

Role of Spatial Integration in the Morphology of the Bony Labyrinth in Modern Humans

Le rôle de l'intégration spatiale dans la morphologie du labyrinthe osseux chez les humains modernes

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Abstract The bony labyrinth corresponds to the osseous wall of the inner ear, the hearing and balance organ located in the petrous pyramids, in the base of the cranium. The morphology of the labyrinth reflects phylogenetic and ecological signals. In hominoid primates, it is also influenced by its anatomical environment. The aim of this study is to determine whether, in the species *Homo sapiens*, the morphological relationships between the labyrinth and the skull result from geometrical constraints linked to equilibrioception, or from spatial constraints due to the inclusion of the inner ear in the petrous bone. Based on CT-scans of the skulls of adult individuals (n=30), two sets of 22 landmarks each were placed on the labyrinth and on the basicranium. The covariations between these two sets were investigated using two-block partial least squares (2B-PLS) analyses. The shape of the labyrinth is significantly correlated with the cranial base, but not with the isolated temporal bone. This indicates that the morphology of the labyrinth mainly results from functional constraints. However, several observations suggest that spatial constraints also have an influence, especially on the cochlea. The associated changes in shape are consistent with the ontogenetic trend, but differ slightly from the phylogenetic trend. These covariations caution against exclusively ecological interpretations of the morphology of the labyrinth.

Keywords Bony labyrinth · Petrous bone · Cranial base · Integration · Geometric morphometrics · *Homo sapiens*

Résumé Le labyrinthe osseux correspond à la paroi osseuse de l'oreille interne, organe de l'audition et de l'équilibre situé dans les pyramides pétreuses, dans la base du crâne.

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La morphologie du labyrinthe reflète des signaux écologique et phylogénétique. Chez les primates hominoïdes, elle est également influencée par son environnement anatomique. L'objectif de cette étude est de déterminer si dans l'espèce *Homo sapiens*, les relations morphologiques entre le labyrinthe et le crâne résultent de contraintes géométriques en lien avec l'équilibrioception ou de contraintes spatiales dues à l'inclusion de l'oreille interne dans le pétreux. À partir de CT-scans du crâne d'individus adultes (n = 30), deux ensembles de 22 points-repères sont placés sur le labyrinthe d'une part et sur le basicrâne d'autre part. Les covariations entre ces deux ensembles sont étudiées à l'aide d'analyses aux moindres carrés partiels à deux blocs (2B-PLS). La forme du labyrinthe est significativement corrélée à celle de la base du crâne, mais pas à celle de l'os temporal pris isolément, ce qui indique que la morphologie du labyrinthe résulte surtout de contraintes fonctionnelles. Cependant, certaines observations suggèrent l'influence de contraintes spatiales, notamment sur la cochlée. Les changements de forme associés sont cohérents avec la tendance ontogénétique observée chez les humains, mais différent de la tendance phylogénétique. L'existence de ces covariations incite à la prudence quant aux interprétations écologiques de la morphologie du labyrinthe.

Mots clés Labyrinthe osseux · Os pétreux · Basicrâne · Intégration · Morphométrie géométrique · *Homo sapiens*

Introduction

The bony labyrinth consists of tubes and cavities embedded in the petrous part of the temporal bone, on each side of the head. It holds and roughly moulds the inner ear, which is a sensory detector for balance and hearing. In mammals, three semicircular ducts detect head rotations, two otolithic organs give the position of the head relative to the vertical axis, and

sounds are sensed by the coiled cochlea. The three semicircular canals are roughly orthogonal, the lateral semicircular canal forms an angle of 20° to 25° relative to the Frankfurt plane, so that it is nearly horizontal at rest, and the angle between the midsagittal plane of the head and the two vertical (anterior and posterior) semicircular canals is about 45° [1]. This geometry allows efficient detection of head rotations in all directions, further improved by the coupling between the labyrinths on both sides of the head [1]. The geometry of the labyrinth is remarkably conservative in mammals, suggesting strong functional constraints [2].

However, some variability exists in the morphology of the labyrinth, both across species [3] and within species [4,5]. The morphology of the bony labyrinth carries both a phylogenetic signal and an ecological signal [6-8]. For instance, the dimensions of the vestibular apparatus differ between aquatic and terrestrial mammals, and in musteloid taxa, the degree of arboreal and fossorial behaviour are reflected by the shape of the labyrinth [7,9,10]. In primates, the cochlear length and the area of the oval window, located on the base of the cochlea, reflect auditory capacities [11,12], whereas the semicircular canal sizes and geometry provide information on posture, locomotor agility and angular head velocity [4,12-15]. The spiral form of the cochlea also results from spatial packing in the petrous bone, at least in humans [16]. In primates, when the cranial base is more flexed and the posterior surface of the petrous pyramids is more vertical, the lateral semicircular canal (particularly its posterior part) tends to be tilted upwards in relation to the rest of the labyrinth [2]. Some correlations are also observed during the prenatal development of humans, but not necessarily the same ones [17]. In the first weeks of gestation, the cranial base angle increases and the petrous pyramids rotate coronally. While the orientation of the labyrinth follows the orientation of the posterior cranial base, the lateral semicircular canal tilts upwards (especially relative to the cochlea), the basal turn of the cochlea rotates coronally and the angle between the two vertical canals increases because of their greater torsion. The morphological changes in the labyrinth observed during ontogeny are associated with the orientation of the petrous bone rather than with retroflexion of the basicranium. Because of the ossification of the otic capsule that surrounds it, the adult size and shape of the labyrinth are attained before 19 weeks of gestation [17]. In adult humans, the upward tilt of the lateral semicircular canal – combined with a smaller posterior canal – is also associated with a relatively more coronally rotated petrous bone, and hence a wider posterior cranial fossa [18].

In this study, we focus on a single species, modern humans, so that the phylogenetic and ecological signals can be ignored. In particular, the differences in locomotor behaviour and sound perception associated with the use of diverse ecological niches are considered as negligible

between individuals. The aim is to determine whether the morphological correlations between the bony labyrinth and the cranial base reflect

- 1) geometrical constraints related to efficient perception of head movements, i.e., functional constraints, or
- 2) spatial constraints linked to the restricted space within the petrous bone, as with cochlear coiling, or
- 3) both spatial and functional constraints.

To do so, we evaluated the integration between the labyrinth and its osseous surroundings, namely the petrous pyramids and, more generally, the basicranium. When the constraints are functional (hypotheses 1 and 3), the shape of the labyrinth is linked to the orientation of the petrous pyramids in the cranial base, and hence to the shape of the basicranium, which is not the case for spatial integration only (hypothesis 2). If there is spatial packing (hypotheses 2 and 3), the shapes of the labyrinth and the petrous pyramids are correlated, whereas they are independent in the absence of spatial constraints (hypothesis 1). In all cases, the sizes of the petrous pyramids and the bony labyrinth are likely to be influenced by the overall size of the cranial base. However, when this general effect is removed, interactions between the shapes and sizes of the labyrinth and the pyramids are to be expected in the presence of spatial constraints (hypotheses 2 and 3), but should disappear in their absence (hypothesis 1).

Materials and methods

The sample consisted of 30 humans aged 20 to 95 years from the Terry anatomical collection, an osteological collection of 1,728 individuals of known ethnic origin, sex, age and cause of death, collected in the U.S.A. in the first half of the 20th century. 18 individuals were Afro-American and 12 of European ancestry. The sex ratio is balanced. Using Amira software (Thermo Fisher Scientific), the skull and the bony labyrinth were virtually extracted from the CT-scans provided by Copes [19]. The 22 landmarks defined by Lebrun et al. [6] were positioned on the labyrinth (Fig. 1, Table 1). 22 landmarks were placed on the cranial base: 7 on the midsagittal plane and 15 on one side; of these, 9 were located on the temporal bone and more specifically on the petrous pyramids (Fig. 2, Table 2).

Statistical analyses were conducted on the landmark coordinates using MorphoJ v1.0e software [20]. The landmark coordinates were aligned, centred and scaled using Procrustes superimpositions [21,22]. They were then regressed against their log centroid size to remove allometric effects [22]. These two operations were performed independently for each set of landmark coordinates: the labyrinth (22 landmarks), the petrous part of the temporal bone (9 landmarks)

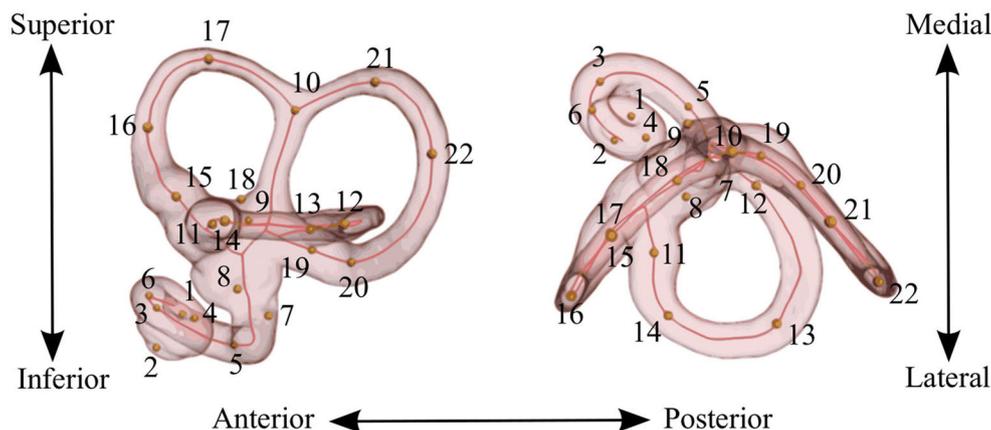


Fig. 1 Position of the 22 landmarks of the bony labyrinth. After Le Maître et al. [15] / *Position des 22 points-repères sur le labyrinthe osseux. D'après Le Maître et al. [15]*

Table 1 Definition of landmarks on the bony labyrinth [6] / <i>Définition des points-repères sur le labyrinthe osseux [6]</i>		
Number	Name	Definition
1	Helix basis	Centre of the first turn of the cochlea
2	Helix apex	Centre of the last turn of the cochlea
3	Helix anteromedial	Anteromedial-most point of the first turn of the cochlea
4	Helix posterolateral	Posterolateral-most point of the first turn of the cochlea
5	Helix inferior	Inferior-most point of the first turn of the cochlea
6	Helix superior	Superior-most point of the first turn of the cochlea
7	Fenestra cochlea	Centre of the round window
8	Fenestra vestibuli	Centre of the oval window
9	Aquaeductus vestibuli	Opening of the vestibular aqueduct in the vestibular wall
10	Crus commune apex	Bifurcation point of the common crus
11	Canalis lateralis ampulla	Centre of the ampulla of the lateral semicircular canal
12	Canalis lateralis posteromedial	Posteromedial-most point of the lateral semicircular canal
13	Canalis lateralis posterolateral	Posterolateral-most point of the lateral semicircular canal
14	Canalis lateralis anterolateral	Anterolateral-most point of the lateral semicircular canal
15	Canalis anterior ampulla	Centre of the ampulla of the anterior semicircular canal
16	Canalis anterior anterolateral	Anterolateral-most point of the anterior semicircular canal
17	Canalis anterior superior	Uppermost point of the anterior semicircular canal
18	Canalis anterior inferior	Inferior-most point of the anterior semicircular canal
19	Canalis posterior ampulla	Centre of the ampulla of the posterior semicircular canal
20	Canalis posterior inferior	Inferior-most point of the posterior semicircular canal
21	Canalis posterior superior	Uppermost point of the posterior semicircular canal
22	Canalis posterior posterolateral	Posterolateral-most point of the posterior semicircular canal

and the cranial base (22 landmarks including on the temporal bone). Finally, two-block partial least squared (2B-PLS) analyses were performed between the labyrinth and either the temporal bone or the whole cranial base, in order to assess the degree of covariation between their shapes [23]. Permutation tests against the null hypothesis of independence between the two blocks were performed with 10,000 randomization rounds. The 3D shape changes associated

with each PLS component were visualized using the *rgl* package in R v3.2.2 software [24,25].

In a second round of analyses, the log centroid size of the cranial base (computed with the 22 landmarks) was regressed out, in order to correct for the effect of the overall skull size on the covariation patterns between the bony labyrinth and the petrous pyramids. The regression residuals of the variables (Procrustes coordinates and / or log centroid

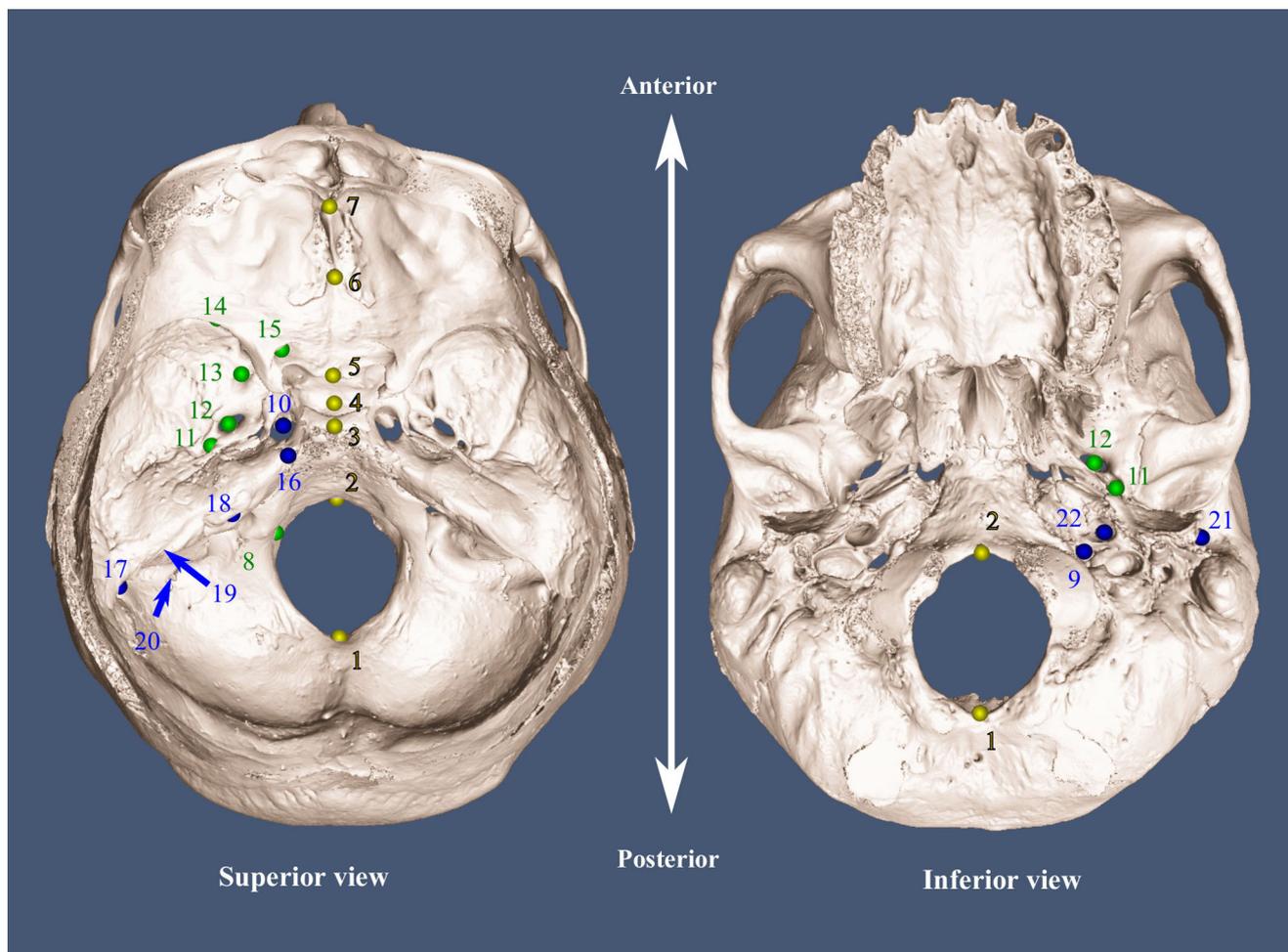


Fig. 2 Position of the 22 landmarks of the cranial base. Yellow: midsagittal plane; blue: temporal bone; green: lateral base excluding the temporal bone. The 9 landmarks in blue were used for the analyses on the temporal bone and all 22 landmarks were used for the analyses on the cranial base / *Position des 22 points-repères sur la base du crâne. Jaune, plan médio-sagittal ; bleu, os temporal ; vert, partie latérale de la base à l'exclusion de l'os temporal. Les 9 points-repères en bleu ont été utilisés pour les analyses sur l'os temporal et l'ensemble des 22 points-repères en bleu ont été utilisés pour les analyses sur la base du crâne*

size) describing these two structures were used as covariates in 2B-PLS analyses to investigate their morphological integration in terms of both size and shape.

Results

The overall correlation between the shapes of the labyrinth and the petrous part of the temporal bone is very low and not significant ($RV=0.3726$, $P=0.4928$). According to the scree plot, the first four PLS components carry the main signal for the correlations and account for 70.9% of the total squared covariance. For each PLS component, the pairwise correlation coefficient is higher than the overall correlation between the two blocks, but all values remain below 0.6 except for

PLS 3 with $r^2 = 0.759$ (Table 3). The first PLS component ($r^2=0.593$) accounts for 25.7% of the total squared covariance. High values correspond to comparatively high, short and narrow petrous pyramids (Fig. 3). Relative to the upper ridge of the petrous bone, the inferior part of the pyramid (that is, the segment linking the jugular and the mastoid foramina) is sagittally rotated. The associated changes in labyrinth shape are a downward translation of the posterior semicircular canal with a shortening of the common crus, a sagittal rotation of the lateral semicircular canal in the horizontal plane, a tightening of the cochlear spiral and the rotation of its basal turn relatively to the semicircular canal system, clockwise when seen from the left side of the head.

The shape of the labyrinth is significantly correlated with the shape of the cranial base ($RV = 0.5327$, $P < 0.05$).

Table 2 Definition of landmarks on the cranial base. The landmarks positioned on the temporal bone are highlighted with a star (*) /
Définition des points-repères sur la base du crâne. Les points-repères positionnés sur l'os temporal sont marqués d'une étoile ()*

Number	Temporal	Name	Notes
1		Opisthion	Posterior-most point of the foramen magnum
2		Basion	Anterior-most point of the foramen magnum
3		Dorsum sellae	Posterior-most point
4		Fossa hypophysialis	Inferior-most point
5		Tuberculum sellae	Posterior-most point
6		Cribriform plate	Posterior-most point
7		Foramen caecum	
8		Hypoglossal canal	
9	*	Jugular foramen	Anterior-most point
10	*	Foramen lacerum	
11		Foramen spinosum	
12		Foramen ovale	
13		Foramen rotundum	
14		Superior orbital fissure	Anterolateral-most point
15		Optic foramen	
16	*	Apex of the petrous pyramid	
17	*	Base of the petrous pyramid	
18	*	Internal acoustic meatus	
19	*	Aquaeductus vestibuli	
20	*	Mastoid foramen	
21	*	External acoustic meatus	
22	*	Carotid canal	

The main signal is conveyed by the first five PLS components (76.0 % of the total squared covariance) for the association with the cranial base. All five pairwise correlation coefficients are above 0.6 and even above 0.7 for PLS 1, 2 and 3 (Tab. 3). The correlation is higher for PLS 1 ($r^2=0.754$), which accounts for 22.0 % of the total squared covariance. Compared to the lower values, high PLS 1 values correspond to an overall shortening, widening and increase in height of the cranial base, with a lateral projection of the middle and posterior fossae and a lengthening of the clivus and its surrounding area, producing a narrower angle with the foramen magnum (Fig. 4a). The morphological changes in the petrous pyramids are similar to the features observed for PLS1 in the previous 2B-PLS analysis on the petrous bone only. The associated changes in labyrinth shape also correspond to PLS1 in the previous analysis, except for the absence of rotation of the lateral semicircular canal in the horizontal plane. PLS 2 accounts for 15.0 % of the total squared covariance ($r^2 = 0.725$). Relatively to the lowest values, the highest correspond to a reduction of the basicranial flexure and an upward rotation of the posterior part of the cranial base, together with the sagittal rotation of the lateral part of the skull, producing a long, low and narrow cranial base (Fig. 4b). These changes in shape are associated

with the rotation of the labyrinth around the lateral semicircular canal, clockwise when observed from the left side of the head. The angle between the two vertical canals is more obtuse and the lateral semicircular canal is more projected along the anteroposterior axis.

The log centroid size of the cranial base significantly ($P<0.005$) predicts 48.9% of the log centroid size of the petrous pyramids and 36.6 % of the log centroid size of the bony labyrinth. Conversely, only a small proportion of the shape of the petrous pyramids (4.2%) and the bony labyrinth (3.4%) are predicted by the log centroid size of the cranial base, and these relationships are not significant ($P=0.2665$ and $P=0.4980$, respectively). When the effect of the overall size of the basicranium is removed, none of the associations between the labyrinth and the petrous pyramids is statistically significant. The correlation between their log centroid sizes is very low ($r^2=0.0462$, $P=0.2541$), as is the association between the shape of the labyrinth and the size of the petrous pyramids ($RV=0.1554$, $P=0.2480$) and between the size of the labyrinth and the shape of the petrous pyramids ($RV=0.0363$, $P=0.9738$). The overall association between the shapes of the labyrinth and the petrous pyramids is not statistically significant ($P=0.4439$), with a RV coefficient as low as 0.3761 (Tab. 3). The first four components (69.9% of

Table 3 Results of the 2B-PLS analyses between the labyrinth and the temporal bone or the cranial base. The RV-coefficients measure the overall association between the two blocks of variables and the r^2 measure the pairwise association for each PLS component (only the first five components are shown, with the % of total squared covariance described). The star (*) indicates $P < 0.05$ / *Résultats des analyses aux moindres carrés à deux blocs entre le labyrinthe et l'os temporal ou le basicrâne. Les coefficients RV mesurent l'association globale entre les deux blocs de variables et les r^2 mesurent l'association entre les deux axes de chaque composante de l'analyse aux moindres carrés (seules les cinq premières composantes sont mentionnées, avec le % du total des carrés des covariances décrit par chacune). L'étoile (*) indique que $P < 0,05$.*

	Cranial base		Petrous bone		Petrous bone - size base regressed out	
	r^2	% tot. cov ²	r^2	% tot. cov ²	r^2	% tot. cov ²
RV-coefficient	0.5327*	-	0.3726	-	0.3761	-
PLS1	0.754	22.0 %	0.593	25.7%	0.622	25.8%
PLS2	0.725	15.0 %	0.587	17.9%	0.684	17.9%
PLS3	0.724	12.6 %	0.759	16.1%	0.618	15.4%
PLS4	0.632	10.4 %	0.576	11.2%	0.576	10.7%
PLS5	0.637	8.0 %	0.551	6.8%	0.666	6.3%

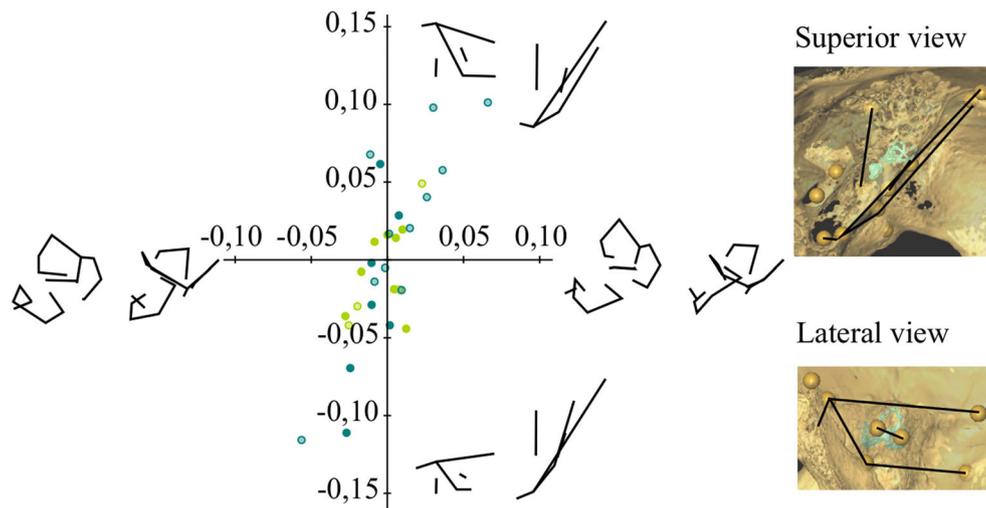


Fig. 3 Scatter plots of the first PLS axes describing 25.7 % of the total squared covariance between the shape of the labyrinth and the shape of the temporal bone. Blue circles: Afro-Americans; green circles: European ancestry; dark filling: men; light filling: women. Wireframes show the shape changes along each axis. Left: lateral view; right: superior view / *Nuage de points pour les premiers axes de la PLS décrivant 25,7 % du total des carrés des covariances entre la forme du labyrinthe et celle de l'os temporal. Cercles bleus : Afro-Américains, cercles verts : individus d'origine européenne ; remplissage sombre : hommes ; remplissage clair : femmes. Les points reliés par des segments représentent les changements de forme le long de chaque axe. À gauche, vue latérale ; à droite, vue de dessus*

the total squared covariance) carry most of the signal. For each PLS component, the proportion of total squared covariance accounted for is very similar to the results of the previous 2B-PLS analysis between the shapes of the labyrinth and the petrous pyramids, in which the log centroid size of the latter had been regressed out instead of the log centroid size of the cranial base (Tab. 3). Here, the pairwise correlations are slightly higher than previously except for PLS3, but all coefficients remain below 0.7.

Discussion

The correlation between the shape of the labyrinth and the shape of the cranial base suggests that geometrical constraints linked to equilibrioception are involved in the morphology of the labyrinth. Along the main axis of covariation, the linear changes in length, width or height of the cranial base do not modify the semicircular canal system, except the translation of one canal and the shortening of the common

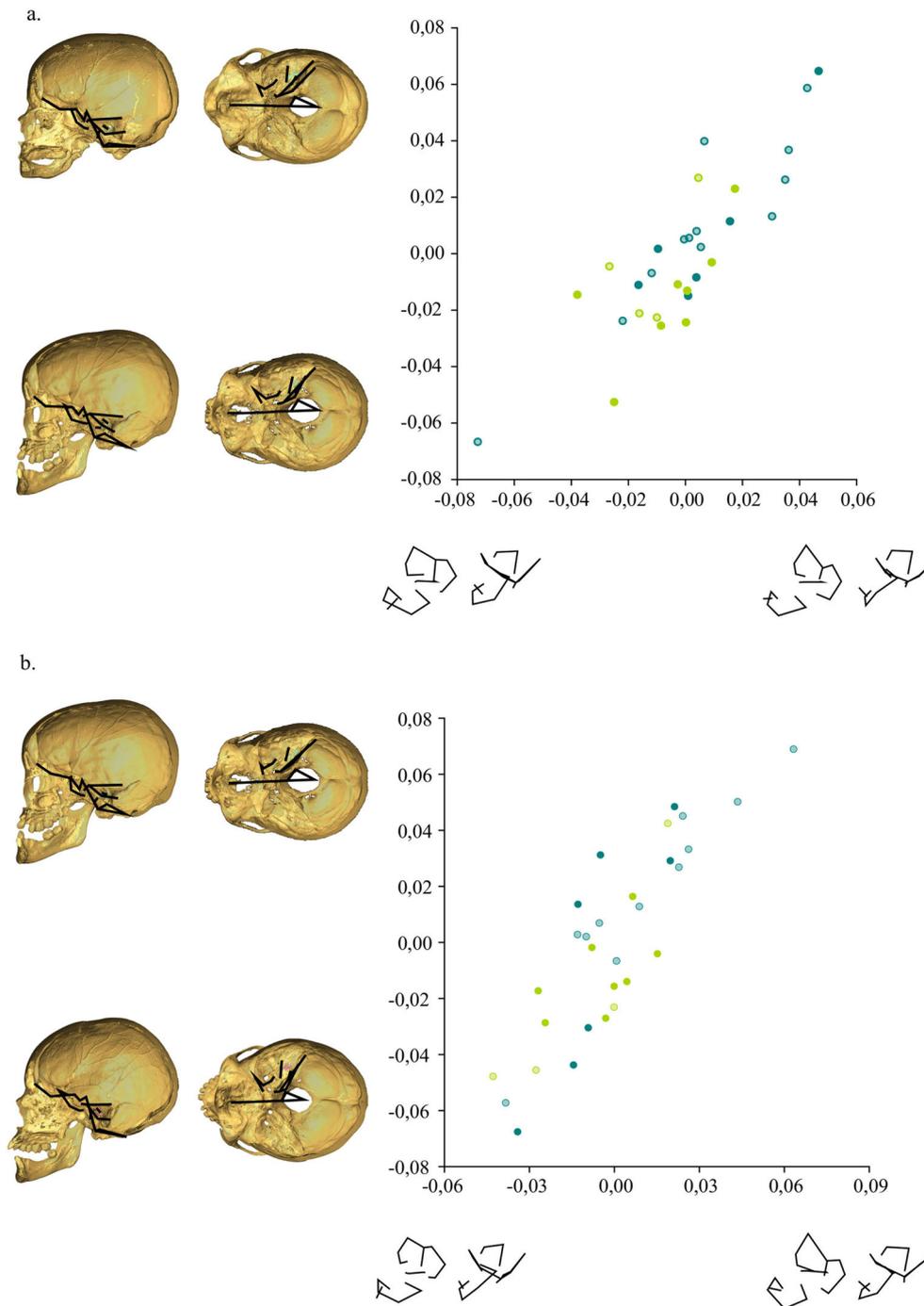


Fig. 4 Scatter plots of (a) PLS 1 and (b) PLS 2 axes describing 22.0% and 15.0% of the total squared covariance between the shape of the labyrinth and the shape of the cranial base. Blue circles: Afro-Americans; green circles: European ancestry; dark filling: men; light filling: women. Wireframes show the shape changes along each axis. Left: lateral view; right: superior view / Nuage de points pour (a) PLS 1 et (b) PLS 2 décrivant respectivement 22,0 % et 15,0 % du total des carrés des covariances entre la forme du labyrinthe et celle de la base du crâne. Cercles bleus : Afro-Américains ; cercles verts : individus d'origine européenne ; remplissage sombre : hommes ; remplissage clair : femmes. Les points reliés par des segments représentent les changements de forme le long de chaque axe. À gauche, vue latérale ; à droite, vue de dessus

crus (Fig. 4a), which have no influence on the parameters that matter for the detection of head movements [26]. By contrast, in the second axis of covariation, the rotations of the petrous pyramid are associated with changes in the geometry of the semicircular canal system (Fig. 4b). The rotation of the petrous pyramid linked to the basicranial flexion is correlated with the rotation of the lateral semicircular canal, in the same direction relatively to the rest of the labyrinth. The sagittal rotation of the petrous pyramids corresponds to the anteroposterior elongation of the labyrinth, with a wider angle between the anterior and the posterior canals. According to biophysical models, the sensitivity of a semicircular duct depends on arc size, cross-sectional area and eccentricity [27-29] and, as the three semicircular ducts are coupled in the mammalian inner ear, their relative angles and dimensions also play a role in the detection of head movements [30]. In both rotations, the angles between the semicircular canals and their dimensions change, and hence the sensitivity of the system. However, these morphological changes tend to maintain the overall orientation of the semicircular canals in the skull: the vertical canals remain symmetrical in relation to the midsagittal plane and the lateral semicircular canal follows the orientation of the posterior cranial base, and hence of the foramen magnum. The correlation between the orientation of the lateral canal and the posterior cranial base is consistent with both the phylogenetic trend in primates [2] and the ontogenetic trend in humans [17]. The association between the width of the posterior basicranial fossa and the translation of a smaller posterior semicircular canal (because of the shorter common crus) also broadly corresponds to the main covariation axis found in a previous study conducted on adult humans, except for the rotation of the petrous bone [18]. This small difference could be due to the use of semi-landmarks that capture shape more finely.

After correction for the overall effect of skull size, there is no correlation between the labyrinth and the petrous bone when size is involved, and the overall correlations between their shapes are not significant. However, spatial constraints could have an effect on the shape of the labyrinth, because the pairwise correlation coefficients for individual PLS components are not too low (r^2 around 0.6 for the five first components) and the associated changes in shape are consistent with spatial integration, since the rotations of the basal turn of the cochlea and of the posterior surface of the petrous pyramid are similar and the sagittal rotation of the lateral semicircular canal follows the rotation of the petrous pyramid (Fig. 3). Some morphological associations revealed when the cranial base is considered also suggest that spatial constraints have an influence: for the first component, the rotation of the cochlea corresponds to the rotation of the petrous pyramid on the head and, as in correlations with the temporal bone, the downward translation of the posterior

semicircular canal follows the increase in height of the posterior surface of the petrous pyramid (Fig. 4a). The association between the orientation of the cochlea and the orientation of the petrous pyramids is similar to the human ontogenetic trend [17] and, together with the changes in coiling shape, consistent with the spatial packing observed for the cochlea in humans [16].

Compared to chimpanzees, our closest relatives, humans have a more flexed cranial base [31] and their petrous pyramids have a more coronal orientation [32]. These features roughly correspond to the changes in shape observed along PLS 2 (Fig. 4b) for the analysis with the whole cranial base, with chimpanzees having morphologies closer to the highest values for humans. Compared to great apes, the lateral semicircular canal in humans is coronally rotated and less posteriorly projected, and the labyrinth overall is rotated around this canal [2,15]. Except for the projection of the lateral canal, this morphology is not consistent with the changes in shape associated with the cranial base for PLS 2, suggesting that the phylogenetic trend might be slightly different to the ontogenetic and intraspecies trends in humans.

Conclusion

It has been known since the early 2000s that the labyrinth and the cranial base are morphologically correlated in primates and during human foetal development. This study shows that this is also the case within adult variability in our species. The shape of the semicircular canals depends on geometrical constraints linked to equilibrioception. The morphological correlation with the petrous pyramids is not significant; however, the shape associations observed could be a sign of some spatial packing of the cochlea in the temporal bone. The patterns observed in adults are consistent with the ontogenetic trend reported previously in humans.

Despite some similarities, the intraspecies covariation pattern in humans is not the same as the phylogenetic pattern in hominoids, suggesting that the intraspecies trend might be different across species. It would be interesting to perform the same study for chimpanzees or gorillas, to determine whether the correlation pattern found in humans is specific to this species or represents a general trend in hominoids. Humans are characterized by very large brains compared to other primates, which induce morphological constraints on the skull as a whole that result in its peculiar basicranial shape. The spatial packing induced by this large brain could be a much stronger determinant of the shape of the labyrinth than ecology, as observed for the semicircular canals of birds [33].

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