components in a bipedal posture, with significant covariation between these two orientations. In summary, a quantitative approach of the functional integration of the human hip joint was performed here to firstly evaluate the degree of concordance between the three-dimensional orientations of both the acetabulum and the femoral neck in the bipedal posture in adult humans and, secondly identify patterns of covariation between these two three-dimensional orientations.

Material and methods

Materials

The study included 83 specimens of modern *H. sapiens* (41 females and 42 males). Of the 83 specimens, 76 specimens (39 females and 37 males) had the right and/or the left hip bone(s) well preserved, resulting in a total sample of 117 hip bones (62 right and 55 left). Of the 83 specimens, 66 specimens (29 women and 37 men) had the right femur and/or the left femur well preserved, resulting in a total sample of 107 femora (53 right and 54 left). Only dry bones

with no appearance of skeletal disease were included in the study. The specimens belong to the SIMON collection (housed at the University of Geneva, Switzerland), the collections of the National Museum of Natural History (Paris, France) and the OLIVIER collection (housed at the Musée de l'Homme, France). The SIMON collection is composed of skeletons dated from the twentieth century and collected in cemeteries from Vaud (Perréard Lopreno and Eades, 2003). The OLIVIER collection is composed of skeletons dated from the 1960s and was collected by Professor G. Olivier. The skeletons belong to French individuals who gave their bodies to science or who have been left without a grave. Bones housed in the collections of the National Museum of Natural History correspond to body donation of French individuals from the twenty-first century.

Data acquisition

Femora and hip bones were successively immobilized using a clamp and three-dimensional coordinates (x, y, z) were recorded in a millimetric orthonormal reference system using a MicroScribe® G2 (Immersion, France) with a precision of ± 0.38 mm according to the manufacturer.

For the hip bones, the three-dimensional coordinates (x, y, z) of nine homologous landmarks (Table 1, Fig. 1) were digitized in order to define a three-dimensional reference space used afterwards to superimpose bones. In addition, the osseous acetabular rim defined between the anterior and posterior horn tips (Bonneau et al., 2012a) was acquired by recording coordinates of successive points using the MicroScribe programmed to take three-dimensional coordinates 1 mm apart. Depending on the bone size, between 120 and 180 points were recorded.

For the femora, the three-dimensional coordinates of eight homologous landmarks (Table 1, Fig. 1) were digitized to define a three-dimensional reference space. In addition, using the stylus of the MicroScribe, which was programmed to take three-dimensional coordinates 1 mm apart, the full exterior surface of the femoral neck defined between the edge of the femoral head articular surface and the intertrochanteric lines was traced and between 900 and 1200 points were recorded.

Table 1
List of homologous landmarks used in the study.

No.	Definition
COXAL	
1	Superior point of the pubic symphysis
2	Anterior superior iliac spine
3	Spinea limitans: tubercle forms by the postero-inferior border of the insertion of the muscle quadratum lumborum, at the level of the lateral border of the iliac crest
4	Posterior inferior iliac spine
5	Extreme of curvature of the greater sciatic notch (deepest point)
6	Top of the ischial spine
7	Most postero-superior point of the ischial tuberosity, i.e., superior border of the insertion of the muscle semi-membranosus
8	On the transversal crest of the ischial tuberosity, point between the insertion of the semi-tendinosus and the adductor magnus
9	Scalenion: tangent point of the line between the acetabular center and the ventral border of the sacroiliac joint (Rickenmann, 1957)
FEMUR	
1	Pretrochanteric tubercle, at the level of the iliofemoral ligament attachment
2	Antero-inferior point of the insertion of the gluteus minimus
3	Superiormost point of the pyramidal muscle attachment
4	Postero-superior point of the posterior intertrochanteric crest
5	Posterior base of the medial condyle
6	Posterior base of the lateral condyle
7	Maximal of curvature of the trochlea in its central part (frontal view)
8	Maximal of curvature of the distal articular surface between the two condyles

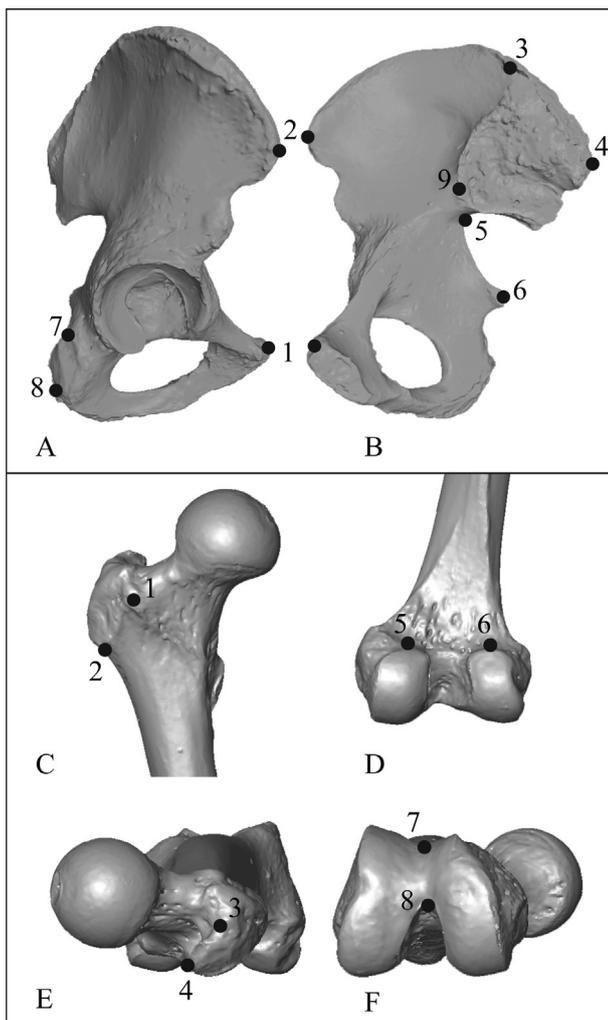


Figure 1. Homologous landmarks used in the study and further described in Table 1. The scans of the bones were performed using a Stereoscan Breukmann® surface scanner. A: lateral view of the right hip bone; B: medial view of the right hip bone; C: frontal view of the proximal part of the right femur; D: posterior view of the distal part of the right femur; E: proximal view of the right femur; F: distal view of the right femur.

Landmarks acquired on both hip bones and femora were chosen for their minimal observer-induced measurement error (see validation of [method](#) section) and their maximal and homogeneous dispersion relative to the overall bone volume.

Superimposition of data

Using a custom-designed function of the Rmorph library (Baylac, 2010) for R v.2.11.0 (R Development Core Team, 2011), a partial superimposition based on the homologous landmarks was performed to reorient the bones that we wanted to compare in a common space. Previously, left bones had been symmetrized to obtain right and left bones in a comparable space. As two separate hip bones and femora exist as a mirror image of each other on the body, a left-right matching symmetry was used in this process (Rohlf and Slice, 1990; Bookstein, 1996; Dryden and Mardia, 1998; Klingenberg and McIntyre, 1998). The superimposition process, based on a Generalized Procrustes Analysis (Gower, 1975; Rohlf and Slice, 1990), corresponds to a scaling step followed by translations and rigid three-dimensional rotations of the bones using the homologous landmarks. The three-dimensional coordinates acquired on osseous

acetabular rims and femoral neck surfaces followed passively the translations and rotations calculated using respectively the nine homologous landmark coordinates acquired on hip bones, and the eight homologous landmark coordinates acquired on femora. In summary, this alignment removes the effect of variation in location and orientation from the three-dimensional coordinates acquired on both the acetabular rim and the femoral neck surface.

This approach used three-dimensional coordinates of homologous landmarks to superimpose the two bones to quantify variation in the three-dimensional orientation of both the acetabulum and the femoral neck. The superimposition used for the comparison of the three-dimensional axes was thus directly dependant on the inter-individual variation of the landmarks used in the process. Consequently, variation observed in the three-dimensional orientations must always be analysed simultaneously with regard to variations of the shape itself. It is important to note that this influence of the landmarks selected in the superimposition process also exists in measurements of traditional angles used in the quantification of the orientation of both the acetabulum and the femoral neck such as the angles of anteversion or inclination. For example, when the angle of anteversion of the acetabulum was measured in the pelvis using the Lewinnek plane of reference (Lewinnek et al., 1978), variations of the anterior superior iliac spines and the superior points of the pubic symphysis influence the position of the pelvis in space and, consequently, the measure of the angle of anteversion. The advantages of the superimposition based on three-dimensional homologous landmarks are, firstly, that variation is distributed among a larger number of points, which renders the superimposition more objective, and, secondly, that variation in the homologous landmarks can be quantified.

Determination of the three-dimensional orientations of both the acetabulum and the femoral neck

Regression planes were computed based on the successive points acquired on the osseous acetabular rims using the least squares method. In other words, the mean distance between the calculated plane and all of the points acquired on the osseous rim was minimized. For each hip bone, a plane ($ax + by + cz + d = 0$) was thus obtained and the three-dimensional orientation of the acetabulum was defined as the direction vector (a, b, c) of this plane (Calandruccio, 1987; Bonneau et al., 2012a).

The three-dimensional axis of the femoral neck was determined using a three-dimensional model based on successive cross-sectional ellipses (Bonneau et al., 2012b). The raw point cloud acquired on the exterior surface of the neck was used in a regression approach based on the least squares method. A custom-designed function in Matlab v.7.8.0 (www.mathworks.com/) was used to model the femoral neck based on successive cross-sectional ellipses. The axis of inertia of the total point cloud was calculated providing a first axis to cut the cloud in equidistant cross-sections, which are separately used to compute an elliptic regression. At the cross-sectional extremities of the point cloud, the points did not represent a complete ellipse and they were eliminated. Based on the centers of the successive ellipses, a PCA (Principal Component Analysis) was performed and the first principal component provided a new axis that was used to reiterate the process. The axis defined by the centers of the successive ellipses obtained in the second process corresponds to the femoral neck axis.

Validation of method

The observer-induced measurement errors were assessed using a method described by Bonneau et al. (2012b) corresponding to a

variant of the protocol proposed by von Cramon-Taubadel et al. (2007). Four stainless steel nails, with a diameter of 1 mm, were implanted homogeneously in each of the six hip bones used to assess measurement error in order to generate a three-dimensional system of reference landmarks. Likewise, five nails were implanted in six femora. Bones were pierced by means of a 0.9 mm diameter drill and stainless steel nails were placed in the holes.

The protocol of data acquisition on hip bones and femora was applied six times. The reference nails were digitized in the center of their head at each acquisition. Based on the nails, a partial superimposition, performed using the custom-designed function of the Rmorph library for R (Baylac, 2010), was used to reorient the different repetitions of a given specimen. The three-dimensional coordinates of data acquired on the bones (i.e., homologous landmarks, successive points acquired on the osseous acetabular rim and point cloud acquired on the femoral neck surface) followed passively the translations and rotations calculated using the nail coordinates. The use of nails to perform the partial superimposition guarantees a minimal variance of the measurement error of the reference landmarks. Acquisitions obtained using the nails guarantee reference landmarks with equal and spherical variance and they are uncorrelated (Richtsmeier et al., 2005).

For each homologous landmark, the intra-observer measurement error was evaluated. The geometric center of the coordinates acquired during the six repetitions on the same homologous landmark was computed. The mean distance between each repetition and this geometric center was then calculated providing the intra-observer measurement error of the landmark of interest. To evaluate the observer-induced measurement error in the determination of the three-dimensional orientation of the acetabulum, regression planes were computed for each repetition on six acetabula. A mean vector of the six direction vectors was calculated. The intra-observer measurement error corresponds to the mean angle between the mean vector and each direction vectors of the six repetitions. Similarly, the intra-observer measurement error induced in the determination of the three-dimensional orientation of the femoral neck was computed.

Intra-specific variation of the three-dimensional orientations of both the acetabulum and the femoral neck

Variations of the three-dimensional orientations of both the acetabulum and the femoral neck in the sample of adult humans with respect to the shape variation of the hip bone and the femur, respectively, were analysed. All analyses were performed using the R graphical and statistical package v.2.11.0 (R Development Core Team, 2011).

A superimposition was performed on the 117 hip bones and the three-dimensional orientations of the acetabula were computed. Similarly, a superimposition was computed on the 107 femora and the three-dimensional orientations of the femoral necks were calculated. To ensure independence of data in statistical analyses, the mean vector of orientation and the mean shape of the right and left sides were computed for the paired specimens. Thus, analyses were performed on a sample of 76 lines for the set of hip bones and 66 lines for the set of femora. Multivariate analyses of covariance (MANCOVA) were performed to test the effect of sex and size, respectively, on the orientation of both the acetabulum and the femoral neck. Interactions between the two factors were also tested. Size corresponded to continuous factors based on the log of the centroid size of the homologous landmarks, i.e., the square root of the sum of the squared distances of each homologous landmark from the center of gravity of all homologous landmarks (Bookstein, 1991; Dryden and Mardia, 1998; Zelditch et al., 2004). Significant differences were explored graphically. Differences between females

and males were explored using the mean orientations of both the acetabulum and the femoral neck of each sex.

In parallel, tangent space projections of the homologous landmarks coordinates were used to compute Principal Component Analyses (PCA). Multivariate analyses of covariance (MANCOVA) were performed on the non-null principal components to test the effect of sex and size on the shape of both the hip bone and femur. Significant differences were explored graphically.

Concordance of the three-dimensional axes of the acetabulum and the femoral neck

The joint concordance evaluates the relationships between the orientations of the neighbouring components of a joint in defined posture, i.e., in a done posture the orientation of one component of the joint was observed in relation to the orientation of the other component. A perfect concordance was concluded when the two orientations are aligned. In order to evaluate the concordance between the axes of the two opposing articulating components of the human hip joint, the two datasets representing the set of hip bones ($N = 76$) and the set of femora ($N = 66$) were reoriented in two anatomical reference positions: bipedal posture and quadrupedal posture on an inclined ground. The reorientation of the datasets was based on the mean configurations of the hip bones and femora, i.e., the average configuration of homologous landmarks. First, the coordinates of the mean configurations of both the hip bones and the femora were mathematically transformed in order to rearticulate the two components of the hip as they are in a standard bipedal posture. Secondly, as the maximal concordance was obtained according to Kapandji (2009) in a quadrupedal posture on an inclined substrate, the articulated process was also applied for this posture.

Patterns of covariation between the three-dimensional orientation of both the acetabulum and the femoral neck

In the total sample of 83 specimens, 57 specimens (26 females and 31 males) were identified as having an associated hip bone and femur from at least one side. When two sides were present for one individual, the right or left side was selected randomly. Finally, in the sample of 57 human specimens, 29 right and 28 left sides were used. Two separate superimpositions of the hip bones and femora were performed as previously described, and the three-dimensional orientations of both acetabula and femoral necks were computed. Because the strength of covariation between the three-dimensional orientations of the acetabula and the three-dimensional orientations of the femoral necks may reduce the degree of functional integration between the two neighbouring components of the hip joint, patterns of covariation between their respective three-dimensional vectors were quantified using both the RV coefficient of Escoufier (Escoufier, 1973; Klingenberg, 2009) and the two block partial least-squares methods (2B-PLS; Bookstein, 1991, 2003; Rohlf and Corti, 2000; Bookstein et al., 2003). These two methods are typically used for assessing integration between two sets of data in geometric morphometrics (Zelditch et al., 2004; Slice, 2005; Klingenberg, 2008; Weber and Bookstein, 2011) and are implemented in the Rmorph morphometric library (Baylac, 2010) for R. The two sets of variables were constituted by the two data matrices formed by the three-dimensional vectors of orientations of the acetabula and the femoral necks, resulting in two 57×3 matrices. Thus, the combined data matrix Y resulting from these two datasets is a 57×6 matrix. Both the RV coefficient and the 2B-PLS analysis are based on the variance-covariance matrix obtained from this combined matrix Y even though the processes are distinct and they differently answer the covariation question.

The *RV* coefficient of Escoufier represents a squared measure of the total amount of covariance scaled by a squared measure of the amounts of variance within the two sets of variables. It can therefore be compared to an extension to matrices of squared correlation coefficient between two variables (for more calculation details see Escoufier, 1973; Klingenberg, 2009). Permutation tests (Good, 2000; Manly, 2007) were used in order to assess the statistical significance of the *RV* coefficient, i.e., observations in the two sets are permuted randomly in order to simulate the null hypothesis of complete independence. As for 2B-PLS analysis, linear combinations of maximized covariance were computed using the singular value decomposition method to maximize the low-dimensional representation of between-block covariation structure (for more calculation details see Rohlf and Corti, 2000). Permutation tests were used in order to assess of statistical significance of the observed singular values and correlations. Visualization of the three-dimensional orientations corresponding to the positive and negative ends of the first 2B-PLS dimension were computed using multivariate regressions. The *RV* coefficient and the 2B-PLS analysis are two complementary methods for exploring patterns of covariation as the former works on the total covariance between two matrices relative to the variance of each matrix while the latter works on two of axes of maximum covariance.

Results

Validation of the method

A mean measurement error of 0.49 ± 0.08 mm was obtained for the nine landmarks acquired on the hip bones with a range of 0.35–0.61 mm. A mean measurement error of 1.38 ± 0.43 mm was obtained for the eight landmarks acquired on the femora with a range of 0.96–2.06 mm (for more details see Table 2).

There is a good reliability in the determination of the three-dimensional orientation of the acetabulum, as the intra-observer measurement errors equalled $0.50 \pm 0.19^\circ$ (range = 0.26° – 0.81°). The intra-measurement error induced by the determination of the

Table 2
Intra-observer measurement error (ME) scores obtained for each homologous landmark used in the superimposition process.

Landmark	ME (mm)
HIP BONE	
1	0.43
2	0.48
3	0.61
4	0.35
5	0.59
6	0.49
7	0.48
8	0.45
9	0.55
FEMUR	
1	2.06
2	2.01
3	1.39
4	1.08
5	1.03
6	1.27
7	0.96
8	1.23

For each landmark, the geometric center of the coordinates acquired during the six repetitions was computed. The mean distance between each repetition and this geometric center was next calculated providing the intra-observer measurement error of the regarded landmark.

Table 3
Results of the MANCOVA's performed to test the effect of sex, and size on the three-dimensional orientation of the acetabulum (a), and the shape of the hip bone (b).

	Df	Pillai's trace	Approx F	Num DF	Den Df	PR (>F)	
a							
Sex	1	0.13	3.51	3	70	0.02	*
Size	1	0.06	1.52	3	70	0.22	NS
Sex × size	1	0.02	0.50	3	70	0.68	NS
Residuals	72						
b							
Sex	1	0.73	4.72	27	46	<0.001	***
Size	1	0.51	1.79	27	46	0.04	*
Sex × size	1	0.40	1.15	27	46	0.33	NS
Residuals	72						

(NS, not significant; * significant at 0.05; ** significant at 0.01; *** significant at 0.001).

three-dimensional orientation of the femoral neck was $1.97 \pm 1.12^\circ$ (range = 0.86° – 2.81°).

Intra-specific variation of the three-dimensional orientation of the acetabulum and the femoral neck

There is a greater variability in the three-dimensional orientation of the femoral neck than the three-dimensional orientation of the acetabulum. A standard deviation of 6.59° (range = 0.41° – 14.18°) compared to the mean vector was obtained for the femoral neck axis while the score of the standard deviation compared to the mean vector obtained for the acetabular axis equalled 4.37° (range = 0.46° – 8.30°).

There is a significant effect of sex on the orientation of the femoral neck axis, while no significant effect was detected on the femoral shape (Table 4). The anteversion of the femoral neck tends to be greater in females than in males, while no difference was observed in the inclination of the femoral neck (Fig. 2). No significant effect of size on the three-dimensional orientation of the acetabulum was detected (Table 4).

There is a significant effect of sex on both the orientation of the acetabulum and the shape of the hip bone (Table 3). Relative to the mean conformation of the hip bone, both the anteversion and the inclination of the acetabulum tend to be greater in females than in males (Fig. 3). The very significant difference in shape between females and males is in accordance with the known high dimorphism of the hip bone. No significant effect of size on the three-dimensional orientation of the acetabulum was detected (Table 3).

Concordance between the three-dimensional axes of the acetabulum and the femoral neck

In the habitual bipedal posture, the articulated hip process demonstrates a lower concordance between the two axes of the

Table 4
Results of the MANCOVA's performed to test the effect of sex, and size on the three-dimensional orientation of the femoral neck (a), and the shape of the femur (b).

	Df	Pillai's trace	Approx F	Num DF	Den Df	PR (>F)	
a							
Sex	1	0.16	3.70	3	60	0.02	*
Size	1	0.07	1.42	3	60	0.25	NS
Sex × size	1	0.03	0.60	3	60	0.62	NS
Residuals	62						
b							
Sex	1	0.47	1.42	24	39	0.16	NS
Size	1	0.49	1.53	24	39	0.12	NS
Sex × size	1	0.39	1.03	24	39	0.46	NS
Residuals	62						

(NS, not significant; * significant at 0.05; ** significant at 0.01; *** significant at 0.001).

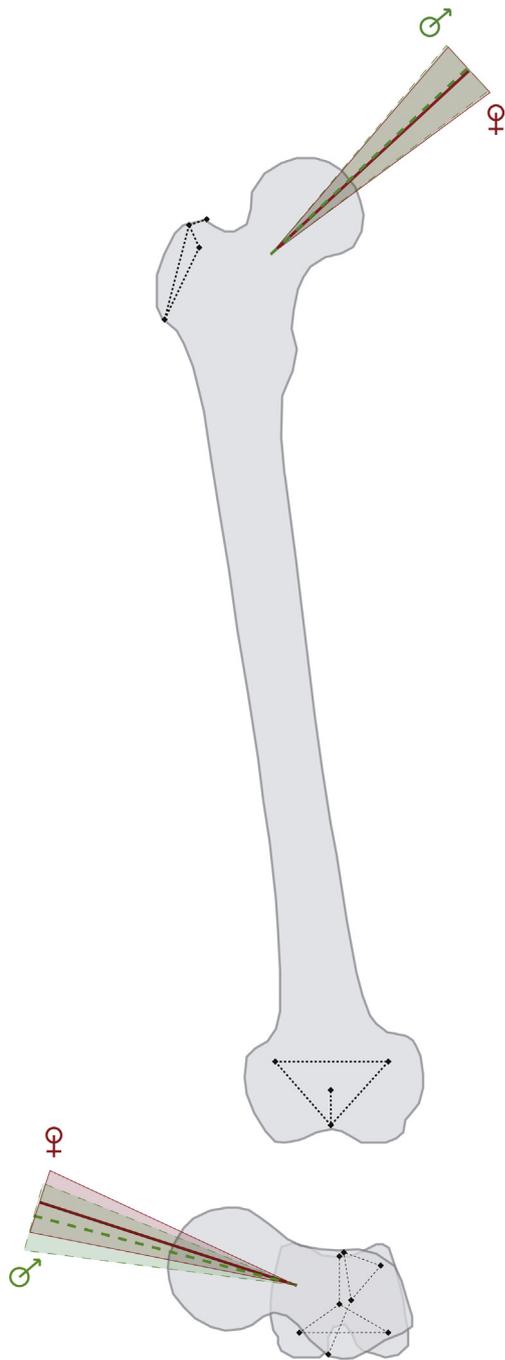


Figure 2. Significant variation between males and females in the three-dimensional orientation of the femoral neck is illustrated. Mean orientations were symbolized for each sex with their corresponding intra-individual variation. A significant difference in the orientation of the femoral neck between males (in dotted green lines) and females (in solid red lines) was detected. In the transverse plane, the anteversion of the femoral neck tends to be greater in females than in males, while, in the frontal plane, no difference was observed in the inclination of the femoral neck. No significant effect of sex was detected on the femoral shape and, thus, the mean shape only is illustrated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

acetabulum and the femoral neck than expected for a strong joint such as the hip joint. Regarding the mean orientations of both the acetabulum and the femoral neck in bipedal posture, a good concordance of the two axes was obtained in frontal view (175°; Fig. 4A) while the concordance was quite poor in the transverse plane (145°; Fig. 4A). Indeed, in the transverse plane, both the

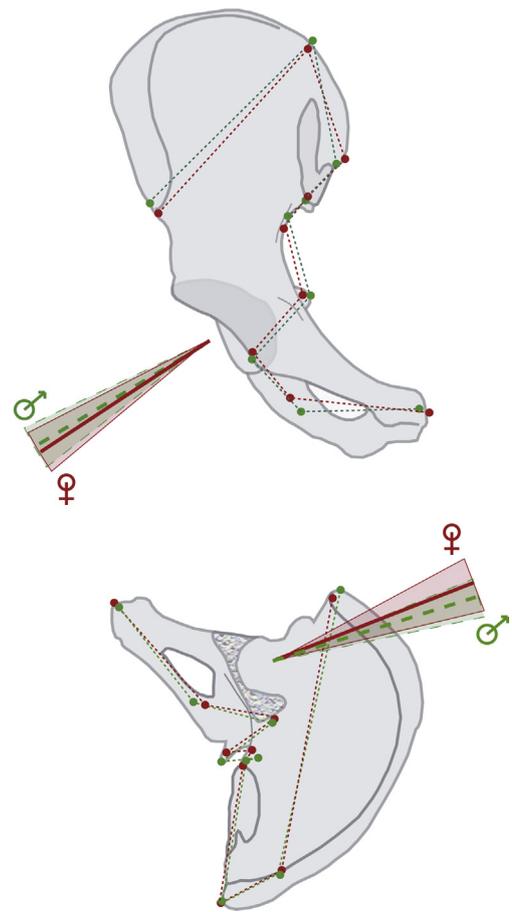


Figure 3. Significant variations between males and females in both the three-dimensional orientation of the acetabulum and the hip bone shape are illustrated. Mean orientations were symbolized for each sex with their corresponding intra-individual variation. A significant difference in the orientation of the acetabulum between males (in dotted green lines) and females (in solid red lines) was detected. In the transverse plane, the anteversion of the acetabulum tends to be greater in females than in males, while, in the frontal plane, the acetabulum shows a greater inclination in females than in males. The significant difference in shape between females (solid red lines) and males (dotted green lines) is in accordance with the known high dimorphism of the hip bone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

acetabulum and the femoral neck present an anteversed orientation resulting in a lower concordance of the two neighbouring components orientations.

Our results demonstrated that the maximal concordance between the two neighbouring components of the human hip joint is obtained in a quadrupedal posture on an inclined substrate as the axis of the acetabulum and the axis of the femoral neck were aligned in this posture whatever the anatomical plane observed (Fig. 4B).

Patterns of covariation between the three-dimensional orientations of both the acetabulum and the femoral neck

The RV coefficient computed based on the combined data matrix Y constituted by the two data matrices formed by the three-dimensional vectors of orientation of the acetabula and the femoral necks equalled 0.20. The associated *p*-value resulting from permutation tests is less than 0.001. As illustrated in Fig. 5A, the RV coefficient associated with the *p*-value demonstrated significant covariation between the three-dimensional orientation of the acetabulum and the three-dimensional orientation of the femoral

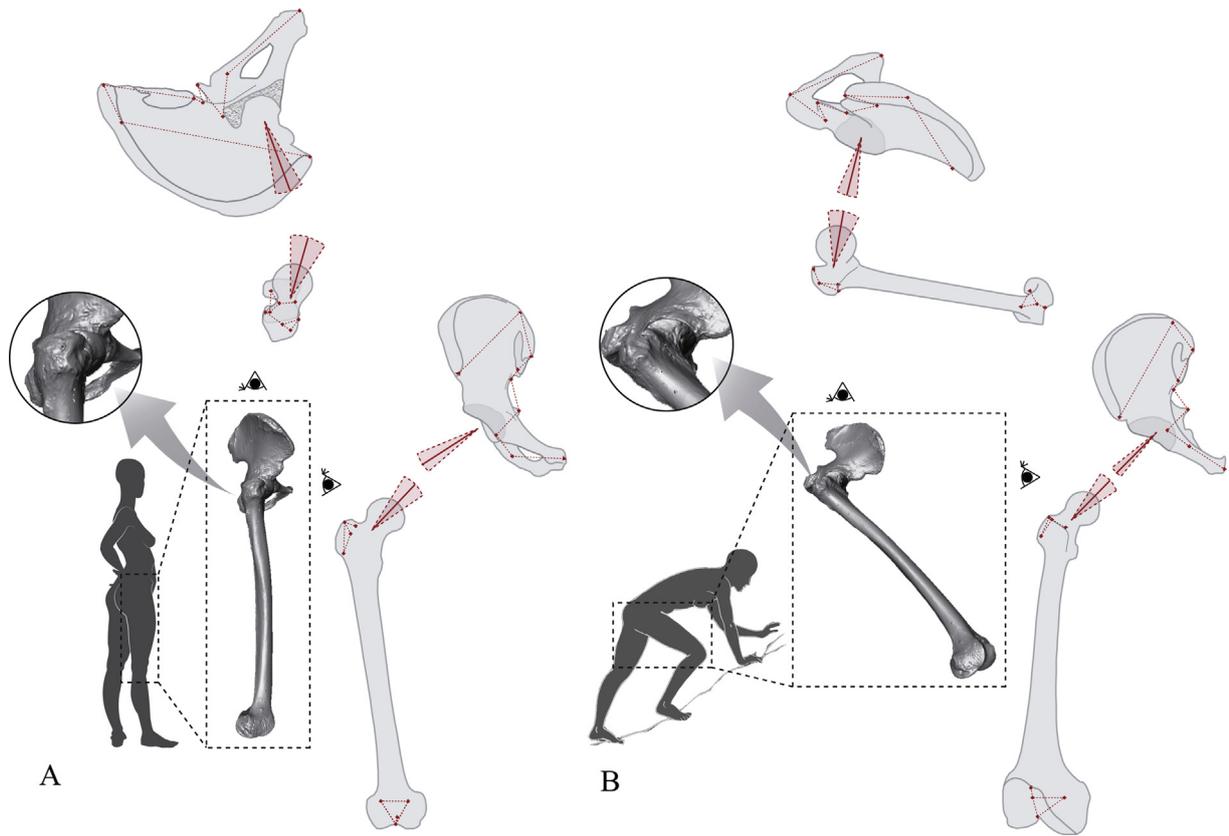


Figure 4. The coordinates of the mean configurations of both the hip bones and the femora were mathematically transformed in order to rearticulate the two components of the hip as they are both in a standard bipedal posture (A) and in a quadrupedal posture on an inclined substrate (B). In each of the postures examined, the mean axes of the acetabulum and the femoral neck (red full lines), computed based on the full sample, were illustrated in a frontal view and a transverse view. Dotted lines illustrated the range of variation of the three-dimensional orientations of the acetabulum and the femoral neck in the set of hip bones ($N = 76$) and the set of femora ($N = 66$). A – In a bipedal posture the antero-posterior part of the femoral head is uncovered. Mainly in the transverse plane, both the acetabulum and the femoral neck present an anteversed orientation resulting in a lower concordance than could be expected for a key joint such as the hip joint. B – A total concordance of the human hip joint may be obtained in a quadrupedal posture on an inclined substrate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

neck. In other words, it follows that changes in the orientation of one of the two neighbouring components of the hip joint is associated with changes in the orientation of the other component of the joint. Analyses performed separately on females and males demonstrated that patterns of covariation remain significant in the sample of males ($RV = 0.33$; $p < 0.01$; Fig. 5B) while they are not significant in the sample of females ($RV = 0.08$; p -value = 0.30; Fig. 5C).

Significant patterns of covariation between the three-dimensional orientations of the two neighbouring components were also detected using the 2B-PLS method. Table 5 shows the covariance (squared singular values), cumulative covariance as proportions of the total, and cross-set correlations for the three dimensions. The first pair of latent variables accounts for ~97% of the total covariance and permutation tests demonstrated that none of the random permutations resulted in a larger percentage than

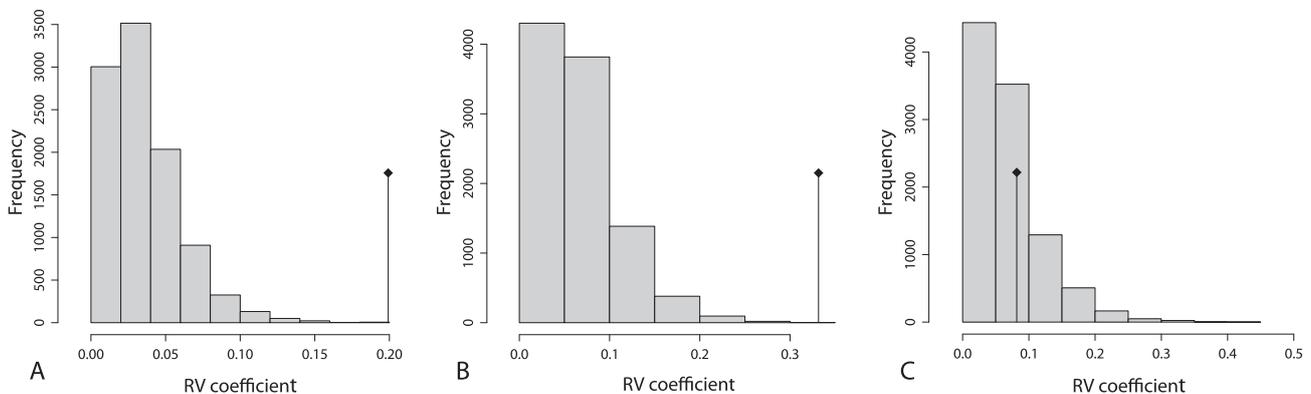


Figure 5. Histograms of the RV coefficients computed based on the combined data matrix Y constituted by the two data matrices formed by the three-dimensional vectors of orientation of the acetabula and the femoral necks for the total sample (A), for the male sample (B) and for the female sample (C). The values of the RV coefficients between the three-dimensional vectors of orientation of both the acetabulum and the femoral neck are indicated by arrows.

Table 5

Results of 2B-PLS analysis performed to test patterns of covariation between the three-dimensional orientations of both the acetabulum and the femoral neck in the total sample (a), the female sample (b), and the male sample (c).

Dimensions	ν_i	$\Sigma\nu_i$	p	r_i	p
a					
1	1.00×10^{-5}	96.61	0.001	0.64	0.001
2	3.52×10^{-7}	100	0.21	0.12	0.28
3	1.83×10^{-12}	100	0.92	0.02	0.73
b					
1	3.03×10^{-6}	65.21	0.45	0.36	0.34
2	1.61×10^{-6}	99.99	0.02	0.26	0.11
3	3.55×10^{-10}	100	0.44	0.24	0.06
c					
1	1.51×10^{-5}	99.52	0.001	0.75	0.001
2	7.29×10^{-8}	99.99	0.70	0.07	0.73
3	1.32×10^{-10}	100	0.36	0.11	0.25

ν_i is the i th covariance, $\Sigma\nu_i$ is the cumulative sum of covariance, and r_i is the correlation for the i th pair of latent variables. Probabilities are based on the observed values plus 9999 random permutations of the association between the three-dimensional axes of both the acetabulum and femoral neck.

that obtained for the first dimension ($p = 0.001$). The correlation for the first pair of variables is 0.64 and was also significant ($p = 0.001$; Fig. 6). No other pair of latent variable was found significant.

Fig. 7 gives visualization of the three-dimensional orientations corresponding to the positive ends (red full lines) and negative ends (blue dotted lines) of the first axis for the orientations of both the acetabulum and the femoral neck. It can be observed that an acetabulum showing an axis with inclination and anteversion is associated with a femoral neck with a greater anteversion.

In Fig. 6, females and males are illustrated in different colours and it can be observed that patterns of covariation between the

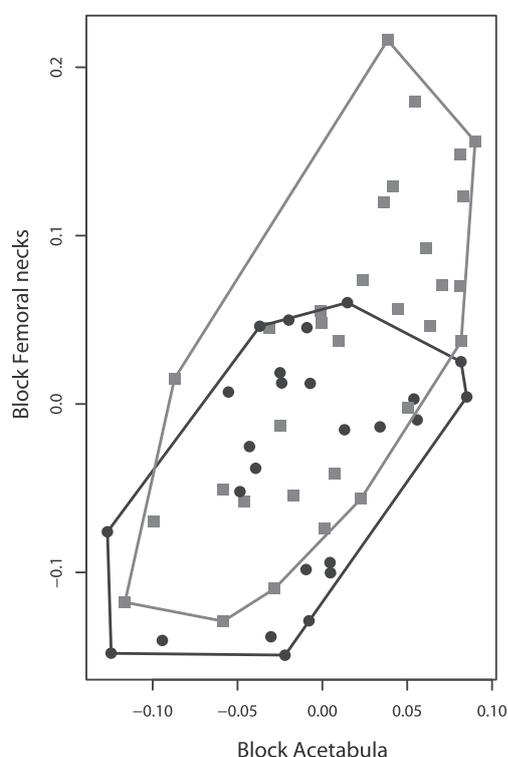


Figure 6. Plot of the first 2B-PLS dimension for the three-dimensional orientation of the acetabulum (ordinate) and the three-dimensional orientation of the femoral neck (abscissa). Correlation is 0.64 ($p < 0.001$). Males are represented in grey squares and females in black spheres.

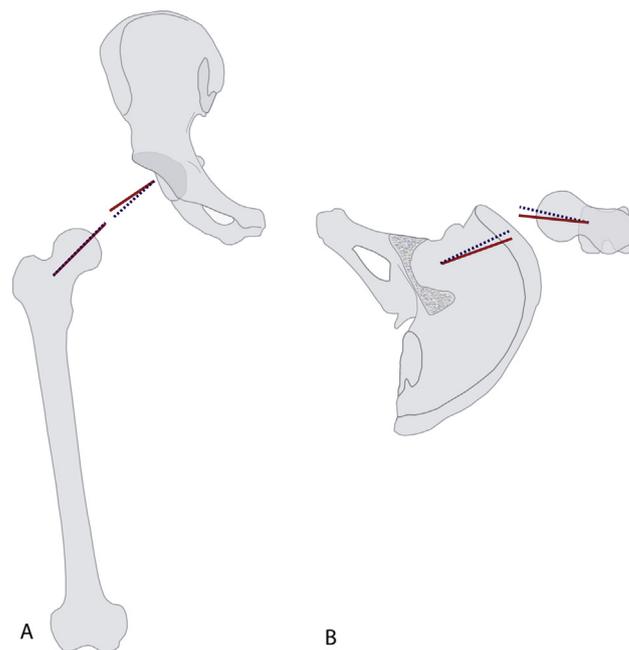


Figure 7. Visualization of the three-dimensional orientations of both the acetabulum and the femoral neck corresponding to the positive ends (in red full lines) and negative ends (in blue dotted lines) of the first 2B-PLS dimension illustrated in Fig. 6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three-dimensional orientations of both the acetabulum and the femoral neck are not the same. Results obtained with distinct analyses between females and males demonstrated that the first dimension remains significant in males (Table 5C) while it is not significant in females (Table 5B).

Discussion

Functional integration at any joint has important implications for joint stability and performance. Thus, this study started from the hypothesis that functional integration at the human hip joint should be favoured over the course of evolution. In order to test our hypothesis, 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. As humans habitually use bipedal locomotion, our prediction was that the hip joint presents a perfect concordance between the axes of the two neighbouring components in this stressful posture, as demonstrated for other vertebrates, such as elephants, horses or ostriches, during their natural locomotion behaviour (Le Damany, 1904). In order to conserve this perfect concordance at the inter-individual level, we suggested that a change in the three-dimensional orientation of the acetabulum is associated with an antagonistic change in the orientation of the femoral neck, resulting in patterns of covariation between the two structures. Both the level of concordance and patterns of covariation were explored in this study using innovative three-dimensional methods. Three-dimensional orientations of both the acetabulum and the femoral neck were accurately determined using methods validated previously (Bonneau et al., 2012a, b). Moreover, the variation and covariation analyses of the orientations of the two neighbouring components in a sample of adult humans used geometric morphometric tools in order to perform the superimposition of data in a three-dimensional reference space. The use of geometric morphometric methods for the establishment of

the reference space leads to the accurate superimposition of functional structures with no recognized homology, using homologous landmarks.

Before approaching the functional integration at the human hip joint, the level of inter-individual variation of the studied sample was evaluated. Analyses of the total sample demonstrated significant differences in the three-dimensional orientations of both the acetabulum and the femoral neck between males and females. Concerning the femoral neck, females tend to present a more anteverted orientation in the transverse plane (Fig. 2), as it has been reported in the literature (Parsons, 1914; Kingsley and Olmsted, 1948; Yoshioka et al., 1987). An explanation for this pattern can be derived by considering the differences in the loading of the femoral neck between the two sexes (Burr et al., 1977). For example, the loading of the femoral neck depends on the moment arms of the abductor and adductor muscles that insert upon the hip bone (Lovejoy et al., 1973; McHenry, 1975; Clark and Haynor, 1987; Ruff, 1995). As a moment arm differs with the origin and position of the muscle, the well known difference in pelvic shape between males and females (Ferembach et al., 1979; Fernández Camacho et al., 1993; Marchal, 2003) necessarily implies changes in the loading of the femoral neck. Given that bone actively remodels (Carter et al., 1987; Carter and Wong, 1988; Frost, 2004; Ruff et al., 2006), this difference in loading will impact the three-dimensional orientation of the femoral neck. More precisely, the proximal attachments of the tensor fasciae latae and the middle and anterior parts of the gluteus medius take place at the level of the anterior superior iliac spine and along the outer edge of the iliac crest. These two muscles play a dominant role in hip abduction (Gottschalk et al., 1989) and their role in the biomechanics of the proximal femur is known to explain the globally forward orientation of the femoral neck in both sexes (Merchant, 1965; Fabeck et al., 2002). Consequently, a difference in the iliac shape between males and females could partly explain a change in the orientation of the abductor forces and thus the dimorphism quantified at the femoral neck orientation. Although the adductor muscles are known to be less involved during normal gait compared with the abductor muscles (a factor of five according to Duda et al., 1997), the same line of reasoning can be applied for the adductor muscles, which are more active during stair climbing (Lyons et al., 1983). The attachments of the adductor muscles, such as the pectineus, at the level of the pubis, suggest that the orientations of both the pubic branch and the ischiopubic ramus branch can induce variation in the antero-posterior oriented force component of the adductor muscles, resulting in variation in the anteversion of the femoral neck.

Concerning the acetabulum, females tend to present a more anteverted orientation in the transverse plane (Fig. 3) as previously documented in the literature (McKibbin, 1970). We suggest that this could be also, at least in part, explained by the different morphology of the pelvic girdle between females and males. Indeed, the acetabulum develops from a cartilaginous complex composed by a lateral cup-shaped part and a medial triradiate part formed by an iliopubic flange anteriorly, an ilio-ischial flange posteriorly, and an ischio-pubic flange inferiorly (Harrison, 1958; Ponseti, 1978; Bucholz et al., 1982; Portinaro et al., 2001). The three physes, located along the exterior borders of the triradiate cartilage, are placed at the center of the different forces that pass through the load hip bone (Bonneau et al., 2012a). Differences in shape and orientation of the three branches of the hip bone (ilium, pubis and ischium) between sexes induce differences in the biomechanical environment of each physis, which can adapt their speed and orientation of growth (Carter et al., 1996; Frost, 2004; Ruff et al., 2006), resulting in a globally different three-dimensional orientation of the acetabulum between females and

males. A good illustration is the high level of correlation demonstrated by Tardieu et al. (2006) between the angle formed by the two ischiopubic rami (or sub-pubic angle) and the angle of acetabular anteversion ($R_{\text{Pearson}} = 0.64$, $p < 0.001$, $N = 51$). The ischiopubic rami in females are known to be significantly more horizontal compared with the more vertical orientation in males, contributing to a global rearrangement in the ischiopubic region between the two sexes (Coleman, 1969; Ferembach et al., 1979; Bruzek, 2002; Marchal, 2003; Tardieu et al., 2013). This rearrangement contributes to the different biomechanical environment at the triradiate cartilage and, consequently, produces a part of the significant difference in the orientation of the acetabulum between females and males. In parallel, no significant effect of size in the three-dimensional orientation of both the acetabulum and the femoral neck was detected when the size difference between sexes was eliminated. Thus, no difference in the orientations of the two components was observed in our sample between short and tall individuals for each sex separately.

As presented above in our analysis of inter-individual variation, the orientations of the acetabulum and the femoral neck are generally studied independent from one another. The core of the present work was to evaluate the degree of integration between the axes of the two neighbouring components of the hip joint using a three-dimensional approach. 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 joint. The presence of significant patterns of covariation reinforces the initial hypothesis predicting a strong level of integration at the human hip joint. Indeed, our results provided evidence that in our sample of 57 individuals a specific variation in the three-dimensional orientation of the acetabulum can be associated with a specific variation in the three-dimensional orientation of the femoral neck. More precisely, our results showed that a femur with a femoral neck in a more anteverted orientation is statistically associated with a hip bone demonstrating a more anteverted and inclined acetabular orientation. This result is in disagreement with the results obtained by Reikerås et al. (1983), who observed no significant correlation between the angle of anteversion of both the acetabulum and the femoral neck. McKibbin (1970) also noted that a high degree of acetabular anteversion is not necessarily associated with a low degree of femoral anteversion. We suspect that this absence of correlation might have been due to the nature of previous measurements. Indeed, the two-dimensional measurements proposed by these authors are greatly dependant on the choice of the anatomical plane of reference of both the hip bone and the femur. Yet, our personal methodological tests demonstrated that the identification of significant patterns of covariation need a very accurate determination of the three-dimensional orientations of both the acetabulum and the femoral neck, in addition to a strong superimposition performed on an adequate number of homologous landmarks in order to minimize the effect of inter-individual variation of the landmark morphology. Although the existence of patterns of covariation agrees with our first functional hypothesis, the nature of these covariations is unexpected because they are not necessarily in the direction that maximizes joint concordance. As it was previously suggested by McKibbin (1970), our preliminary expectation was that a high degree of femoral anteversion would be associated with a low degree of acetabular orientation in order to increase the level of joint concordance. However, in the present sample of 57 individuals, acetabula with high level of anteversion are statistically associated with anteverted femoral necks. In addition, the level of concordance of the mean orientations of both the acetabulum and the femoral neck in our total sample is not as

great as expected. Although the concordance in the frontal plane appears quite good (around 175°), the angle formed by the two axes of the neighbouring components in the transverse plane is closer to 145° than the 180° expected. However, the level of concordance at an articulation is of main importance in joint stability. The concordance defined partly the level of joint congruence, although other parameters such as the articular surface area have to be included. In the case of the human hip joint, the ball and socket configuration results in an articulation with a high level of congruence. However, the present study provides evidence that the imperfect concordance of the two axes reduces the full capacity of congruence at the joint, resulting in an uncovered femoral head at the anterior part (Fig. 4A). Thus, the anterior part of the articular surface of the femoral head does not contribute to the transmission of the forces between the hip bone and the femur in the bipedal posture, focussing the stress distribution on a smaller area. This observation is particularly true for women who present a higher mean anteversion in both the acetabulum and the femoral neck than men. Although some problems of stability were known in the neonates in which the femoral head tends to subluxate (Le Damany, 1908; McKibbin, 1970; Seringe et al., 1981; Seringe and Kharrat, 1982), the stability of the normal hip joint in human adults is enough to ensure an efficient bipedal gait and posture. Indeed, this diarthrotic joint (Walmsley, 1928) represents one of the more stable joints of the body. Soft tissues surrounding the hip joint contribute to increase stability. Indeed, in addition to deepening the acetabular socket and extending the coverage of the femoral head, the acetabular labrum ensures a progressive transmission of the forces to the osseous acetabular rim and the femoral head (Ferguson et al., 2000b) and acts like a sealant, resulting in a vacuum phenomenon that favours coaptation (Takechi et al., 1982; Ferguson et al., 2000a, 2003). The articular capsule is reinforced by strong ligaments to further increase the stability of the hip. Moreover, muscles crossing the hip joint (e.g., the gluteus minimus) function as hip stabilizers by pulling the femoral head into the acetabulum (Gottschalk et al., 1989). Consequently, as it was discussed by Le Damany (1908) the stability appears to be ensured as long as the axis of the femoral neck remains within the rim of the socket of the acetabulum. Le Damany (1908) proposed a value maximal of 120° between the orientation of the acetabulum and the orientation of the femoral neck in the transverse plane, above which the hip joint becomes instable. However, as it was suggested by Reikerås et al. (1983), the absence of total concordance between the axes of the acetabulum and the femoral neck might explain some pathologies such as osteoarthritis. Reikerås and Hoiseth (1982) established a relation between large femoral anteversion and premature osteoarthritis.

An integrative vision of the full pelvi-femoral complex is the key to put our results in a larger biomechanical context. As discussed above, the three-dimensional orientations of both the acetabulum and the femoral neck are greatly dependent on the pelvic girdle shape. Another strong demonstration is the relationships established between the proportion of the biacetabular breadth, defined between the centers of the two acetabula, and both acetabular and femoral neck orientations. A change in the proportion of the biacetabular breadth compared to the overall pelvic girdle has an influence on the global conformation of the pelvic cavity and thus on the outline of the innominate (Berge, 1993). Regarding the acetabular development via the triradiate cartilage (Harrison, 1958; Ponseti, 1978; Bucholz et al., 1982; Portinaro et al., 2001), we understand how changes in the biacetabular breadth proportion could impact the acetabular orientation. In parallel, the biacetabular breadth plays a central role in the Pauwels' balance (Pauwels, 1935, 1954; McLeish and Charnley, 1970; Lovejoy et al., 1973; Pauwels, 1980; Clark et al., 1987; Ruff, 1995; Heimkes et al., 1997). The hip joint can be viewed as the fulcrum of an off-center type 1 lever

when body weight represents the motive force and the resistive force is created by the abductor muscle actions. The body weight forces arrive at the lower lumbar vertebrae, i.e., a position that can be projected at the mid-biacetabular breadth. Consequently, the wider the biacetabular breadth is, the higher will be the body weight moment arm at the center of the joint. According to Newton's first law, the abductor muscle forces have to increase to ensure the equilibrium. During growth, changes in the proportion of biacetabular breadth and femoral neck length result in a variation of the orientation to the resultant force, which explains the more vertical orientation acquired by the epiphyseal plate of the femoral head during growth (Heimkes et al., 1993, 1997) and, thus, the decrease of the neck-shaft angle (Tardieu and Preuschoft, 1996; Tardieu and Damsin, 1997). Consequently, this example shows that a difference in the shape of the pelvis can be responsible for a difference in the acetabular orientation but also for the femoral neck orientation. It is the first element in understanding the complex relationships between the orientations of the two neighbouring components of the hip joint and thus the nature of their covariation. In reality, the interrelations between the three-dimensional orientations of the two neighbouring components of the hip joint are complicated, implying numerous parameters. For example, as discussed above, the biacetabular breadth induces modifications in both the biomechanical systems governing the three-dimensional orientations of the acetabulum and the femoral neck. However, the biacetabular breadth is also correlated to the femoral bicondylar angle (Pauwels, 1980; Tardieu and Preuschoft, 1996; Shefelbine et al., 2002). Indeed, a greater biacetabular breadth increases the moment at the knee, resulting in a change in stress distribution in the cartilaginous epiphysis during growth and thus modification of the final femoral bicondylar angle (Shefelbine et al., 2002). Thus, a change in the biacetabular breadth has consequences on the global position of the femur during locomotion, which induces indirect variation on the femoral neck biomechanics. More precisely, an example is the influence of the action of the iliotibial tract in relation to the knee extensors and the vastus lateralis on the growth orientation and speed of the apophyseal plate of the greater trochanter, frequently underestimated in hip biomechanical models (Taussig et al., 1976; Heimkes et al., 1993). As these structures follow directly the orientation of the femoral shaft, the action of their forces depends on the femoral position. Consequently, for a full understanding of the complex relationships between the three-dimensional orientations of the two components of the hip joint and the nature of their co-variations, more studies testing a large number of different parameters independently should be performed. In the study of Ruff (1995), not only the effect of the biacetabular breadth and the inclination of the iliac flare on the frontal orientation of the femoral neck were analysed, but also the effect of the femoral neck length. The effect of the femoral neck length during growth of the epiphyseal plate, which partly controlled the femoral neck orientation, was also explored by Heimkes et al. (1993, 1997). Studies on an extended number of parameters are needed in order to better identify their analytic effect on the three-dimensional biomechanics of the femoral neck, but also of the acetabular region, especially as biomechanical analyses are complicated by the combination of translational and rotational movements of the limb during bipedal locomotion (Levens et al., 1948; Merchant, 1965; Fabeck et al., 2002; Neptune and McGowan, 2011). Although our integrative vision of the full pelvi-femoral complex is currently incomplete, it appears that the two biomechanical systems governing the three-dimensional orientations of the acetabulum and the femoral neck are deeply interconnected. These interconnections are not as simple as firstly expected. A morphological change in the pelvi-femoral complex might impact both the acetabular and the femoral neck

orientations. However, the nature of impacts is frequently more complex than simple antagonist effects on the two orientations. Moreover, the biomechanical systems governing the three-dimensional orientations of the two neighbouring components of the hip joint also separately include their own forces. We already addressed the role of the pelvic girdle morphology on the triradiate cartilage, revealing the strong weight of the bone morphology on the three-dimensional orientation of the acetabulum. Regarding the proximal part of the femur, different sources of growth have to be considered. The periosteum, which covers the entire femoral neck (Bagi et al., 1997), produces the cortical bone. The capital epiphyseal plate and the apophyseal plate of the greater trochanter are two separate plates in humans and in hominoids in general (Taussig et al., 1976; Serrat et al., 2007) that produce trabecular bone. These two growth plates are connected by a thin layer of cartilage or isthmus (Siffert, 1981; Serrat et al., 2007) that contributes to the lateral width of the neck (Siffert, 1981). Numerous muscles surround the proximal femur, and the greater trochanter is the place for many muscular insertions and origins. Yet, the muscular environment contributes in the control of speed and orientation of the different sources of growth. For example, the iliotibial tract in relation to the knee extensors and the vastus lateralis play, together with the abductor muscles, an important role in the pressure forces acting on the apophyseal plate of the greater trochanter (Heimkes et al., 1993; Skuban et al., 2009). Inter-individual variation in the morphology of these structures or in the weight-bearing behaviour might consequently produce variation in the resultant force received by the apophyseal plate, which will adapt its speed and orientation in order to minimize the shear stress, and thus avoid degeneration or premature ossification (Carter et al., 1987; Carter and Wong, 1988). Thus, we understand how the level and kind of activity, which changes according to the geo-economical environment in children, can play an important role in the final orientation of the femoral neck (Anderson and Trinkaus, 1998). Although interconnected, the two biomechanical systems governing the orientation of the acetabulum and the femoral neck are not faced with identical constraints: the acetabular region mainly governed by the pelvic girdle morphology and the proximal femur greatly governed by the muscular environment. As a result, the two articular axes do not necessarily demonstrate covariance in the sense of the maximisation of their concordance.

The problem concerning the degree of concordance at the human hip joint can be considered in an evolutionary context. The hip joint of modern humans evolved from an ancestral joint that was adapted to different functions related to both locomotion and the need to give birth of the last ancestor. We suggested that the lower degree of concordance between the three-dimensional axes of both the acetabulum and the femoral neck in the bipedal posture might partly be due to the phylogenetic history of our species. On the one hand, the evolution of the human hip joint has been constrained by the pre-existing structure passing by the most recent non-bipedal ancestor. On the other hand, the demonstrated link between the pelvic shape and the acetabular orientation implies also constraints related to the obstetrical role of the female pelvis from which the shape has evolved in response to the increase in head size and brain volume (Berge et al., 1984; Tague and Lovejoy, 1989; Berge, 1992; Rosenberg, 1992; Häusler and Schmid, 1995; Ruff, 1995; Ruff et al., 1997; Rosenberg and Trevathan, 2002; Lovejoy, 2005a, b; Bouhallier and Berge, 2006). Other functions recognized to influence pelvic shape in the course of evolution are functions related to the support of body viscera (Tague and Lovejoy, 1989) and thermoregulatory constraints, which limit enlargement of the pelvis (Ruff, 1991). In summary, although natural selection optimizes performance of the human hip joint in function of locomotion, the adaptation is also dependent on, first, the physical constraints of

the inherited structure and, second, the trade-off with other functions. We propose that the long phylogenetic history of the human hip joint, before its functions of support and transmission during permanent bipedal locomotion, might explain the level of concordance currently observed. This explanation follows from the observation, already noted by Kapandji (2009) and quantified in this study, that the total concordance of the human hip joint is obtained in a quadrupedal posture on an inclined substrate (Fig. 4B). Although many evolutionary traits at the human hip joint morphology are known to be functionally involved in habitual bipedal locomotion (McHenry and Corruccini, 1978; Stern and Susman, 1983; Asfaw, 1985; Ruff, 1988; Ruff and Runestad, 1992; MacLatchy and Bossert, 1996; Ohman et al., 1997; Rafferty, 1998; Häusler, 2002; Lovejoy, 2005a), our results suggested that the quadrupedal origin of our species might be recorded in the three-dimensional orientations of the two neighbouring components of the human hip joint. This suggestion might help to understand the different results obtained between females and males in the present functional integrative analysis. No significant pattern of covariation was obtained for the sample of females, and the degree of concordance of the mean three-dimensional orientations of the acetabulum and the femoral neck is lower in females than males. Although additional analyses are needed in order to obtain statistically powerful results, we propose that this difference might be due to the more constrained shape of the female pelvis morphology due to the need for a wide birth canal. Indeed, the evolution of the pelvis morphology in females is known to be greatly constrained by the need to give birth (Berge et al., 1984; Tague and Lovejoy, 1989; Berge, 1992; Rosenberg, 1992; Häusler and Schmid, 1995; Ruff, 1995; Ruff et al., 1997; Rosenberg and Trevathan, 2002; Lovejoy, 2005a, b; Bouhallier and Berge, 2006). However, the interrelations between pelvis morphology and acetabular orientation are strong, regarding the development of the hip bone at the triradiate cartilage (Harrison, 1958; Ponseti, 1978; Buchholz et al., 1982; Portinaro et al., 2001). The orientation of the acetabulum is, thus, strongly dependent on the genetic constraints acting on the female pelvis in relation with its parturition function. Although in a relative weaker proportion than the acetabular orientation, the pelvic morphology also has influence on the orientation of the femoral neck. Thus, we suggested that the female morphology of the pelvis might limit the evolution of the hip joint orientations in relation with its function of parturition resulting in a lower concordance than it could be achieved with a male morphology of the pelvis. In summary, we proposed that in females the optimisation of the hip in function of locomotion also could trade-off with the parturition function.

To better understand the evolution of the human hip joint and the constraints acting thereupon, it should be important to study an extended sample of hominoids and other primates. Although changes in the shape of both the proximal femur and the acetabular region among hominoids have been already investigated in the literature (McHenry and Corruccini, 1978; Stern and Susman, 1983; Asfaw, 1985; Ruff, 1988; Ruff and Runestad, 1992; MacLatchy and Bossert, 1996; Ohman et al., 1997; Rafferty, 1998; Lovejoy, 2005a), few analyses have studied the orientations of these two structures (Tayton, 2007) and even fewer have attempted to quantify their three-dimensional orientations.

Acknowledgements

We thank Geneviève Perréard, who is in charge of the collection SIMON, for the cordial welcome in her laboratory in Geneva and her help for data acquisition. We also thank Christine Lefèvre for allowing us access to the collections of Comparative Anatomy of the National Museum of Natural History in Paris and Philippe

Menecier in charge of the collections of the Musée de l'Homme (MNHN, Paris). Special thanks to Camille Dégardin for her help in the illustrations, and to Anthony Herrel for his comments and help with the paper. We also thank Caroline Simonis for her great help in the morphometrical analyses and her comments. Comments by Chris Ruff significantly improved this manuscript. This study benefited from the morphometrics facility of the Paris Muséum (UMS 2700 CNRS – MNHN: 'Plateforme de Morphométrie'). Financial support from the Société d'Anatomie de Paris and the Action Transversale Muséum 'Formes possibles, formes réalisées' of the National Museum of Natural History are gratefully acknowledged. Last, we are grateful to the anonymous reviewers who provided interesting and helpful comments on this work.

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