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Motion from the past. A new method to infer vestibular capacities of extinct species

Mouvements anciens. Une nouvelle méthode permettant de déduire les capacités vestibulaires d'espèces éteintes

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ABSTRACT

The vestibular system detects head movement in space and maintains visual and postural stability. The semicircular canal system is responsible for registering head rotation. How it responds to head rotation is determined by the rotational axis and the angular acceleration of the head, as well as the sensitivity and orientation of each semicircular canal. The morphological parameters of the semicircular canals are supposed to allow an optimal detection of head rotations induced by some behaviours, especially locomotor. We propose a new method of semicircular canal analysis, based on the computation of central streamlines of virtually reconstructed labyrinths. This method allows us to ascertain the functional structure of the semicircular canal system and to infer its capacity to detect particular head rotations, induced by particular behaviours. In addition, this method is well-suited for datasets provided by any kind of serial sectioning methods, from MRI to μCT scanning and even mechanical serial sectioning, of extant and extinct taxa.

RÉSUMÉ

Le système vestibulaire permet de détecter les mouvements de la tête dans l'espace et de maintenir un équilibre visuel et postural. Le système des canaux semi-circulaires est responsable de la détection des rotations de la tête. La façon dont il répond aux rotations est déterminée par l'axe de rotation et l'accélération angulaire de la tête, ainsi que par la sensibilité et l'orientation de chaque canal semi-circulaire. Les paramètres morphologiques des canaux semi-circulaires sont supposés permettre une détection optimale des rotations de la tête induites par certains comportements, en particulier locomoteurs. Nous proposons une nouvelle méthode d'analyse des canaux semi-circulaires, basée sur le calcul de lignes de

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flux centrales, à partir de reconstructions virtuelles de labyrinthes. Cette méthode permet de déterminer la structure fonctionnelle du système des canaux semi-circulaires et d'en déduire sa capacité à détecter des rotations de tête induites par des comportements particuliers. Elle est applicable à des jeux de données issus de tout type de méthodes de sections sériées, de l'IRM aux scanners μCT en passant par le sectionnement sérié mécanique, et ce, pour des taxons actuels et éteints.

1. Introduction

The vestibular system of vertebrates is involved in the coordination of movement, gaze control, and maintaining balance. One of its main tasks is to compensate for uncontrolled head movements to maintain head and gaze stability in space (Berthoz, 1997). Its peripheral detector, the labyrinth or inner ear, is able to detect angular and linear motions and to send this information to the brain through mechanosensorial hair cells (Rabbitt et al., 2004). The semicircular canal system of the labyrinth detects angular motion of the head. In physiological conditions, the semicircular canals system is receptive to angular acceleration of the head but encodes the angular velocity (Mayne, 1950; Oman et al., 1987; Rabbitt et al., 2004). The labyrinth of jawed vertebrates is composed of three semicircular ducts, connected to a set of end organs which contain otolithic masses: the utricle, the saccule and the lagena (Fig. 1). These membranous organs are the functional organs of the system. They are enclosed in bony structures termed the semicircular canals and the vestibule. The semicircular canals, which closely follow the path and shape of the semicircular ducts (Blanks et al., 1975; Bradshaw et al., 2010; Hullar, 2006; Ifediba et al., 2007; Spoor, 2003), and remains of the otic capsules are often well preserved in fossil skulls. Thanks to the ever improving imaging tomography methods in palaeontology, it is now possible to conduct studies of fossil labyrinths in a noninvasive and much faster way than ever before (Spoor and Zonneveld, 1995). It has been suggested that the semicircular duct morphology allows the optimal detection of animals' head movements (Gray, 1907; Gray, 1908; Jones and Spells, 1963; Wilson and Melvill Jones, 1979). Morphological parameters, such as length and cross-section area of the semicircular ducts, are primarily correlated with the body mass (Jones and Spells, 1963; Howland and Masci, 1973). However, it was suggested that these parameters were also linked to the animals' locomotor behaviour (Clarke, 2005; Georgi, 2008; Sipla, 2007; Spoor et al., 1996). This latter relation is of particular interest because it bears information on locomotor behaviour of extinct taxa (Spoor, 2003). Therefore, a certain amount of analyses relating semicircular canal size to locomotor behaviour and agility, taking body mass into account, have been undertaken (Clarke, 2005; Silcox et al., 2009; Sipla, 2007; Spoor et al., 1994; Spoor et al., 2002; Walker et al., 2008). They provided interesting results and supported the existence (although criticized; Graf and Vidal, 1996) of a relation between semicircular canal morphology and locomotor behaviour.

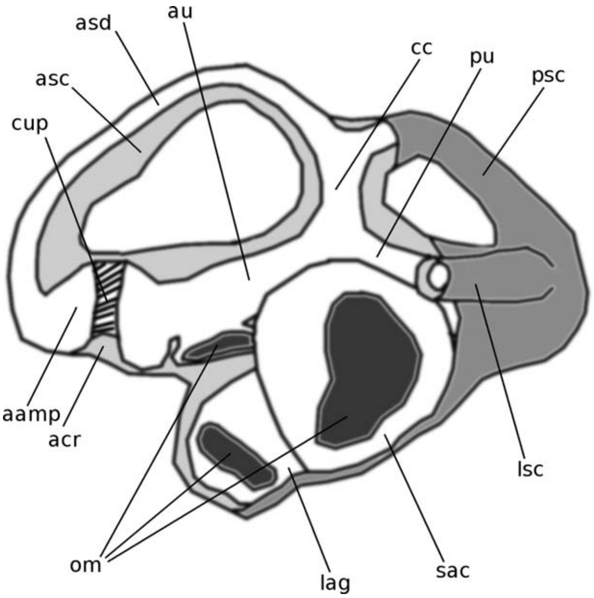

Fig. 1. Lateral view of a schematic labyrinth. The bony labyrinth is in grey. **aamp**: anterior ampulla; **acr**: anterior crista; **asc**: anterior semicircular canal; **asd**: anterior semicircular duct; **au**: anterior utricle; **cc**: common crus; **cup**: cupula; **lag**: lagena; **lsc**: lateral semicircular canal; **om**: otolithic masses; **psc**: posterior semicircular canal; **pu**: posterior utricle; **sac**: saccule.

Fig. 1. Vue latérale d'un labyrinthe schématique. Le labyrinthe osseux est en gris. **aamp**: ampulla antérieure; **acr**: crista antérieure; **asc**: canal semi-circulaire osseux antérieur; **asd**: canal semi-circulaire membraneux antérieur; **au**: utricule antérieur; **cc**: crus commune; **cup**: cupula; **lag**: lagena; **lsc**: canal semi-circulaire latéral; **om**: masses otolithiques; **psc**: canal semi-circulaire postérieur; **pu**: utricule postérieur; **sac**: saccule.

2. Structure of the semicircular canals system

2.1. Morphological structure

The semicircular canal system is commonly described in jawed vertebrates (gnathostomes) as an idealized structure that consists of three functional pairs of roughly circular canals which retain specific angular relationships between them and with the reference planes of the head (Graf, 1988). In this arrangement, each of the three ipsilateral semicircular canal of one labyrinth (i.e. semicircular canals of the same labyrinth) is supposed to be oriented orthogonally, relative to the other two. The vertical semicircular canals (anterior and posterior) form an angle of 45° with the sagittal plane. The synergistic semicircular canal pairs (i.e. semicircular canals of the same functional pair) consist of the two lateral semicircular canals, but also

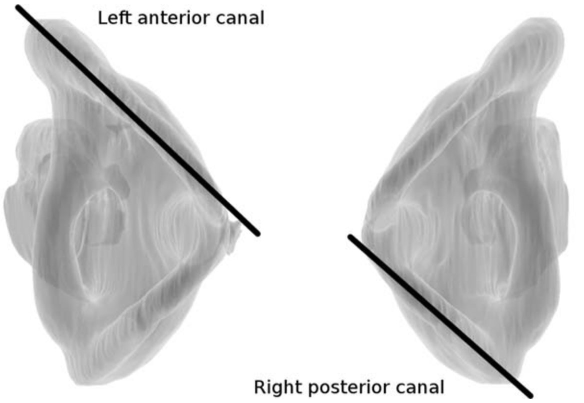

Fig. 2. Dorsal view of the labyrinths of a crocodile showing one synergistic functional pair composed of the left anterior semicircular canal and the right posterior semicircular canal.

Fig. 2. Vue dorsale des labyrinthes d'un crocodile montrant une paire fonctionnelle synergiste, composée du canal semi-circulaire antérieur gauche et du canal semi-circulaire postérieur droit.

of two pairs composed of the anterior semicircular canal of one labyrinth that is coupled with the posterior semicircular canal of the other labyrinth (Fig. 2). The synergistic semicircular canals are considered as being parallel and work in a push-pull fashion (if one semicircular canal is excited, the other one is inhibited). This idealized system allows one to easily resolve any head rotation through the semicircular canals responses. This easily applied system does not, however, exactly mirror the real system. Actually, it has long been known that the ipsilateral semicircular canals are not orthogonal (Blanks et al., 1975; Bradshaw et al., 2010; Brichta et al., 1988; Calabrese and Hullar, 2006; Cox and Jeffery, 2008; Curthoys et al., 1975, 1977; Dickman, 1996; Ghanem et al., 1998; Hullar and Williams, 2006; Ifediba et al., 2007; Mazza and Winterson, 1984; Muller, 2000), nor are the synergistic semicircular canals parallel to each other (Blanks et al., 1975, 1985; Brichta et al., 1988; Calabrese and Hullar, 2006; Curthoys et al., 1975, 1977; Dickman, 1996; Ghanem et al., 1998; Hullar and Williams, 2006; Mazza and Winterson, 1984). The angles between vertical semicircular canals and the head reference planes vary in different taxa and in different canals (Brichta et al., 1988; Curthoys et al., 1975; Hullar and Williams, 2006; Mazza and Winterson, 1984; Muller, 2000). The semicircular canals' shape is not strictly circular but range from ellipsoidal to triangular to various shapes (Brichta et al. 1988; Dickman, 1996; Georgi, 2008; Gray, 1907, 1908; Lindenlaub et al., 1995; Oman et al., 1987; Retzius, 1881, 1884; Sipla, 2007). Curvature radius (or lengths) of ipsilateral semicircular canals and cross-section areas of the semicircular ducts may differ drastically in the three ipsilateral canals (Blanks et al., 1985; Calabrese and Hullar, 2006; Dickman, 1996; Howland and Masci, 1973; Hullar and Williams, 2006; Lindenlaub et al., 1995; McVean, 1999; Muller, 1999). In addition, the semicircular canals are not planar, and torsion commonly appears along their slender parts (Blanks et al., 1985; Bradshaw et al., 2010; Curthoys et al., 1975; Dickman, 1996; Ifediba et al., 2007; Sato et al., 1993). Head rotation is therefore much more complicated to analyse on the basis of the semicircular canal system if all these different patterns are considered. They also complicate the study of the optimisation of the system for the detection of particular rotations.

2.2. Functional structure

The real structure of the semicircular canal system is much more complex than the idealized structure described above. For the purpose of functional consideration, its complicated structure can be simplified. The semicircular canal system basically works with two sets of three interconnected semicircular ducts (Muller, 1999; Rabbitt, 1999). They are filled with a fluid of water-like density, the endolymph. In most gnathostomes, each of these semicircular ducts originates in an ampulla on one side and ends in the common crus or the utricle on the other side. A composite gelatinous structure, the cupula, which is surrounded by connective tissue, fills the entire ampulla in cross-section (Muller, 1999; Oman et al., 1987; Rabbitt et al., 2004). Mechanosensory cells are located at the surface of the crista, in the ampulla, and some of their ciliae are embedded inside the cupula. During a rotation, the membranous labyrinth, which is firmly attached to the bony labyrinth (Rabbitt, 1999), moves with the head, whereas the endolymph lags behind because of its inertia. Before forces of friction compensate endolymph inertia, a certain amount of endolymph is displaced in the opposite direction of the rotation and exerts some pressure on the cupula, forcing it to bend and to activate hair cells via shear strain (Rabbitt et al., 2004). Mechanoelectrical transduction is done in a way that is proportional to cupular bending. In a given semicircular canal, the maximal cupular bending with respect to angular acceleration (i.e. maximal gain) occurs when the axis of rotation reaches an optimal position and decreases following a cosine rule to reach a near zero displacement when the semicircular canal is rotated around an axis that is perpendicular to its maximal response axis (this defines its null plane; Ifediba et al., 2007; Rabbitt, 1999; Rabbitt et al. 2004). For a given angular acceleration, the maximal achieved bending depends on the sensitivity of the semicircular canal. The sensitivity depends on the length of the semicircular canal, the area enclosed by the canal in its maximal response plane, and the cross-section areas of the semicircular duct and the ampulla (Jones and Spells, 1963; McVean, 1999; Muller, 1999; Oman et al., 1987; Squires, 2004; ten Kate et al., 1970) (Fig. 3). Therefore, the more sensitive the semicircular canal, the more the cupula is deflected for the same impulse. Since semicircular canal response, i.e. cupula deflection, depends on (1) the axis of rotation and angular acceleration of the head; (2) the sensitivity of the semicircular canal; and (3) the axis of maximal response of the canal, it is possible to describe any given semicircular canal response to rotations with a vector. The direction of this vector corresponds to the axis of maximal response of the semicircular canal, the sense of this vector corresponds to an excitatory rotation following the right-hand rule (a counter-clockwise rotation around the vector correspond to semicircular canal excitation; see Ezure and Graf

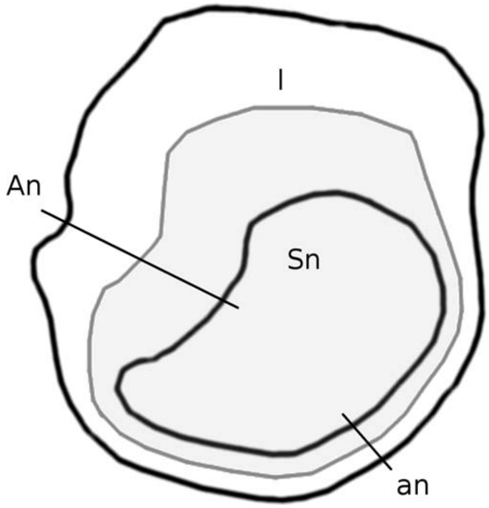

Fig. 3. Sketch of a semicircular duct which shows the main morphological parameters that determine its sensitivity. **An**: cross-section area of the ampulla; **an**: mean cross-section area of the slender part of the semicircular duct; **l**: semicircular canal length; **Sn**: area enclosed by the semicircular canal in its maximal response plane.

Fig. 3. Schéma d'un canal semi-circulaire membraneux présentant les principaux paramètres morphologiques influençant sa sensibilité. **An**: aire de la section de l'ampulla; **an**: aire moyenne des sections de la partie fine du canal semi-circulaire membraneux; **l**: longueur du canal semi-circulaire; **Sn**: aire entourée par le canal semi-circulaire dans son plan de réponse maximale.

(1984)), and the magnitude of this vector corresponds to the sensitivity of the semicircular canal. The response to any rotation of that particular semicircular canal can then be deduced by making the dot product between this vector and the angular acceleration vector. In applying that for the six semicircular canals, we obtain what we call the functional structure of the semicircular canal system. This vectorial structure, which directly derives from the morphology of both labyrinths, has the shape of an octahedron and contains all the parameters needed to analyse the sensitivity of the system to rotations (Fig. 4). It should be noted that organisms with different semicircular canal morphologies, but with the same SCFS, will present the same response intensity to the same path of rotation. However, the temporal response dynamic of these systems, i.e. the behaviour of the cupulae with regard to time during a rotation, may vary according to other morphological and physiological parameters (Rabbitt, 1999). We take into account that: (1) all the parameters of labyrinth morphological structure show some degree of variation; and (2) previous studies relating semicircular canals structure and behaviour of extinct taxa only relied on few parameters of this morphological structure, neglecting in particular the spatial orientation and the shape of the semicircular canals. We consider that the use of the SCFS in such studies may be an improvement in regard to the methods commonly used, because of its simplicity and its full description of labyrinth directional sensitivity based on its complete morphology.

3. Materials and methods

Our proposed method allows us to easily extract morphological and functional parameters from the semicircular canal system of extant and extinct taxa and to use them, along with behavioural information based on extant taxa, to infer locomotor behaviours of fossil vertebrates without using postcranial data (Spoor, 2003; Spoor et al., 2007). Our method can also be used to explain the relation between the spatial configuration and the functioning of the semicircular canal (and/or duct) system. This method uses the SCFS and requires the computation of the central streamlines of the labyrinth, a complex of curves which correspond to the mean ideal flow circulating through each part of the labyrinth. Information about the real pressure exerted on the cupula during a head rotation is biomechanically obtained by integrating the endolymph velocity field along central streamlines (Ifediba et al., 2007; Oman et al., 1987; Rabbit, 1999).

3.1. Data acquisition

3.1.1. Three-dimensional model of the labyrinth

For the analysis, we need to compute a three-dimensional triangle mesh model of the semicircular canal system. This kind of reconstruction is easily obtained by using datasets provided by virtual serial sectioning methods, such as MRI (Cox and Jeffery, 2008), CT (Della Santina et al., 2005, Spoor and Zonneveld, 1995) and μCT scans (Calabrese and Hullar, 2006; Hullar and Williams, 2006; Uzun et al., 2007), synchrotron light μCT (personal obs.), but also by using datasets provided by mechanical serial sectioning methods, commonly used in microscopy, after digitization of the slices (Hofman et al., 2009; Sato et al., 1993). The reconstruction is done by manually or automatically filling the inside of the labyrinth, slice by slice, and then stacking the resulting selections to compute a tri-

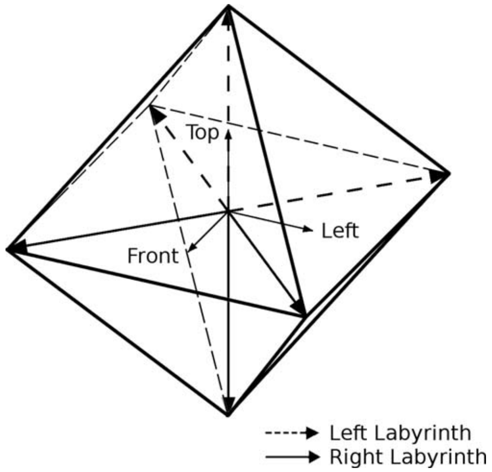

Fig. 4. Functional structure of the semicircular canals system (SCFS) of an idealized model. The tips of the vectors correspond to the vertices of an octahedron.

Fig. 4. Structure fonctionnelle du système des canaux semicirculaires (SCFS) d'un modèle idéal. Les sommets des vecteurs forment les sommets d'un octaèdre.

angle mesh of the labyrinth. This raw three-dimensional model is aliased and can be smoothed by using 3D imaging software. Virtual shrinkage can occur during smoothing, leading to a reduction of the cross-section area of the semicircular canal. Central streamline computation is much more constrained by the path of the semicircular canal than by its cross-section area. Since shrinkage does not really affect the path of the semicircular canals, streamline computation based on the smoothed models remain possible. Smoothed models allow a faster computation of the streamlines. Comparisons between the central streamlines computed from raw and smoothed models are underway. However, if the semicircular canals paths are similar in the two models, the streamlines will not be really different. In any case, the quality of the reconstruction strongly depends on the method used to obtain the slices and on the dataset voxel resolution. Most methods deliver a high enough voxel resolution to reconstruct the bony labyrinth but only microscopic serial sectioning (Hofman et al., 2009), synchrotron light μCT (personal obs.) and, under certain conditions, μCT scanners (Uzun et al., 2007), produce a sufficient voxel resolution to virtually reconstruct the membranous labyrinth and the semicircular ducts in great detail. As an empirical parameter, it seems that when fifty slices of a dataset composed of isometric voxels cut the labyrinth along its anteroposterior axis (e.g. which correspond to a voxel resolution of $\sim 200\,\mu\text{m}$ for a human labyrinth), the triangle mesh calculated with this dataset is precise enough to allow a correct central streamlines computation (personal obs.). Central streamlines computed from triangle meshes based on larger datasets, i.e. with a higher voxel resolution, do not seem to show a better shape fidelity. On the other hand, a smaller voxel resolution can lead to serious artefacts in the streamlines shape. Since the labyrinth size shows a strong negative allometry with the body mass (Jones and Spells, 1963; Muller, 1999; Spoor et al., 2007), the same acquisition methods can be applied to a wide range of taxa with some limitations for very small taxa.

3.1.2. Central streamlines computation

The analysis of the vestibular capacities is based on the central streamlines of the semicircular canal system. The central streamlines consist of unidimensional representations of the studied object. These streamlines retain the topology of the object and are centred inside it (Cornea et al., 2007). Semicircular canals are essentially tubular, which makes the central streamline computation easier. We do not recommend to use the centroids of the cross-sections of the semicircular canals derived from the raw slices in order to reconstruct the central streamlines (unlike the method used by Calabrese and Hullar, 2006; Hullar and Williams, 2006; Ifediba et al., 2007). Such centroids only reflect the passage of the central streamlines when the plane of the cross-section is perpendicular to the streamline. This is the case when the shape of the cross-section approximates an almost conical contour. Since the semicircular canal path changes all along its length, the cross-sections along the fixed axis of the raw slices cannot always be perpendicular to the streamlines. The error may be important when the cross-sections become tangent to the central streamlines, leading to artefacts in these areas (Calabrese and Hullar, 2006). We therefore recommend also not to use the raw grey levels of volumetric data for central streamlines computation (unlike the method used by Bradshaw et al., 2010). Raw grey levels can show a high degree of heterogeneity in fossils, especially when the areas of interest are filled with sediment of heterogeneous density (personal obs.). The presence of heterogeneous grey levels inside the areas of interest is not compatible with an automatized computation. We rather recommend the use of triangle meshes based on a slice-by-slice reconstruction of the labyrinths, especially in the case of fossil taxa. We have developed our own software in order to calculate the central streamlines of triangle mesh models (see technical appendix) but there is also a large number of methods for central streamline computation (see review in Cornea et al. (2007)). After computation, the semicircular canal system is represented by two sets of six streamlines, one per labyrinth. (Fig. 5). Each set is made of three streamlines which represent the anterior, posterior and lateral semicircular canals, respectively, a streamline which represents the common crus, and two streamlines which represent the anterior and posterior utricles (Ifediba et al., 2007; Rabbitt, 1999). The streamlines of the canals extend from the ampullae to the junction of

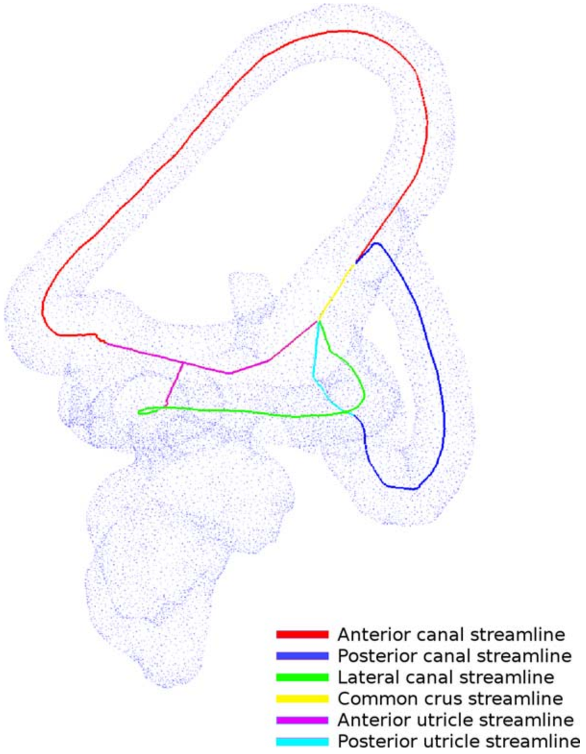

Fig. 5. Lateral view of the left labyrinth of *Aepyornis maximus* (MNHN 1910.12), an extinct giant bird, which shows the central streamlines of the three semicircular canals, of the common crus, and of the utricular parts.

Fig. 5. Vue latérale du labyrinthe gauche d'*Aepyornis maximus* (MNHN 1910.12), un oiseau géant éteint, montrant les lignes de flux centrales des trois canaux semi-circulaires, de la crus commune, et des parties utriculaires.

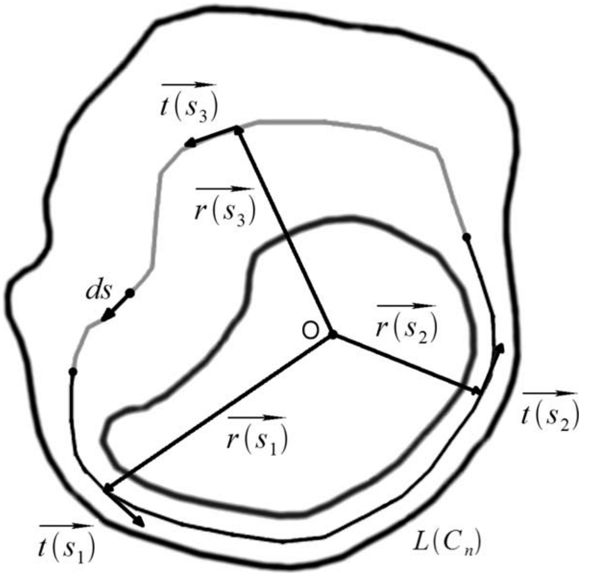

Fig. 6. Sketch of a semicircular canal duct which shows the main parameters which allow the calculation of the sensitivity vector $\overrightarrow{X_n}$.*O*: head-fixed origin of the radius vector $\overrightarrow{r(s)}$, $\overrightarrow{t(s)}$: unit tangent vector of the central streamline at the point *s*, $\overrightarrow{r(s)}$: vector linking the *O* point with the *s* point of the central streamline, *ds*: length of a segment of the central streamline, $L(C_n)$: length of the slender part of the semicircular canal. The $\overrightarrow{r(s)}$ and $\overrightarrow{t(s)}$ vectors are shown for three locations on the central streamline.

Fig. 6. Schéma d'un canal semi-circulaire membraneux présentant les principaux paramètres qui permettent le calcul du vecteur de sensibilité $\overrightarrow{X_n}$. *O*: point d'origine fixe du rayon vecteur $\overrightarrow{r(s)}$, $\overrightarrow{t(s)}$: vecteur unitaire tangent à la ligne de flux centrale au point *s*, $\overrightarrow{r(s)}$: vecteur reliant le point *O* et le point *s* de la ligne de flux centrale, *ds*: longueur d'un segment de la ligne centrale, $L(C_n)$: longueur de la partie fine du canal semi-circulaire. Les vecteurs $\overrightarrow{r(s)}$ et $\overrightarrow{t(s)}$ sont représentés pour trois points de la ligne de flux centrale.

the canals with the common crus or the utricle. The streamline of the common crus extends from the junction of the anterior and posterior canals to the junction of the common crus and the utricle. The streamlines of the anterior and posterior utricles extend from the junction with the common crus to the ampullae of the anterior and posterior canals, respectively. Some parts of the streamlines cannot be inferred from the morphology of the bony labyrinth. It is especially true for the utricle which is often represented by incomplete streamlines. In such cases, we choose to represent the missing parts of the streamlines by line segments in order to limit the number of hypotheses. Only the utricle has to be taken into consideration in the analysis, because the other otolithic end organs are not functionally connected with the semicircular canal system. The streamlines are connected at the level of natural trifurcation points (see Fig. 5). It should be noted that the distal end of the lateral canals streamlines can be connected with the utricle at the base of the common crus or near the posterior ampulla (Ghanem et al., 1998), depending on the considered taxa.

3.1.3. Parameter acquisition

3.1.3.1. Morphological parameters. Several parameters can be calculated with the twelve streamlines. A streamline is composed of ordered, three-dimensional points and its length can be calculated by adding up the distance between each pair of points. The length of an entire semicircular canal and of all of its parts can then be readily measured. We can also plot the cross-section area variation, relative to the position of the section, in order to characterize the different parts of the semicircular canal. The cross-section area can vary from zero to one order of magnitude along a semicircular duct pathway (Curthoys and Oman, 1986, 1987; Ghanem et al., 1998; Ifediba et al., 2007; Oman et al., 1987; ten Kate et al., 1970). However, this area seems relatively constant along the slender part of each semicircular duct (Curthoys and Oman, 1986, 1987; Bradshaw et al., 2010; ten Kate et al., 1970). For the bony labyrinth, we found a similar pattern of variation when we plotted the squared cross-section area, relative to the position of the section in the semicircular canal. We choose to use this property, in order to characterize the slender part of the three semicircular canal streamlines, and to locate two particular landmarks per canal. These landmarks are located on the points of the central streamlines where the cross-section area of the semicircular canals becomes significantly larger than the mean cross-section area along their slender part (this method is similar to that used by Bradshaw et al. (2010)). The first landmark is located at the transition from the slender semicircular ducts to the ampullae. The second landmark is located at the transition from the slender semicircular duct to the common crus for the vertical semicircular canals, and at the transition from the slender semicircular duct to the utricle for the lateral semicircular canals. A set of equidistant semilandmarks can then be automatically calculated between these two landmarks on each semicircular canal streamlines (semi-landmarks calculation is similar to the method used by Georgi (2008), but, in this case, it is done in a three-dimensional space). All these sets of landmarks can then be analysed by using three-dimensional geometric morphometry (see reviews in Mitteroecker and Gunz (2009), and Adams et al. (2004)).

3.1.3.2. Functional structure of the semicircular canals system. Since we have calculated the central streamlines of each semicircular canal, we can now calculate their sensitivity vectors $\overrightarrow{X_n}$. According to Oman et al. (1987), Rabbitt (1999) and Rabbitt and Damiano (1992), we found the following equation (see biomechanical appendix for details):

$$\overrightarrow{X_n} = \frac{a_n \overrightarrow{S_n}}{A_n L(C_n)} \tag{1}$$

In this equation, a_n represents the mean cross-section area of the slender part of the semicircular duct, A_n represents the total area of the cupula surface and $L(C_n)$ represents the length of the slender part of the semicircular duct. $\overrightarrow{S_n}$ is a vector whose direction corresponds to the maximal response axis of the semicircular duct and whose magnitude equals the area enclosed by the projection of the central streamline of the semicircular canal on its maximal response plane (Oman et al., 1987):

$$\overrightarrow{S_n} = \rho \int \left(\overrightarrow{r(s)} \times \overrightarrow{t(s)}\right) \mathrm{d}s \tag{2}$$

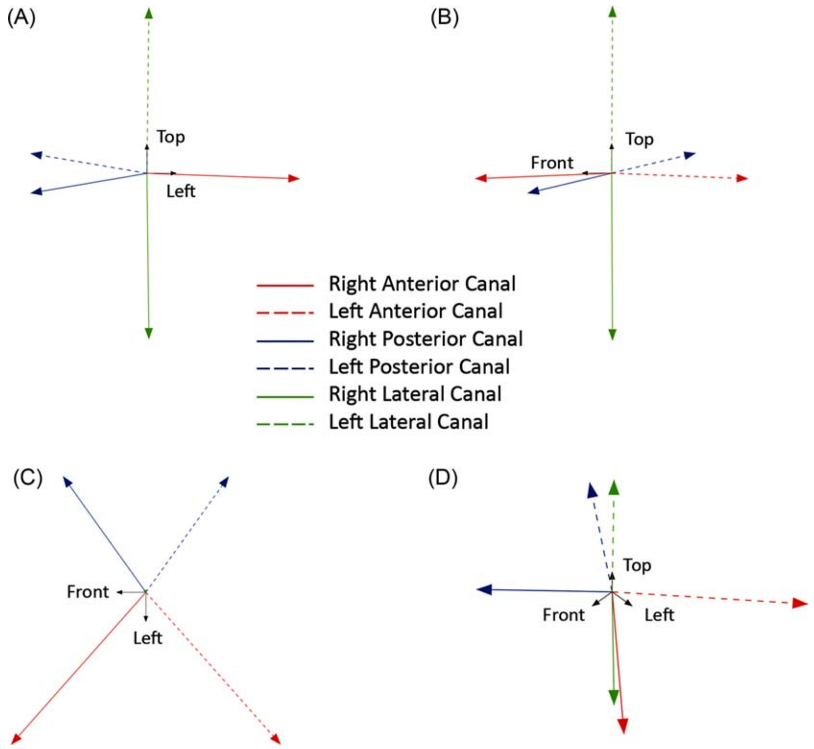

Fig. 7. Functional structure of the semicircular canals system of *Aepyornis maximus* in (A) frontal view, (B) left lateral view, (C) dorsal view and (D) isometric view.

Fig. 7. Structure fonctionnelle du système des canaux semi-circulaires d'*Aepyornis maximus* en vues (A) frontale, (B) latérale gauche, (C) dorsale et (D) isométrique.

$\overrightarrow{S_n}$ is calculated by integrating the cross product between (i) a radius vector $\overrightarrow{r(s)}$ directed from a head-fixed origin O to a point of the central streamline and (ii) the unit tangent vector $\overrightarrow{t(s)}$ of the central streamline at this point, along the entire length s of the central streamline (Fig. 6). ρ is the density of the endolymph. ρ is similar to water density and is constant for a given labyrinth. The ratio $\frac{a_n}{A_n}$ is the sensitivity factor. If we suppose this factor to be constant in the six semicircular ducts of the same individual, which seems to be an acceptable assumption (Curthoys et al., 1977), we can then calculate:

$$\overrightarrow{X'_n} = \frac{\overrightarrow{S_n}}{L(C_n)} \tag{3}$$

The magnitudes of these normalized sensitivity vectors $\overrightarrow{X'_n}$ will be proportional to the magnitudes of the corresponding $\overrightarrow{X_n}$ vectors. However, the shape of the SCFS resulting from the two sets of vectors will be the same. The raw and normalized SCFS are thus equally informative regarding the directional sensitivity. For a more precise estimation of the sensitivity of the vertical semicircular canals, one can take the common crus into account in the calculation of $\overrightarrow{X'_n}$. We know that the ratio between the cross-section radii of the semicircular ducts and the common crus is about $\sqrt{2}$ (Muller and Verhagen, 2002a). In that case, we have:

$$\overrightarrow{X'_n} = \frac{\overrightarrow{S_n}}{L(C_n) + \frac{L(CC_n)}{2}} \tag{4}$$

where $L(CC_n)$ represents the length of the common crus part of the semicircular canal. Due to their large cross-section areas and small lengths, the utricle and ampullae have hardly any effect on the calculation of the sensitivity and can thus be ignored. These simplified equations allow us to study the directional sensitivity using bony labyrinths, which are the only kind of information available in fossils. As in previous studies, the calculated sensitivity increases with the area enclosed by the semicircular canal (McVean, 1999; Oman et al., 1987). However, for equal area enclosed by the semicircular canal, the sensitivity decreases with an increase of the semicircular canal length (Cox and Jeffery, 2010; McVean, 1999; Oman et al., 1987; ten Kate et al., 1970) and with a relative increase of the length of its slender part (Oman et al., 1987). The application of Eqs. (3) and (4) to the six semicircular canals results in a set of six vectors (Fig. 7). This set is composed of one vector per semicircular canal. The respective directions of the vectors correspond to the axes of maximal response of the semicircular canals. The respective senses of the vectors correspond to an excitatory rotation following the right-hand rule. The respective magnitudes of the vectors are proportional to the sensitivity of the semicircular canals. We call this set of vectors the SCFS, which is an octahedron whose shape is not sensitive to scaling effects.

3.1.4. Reference axes

Since many kinds of datasets can be analysed by this method, a common coordinate system is needed for suitable comparison. Considering the various kinds of existing systems (Blanks et al., 1975, 1985; Brichta et al., 1988; Calabrese and Hullar, 2006; Curthoys et al., 1975; Hullar and Williams, 2006; Mazza and Winterson, 1984) and the fact that they are unsuited to datasets at large phylogenetic scales, because they are species-specific, we choose to use the semicircular canal system itself as a reference. In this system, the horizontal plane corresponds to the plane of the synergistic pair of lateral semicircular canals, which is generally considered as essentially perpendicular to the gravity (Brichta et al., 1988; de Beer, 1947; Girard, 1923; Hullar, 2006; Muller and Verhagen, 2002b). The sagittal plane corresponds to the bilateral symmetry plane of the skull and the coronal plane corresponds to the plane which is orthogonal to the other two. The calculation of the coordinates of the reference axes is explained in the technical appendix. This change of reference not only applies to the labyrinths, but also to all objects once reconstructed from the slices in the same reference system, such as the skull or cranial endocasts.

3.2. Data analyses

The SCFS can be used in different kinds of analyses in order to infer the behaviour of extinct taxa and to clarify the functioning of the semicircular canal system.

3.2.1. Scale analysis

Scale analyses deal with scaling factors, such as length and mass. They consist of bringing the studied objects to the same scale and analysing their differences. One typical scaling factor used in such analyses is the body mass. Actually, there is a law relating the body mass of an animal and the size of its labyrinth (Jones and Spells, 1963; Howland and Masci, 1973; Muller, 1999; Spoor et al., 2007). The mean cross-section area of the slender semicircular ducts and semicircular canal lengths are correlated with the body mass and show a strong negative allometry with it. Some authors used this correlation to show that, taking body mass into account, the more agile the animal, the longer its semicircular canals (Sipla, 2007; Spoor et al., 2007). They explained this relation by the fact that the length of the semicircular canals affects sensitivity, which should be higher in agile animals. However, sensitivity not only depends on semicircular canals length but also on the area enclosed by the semicircular canals, i.e. the shape of the semicircular canals, and on the cross-section area variation along the entire semicircular duct (Muller, 1999; Oman et al., 1987; Rabbitt et al., 2004; ten Kate et al., 1970; Squires, 2004). It would then be more appropriate to use the normalized sensitivities, whose calculation takes into account all these parameters, instead of the length or radius of curvature of the semicircular canals to show such a correlation. Moreover, the natural rotation axes involved during movements seem to be mainly restricted to the pitch, roll and yaw axes (Fig. 8), and so do not correspond to the semicircular canal axes of maximal response (Muller and Verhagen, 2002b). The response of a semicircular canal follows a simple cosine rule which leads to a maximal sensitivity when the semicircular canal is rotated around its axis of maximal response. It would then be interesting to consider the projections of the sensitivity vectors on the main axes of rotation, instead of only considering their magnitudes. Another point which can be improved, with regard to the current methods, concerns the scaling factor (ten Kate et al., 1970). In fact, the use of the body mass seems unsuited for the study of particular taxa, such as sauropod dinosaurs. These animals present huge estimated masses and generally possess a small skull, which can be viewed as functionally separated from the body by a long neck. This may imply that their decrease in head mobility was not as important as their mass increase. Moreover, body mass in fossils is difficult to estimate, all the more if they are only represented by fragmentary skeletons (Sipla, 2007). Since it is the head that must be stabilized in all the cases, we propose to use skull parameters instead of body mass in scale analyses.

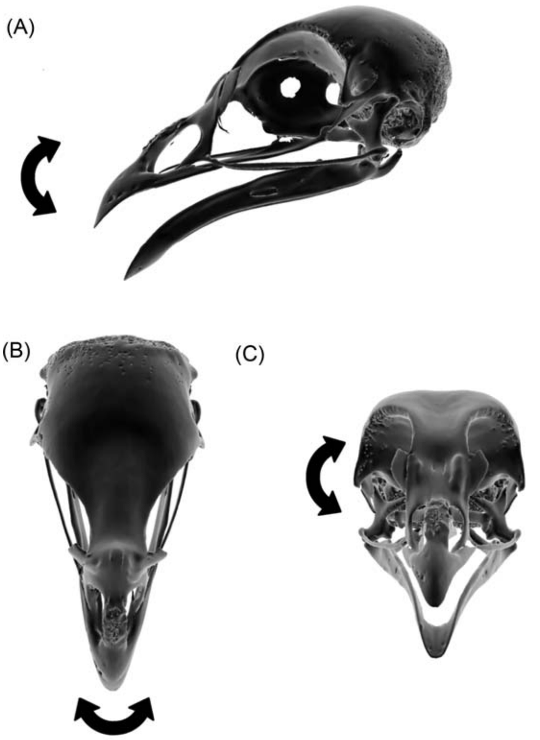

Fig. 8. The three natural rotations. (A) Pitch, (B) yaw and (C) roll.

Fig. 8. Les trois rotations naturelles. (A) Le tangage, (B) le lacet et (C) le roulis.

3.2.2. Shape analysis

Shape analyses are not sensitive to scaling effects and can be used to study interspecific variation of conformation without considering body mass or other scaling factors. Unlike the scale analyses which allow studying the varia-

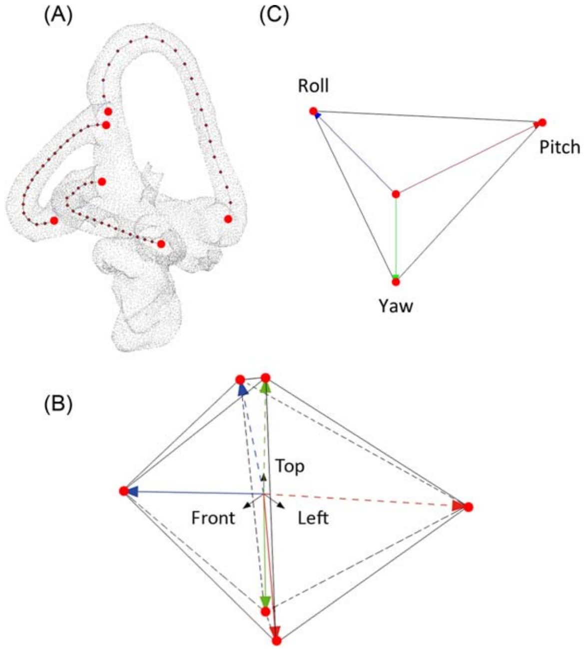

Fig. 9. Landmarks used in the shape analyses based on (A) the semicircular canals morphology, (B) the functionnal structure of the semicircular canals system and (C) the total response of the system for the three natural rotations.

Fig. 9. Points de repère utilisés pour les analyses de forme basées sur (A) la morphologie des canaux semi-circulaires, (B) la structure fonctionnelle du système des canaux semi-circulaires et (C) la réponse totale du système pour les trois rotations naturelles.

tion of parameters between taxa, shape analyses only rely on the grouping of similar conformation and knowledge of the behaviour of extant taxa in order to infer the behaviour of extinct taxa. The shape analysis is mainly based on the study of the octahedral conformation of the SCFS, since it is supposed to be a relevant structure for the function of the semicircular canal system and its behavioural inferences. The main hypothesis here is that taxa which share similar behaviour also share similar octahedral structures. This suggests that, contrary to the general shape of the semicircular canals, which is supposed to be mainly constrained by phylogeny, the SCFS is much more related to the pattern of head movements which occur in each taxon. In order to test this hypothesis, we can analyse the differences in the composition of groups resulting from shape analysis of the semicircular canal system morphology on the one hand, and functional structure on the other. The morphological analysis can be achieved through a geometrical morphometric analysis of the three-dimensional shape variation of the slender parts of the semicircular canals (Georgi, 2008). It can be achieved by making principal components analysis and/or discriminant analysis which use the main landmarks and the semi-landmarks calculated in the above sections (Fig. 9A). The functional analysis can be done by the same method, but by using vector coordinates instead of the morphological landmarks (Fig. 9B). The groups resulting from these analyses can support major phylogenetic constraints in the shape of the system if the composition of the groups accords with the phylogeny. The groups can also support major functional constraint in the shape of the system if the groups are made up of taxa with similar behaviour. It must be remembered that taxa sharing recent divergence generally share similar behaviour, and thus a group composed of such taxa cannot be used to estimate whether the constraints on the shape of the system are related to phylogeny rather than to function. It must also be remembered that a functional structure emerges from the corresponding morphological structure; therefore, the functional structure only provides us with functional information, whereas a morphological structure provides us with both functional and non functional (presumed neutral, inherited structures) information. Hence, only groups resulting from the shape analysis of the functional structure, and composed of taxa sharing an ancient divergence and similar behaviours, can allow us to test this particular functional structure predictability for these behaviours. Finally, morphological comparisons between taxa sharing a recent divergence and showing different behaviour provide the opportunity to analyse the structural plasticity of the canals that allows the functional structure to be optimized in regard to behaviours.

3.2.3. *Response analysis*

The two previous analyses can be used for interspecific comparisons, while the third type of analysis we propose focuses on the response heterogeneity in a single system. Some previous studies suggested that the semicircular canal system may need an increased sensitivity for particular rotations in order to counteract increased imbalance along these axes induced by particular behaviours (Brichta et al., 1988; Calabrese and Hullar, 2006; Hullar and Williams, 2006; Mazza and Winterson, 1984; Spoor et al., 1994, 2007; Yang and Hullar, 2007). We developed three different sets of subanalyses to better characterize these particular rotations. The first subanalysis, named total response analysis, (Fig. 10A) analyses the stimulation of the system as a whole, for all axis of rotation in space, not taking the inhibitory or excitatory nature of the stimulation into account (see technical appendix). Thus, we can directly observe the direction of rotation that mostly deflects the cupulae of the semicircular canals. A similar method is used by Hullar and other authors but differs from the present method by using twelve semicircular canal vectors instead of six (Calabrese and Hullar, 2006; Hullar and Williams, 2006; Yang and Hullar, 2007). This first subanalysis, the total response analysis, shows how the system responds to rotations and provides information, otherwise not detectable, on the head postures suited for optimal detection of some natural rotations (Fig. 11). Moreover, the three-dimensional structure of the total response can be simplified according to the sensitivity of the system along its three natural rotation axes (pitch, roll, yaw, see Fig. 8). This simplified sensitivity structure is a tetrahedron and can be studied with the shape analysis (Fig. 9C). The use of tetrahedral and octahedral functional data in the shape analysis allows us to test hypotheses on the semicircular canal system functioning. The same tetrahedral conformation can emerge from different octahedral conformations. While tetrahedral data represents the sensitivity of the whole system for the rotations around the three natural

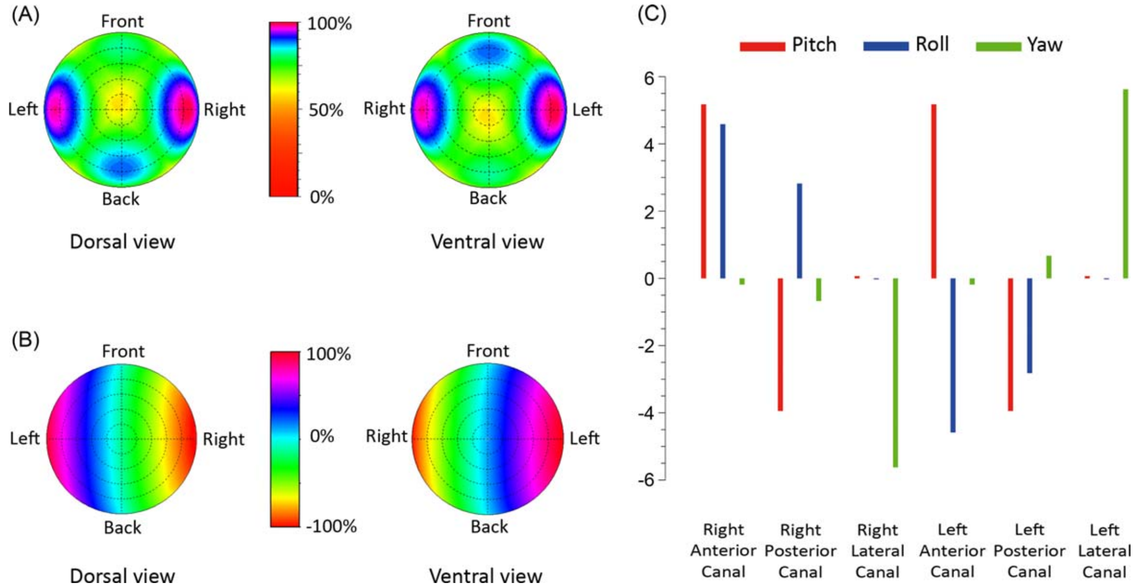

Fig. 10. A. Total response analysis of the SCFS of *Aepyornis maximus*. The color scale represents the response as a percentage of the maximal response obtained. B. Global response analysis of the SCFS of *A. maximus*. The color scale represents the response as a percentage of the maximal response obtained. A positive value corresponds to a global excitation and a negative value to a global inhibition. C. Activation pattern analysis of the SCFS of *A. maximus* for the three natural rotations. A positive value corresponds to excitation and a negative value to inhibition. The pitch rotation corresponds to a nose down rotation along a lateral axis. The roll rotation corresponds to a right directed rotation along an anteroposterior axis. The yaw rotation corresponds to a left directed rotation along a dorsoventral axis.

Fig. 10. A. Analyse de réponse totale du SCFS d'*Aepyornis maximus*. L'échelle de couleur représente la réponse en pourcentage de la réponse maximale obtenue. B. Analyse de réponse globale du SCFS d'*A. maximus.* L'échelle de couleur représente la réponse en pourcentage de la réponse maximale obtenue. Une valeur positive correspond à une excitation et une valeur négative à une inhibition. C. Analyse du patron d'activation du SCFS d'*A. maximus* aux trois rotations naturelles. Une valeur positive correspond à une excitation et une valeur négative à une inhibition. La rotation en tangage correspond à une rotation vers le bas, le long d'un axe latéral. La rotation en roulis correspond à une rotation vers la droite, le long d'un axe antéropostérieur. La rotation en lacet correspond à une rotation vers la gauche, le long d'un axe dorsoventral.

axes, octahedral data informs us how these rotations are individually sensed by each semicircular canal. Different encoding strategies for the same total sensitivity conformations can then be studied in comparing these two kinds of datasets.

The second subanalysis is named global response analysis (Fig. 10B). It works on the same principle as the total response analysis but also considers the excitation and inhibition of the semicircular canals. For a head rotation at reasonable speed, the spike frequencies in afferent responses as well as the cupula displacement are considered to have a linear relationship (Hullar and Williams, 2006). Not so for high velocity movements, where this relationship is falsified in accordance to what is termed the second Ewald's law (semicircular canal excitation is a relatively better stimulus than semicircular canal inhibition). Inhibitory stimulation can only decrease the spike frequency in the afferent response to zero, whereas the increased firing rate due to excitatory stimulation never meets such a boundary (van Egmond et al., 1949). Considering Edwald's law, it can be hypothesized that a break in the balance between excitation and inhibition under a particular rotation may characterize some adaptation in order to counteract the Ewald's law for head movements of increased velocity along this axis. The global response analysis is used to search for configurations of the SCFS that break the balance and give a global excitatory or inhibitory response under certain rotations.

The third subanalysis explains the pattern of semicircular canal activation caused by the main rotations (Fig. 10C). It shows the response of the six semicircular canals for a left directed yaw, a pitch directed nose-down, and a right directed roll. This allows us to directly observe the relative importance of each natural axis of rotation, the pattern of activation and inhibition of the six semicircular canals for each of these rotations, and the relative magnitude of the responses of the six semicircular canals, in a single graphic.

4. Discussion

4.1. Bony vs. membranous labyrinth

The previously described methods can be used on both the bony labyrinth and the membranous labyrinth. Even though the analyses of the two structures return fairly similar results, the analysis of the membranous labyrinth is in all more conclusive because it is the functional part of the system. The latter preferred method is not always applicable especially in extinct taxa, in which only the bony labyrinth is available for study. The membranous semicircular ducts and bony semicircular canals have different cross-section areas that can vary by over one order of magnitude (Curthoys and Oman, 1987; Graf and Vidal, 1996; Ifediba et al., 2007). To attain reliable results and to correct for the missing semicircular ducts in fossils, it is important to know to what degree the general shape of the

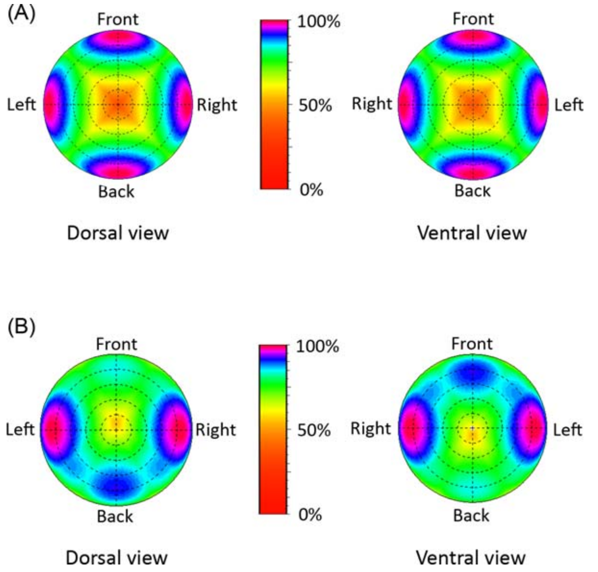

Fig. 11. Total response analysis of the semicircular canals system of *Homo sapiens* based on (A) data of the curvature radii of the semicircular canals (from Spoor et al., 1994) when assuming an orthogonality of the semicircular canals and (B) based on the SCFS of a three-dimensional model of the labyrinth of *Homo sapiens*. The color scale represents the response as a percentage of the maximal response obtained. The analysis of the SCFS shows a more important sensitivity for the detection of pitch rotations than for the detection of roll rotations, whereas the analysis based on the curvature radii alone does not show any differences between these two kinds of rotations. It can also be noted that the analysis of the SCFS informs us that an upside rotation of the head of around 20° from the lateral semicircular canals plane allows an optimal detection of the roll rotations. The turned-up position of the lateral semicircular canals in men was already known but lacked of explanation.

Fig. 11. Analyse de réponse totale du système des canaux semi-circulaires d'*Homo sapiens*, effectuée à partir (A) de données sur les rayons de courbure des canaux semi-circulaires (tirées de Spoor et al., 1994) en considérant une orthogonalité des canaux semi-circulaires et (B) à partir du SCFS d'un modèle tridimensionnel du labyrinthe d'*Homo sapiens*. L'échelle de couleur représente la réponse en pourcentage de la réponse maximale obtenue. L'analyse du SCFS nous montre une sensibilité plus importante pour le tangage que pour le roulis, alors que l'analyse des rayons de courbure seuls ne montre pas de différence entre ces deux types de rotations. Notons également que l'analyse du SCFS nous informe que relever la tête d'environ 20° par rapport au plan des canaux semi-circulaires latéraux permet une détection optimale du roulis. La position relevée des canaux semi-circulaires latéraux chez l'homme est connue, mais n'avait jamais été expliquée.

semicircular canals follows that of the semicircular ducts. It is generally assumed that the path of the semicircular ducts and semicircular canals do not deviate very much (Blanks et al., 1975; Bradshaw et al., 2010; Hullar, 2006; Ifediba et al., 2007; Spoor, 2003). Studies have shown that the semicircular ducts seem to be located along the outermost wall of the semicircular canals (Blanks et al., 1975; Curthoys and Oman, 1987; Curthoys et al., 1977; Ifediba et al., 2007). This means the area enclosed by the central streamlines of the semicircular ducts may be larger than that enclosed by the central streamlines of the semicircular canals. Also, the cross-section area variation along the whole length of semicircular ducts can only be calculated with the membranous labyrinth. The exact knowledge of this pattern of variation may lead to a more precise calculation of the vectors, but the shape of the resulting SCFS should not really deviate from the one calculated with the bony labyrinth, because of the assumed constancy of the sensitivity factor for the three semicircular canals of the same labyrinth. Under this assumption, the critical parameters consist of the relative lengths of each part along a semicircular canal pathway, lengths that can be estimated on the basis of the bony labyrinth alone. Nevertheless, it must be noted that this ratio is not supposed to be constant when considering different taxa. Thus, even if the shape of the SCFS is unaffected, the size of these structures may vary independently in different taxa. Thus, the study of the membranous labyrinth may give us an insight on the absolute sensitivities of the canals, which can be important for all the scale analyses. Another problem poses the location of the utricle in a fossil specimen. The utricle is clearly identifiable in a membranous labyrinth but inferring its former location on the bony vestibule is not always possible. Without knowing its proper location, the central streamlines cannot be completely calculated. If only the bony labyrinth is available, the missing parts of the utricular streamlines are therefore arbitrarily filled with line segments. The larger cross-section areas of the bony labyrinth, the exact path of the membranous duct in the bony canal, and the location of the utricle are unknown parameters that, when considering a fossil specimen, can distort the end result from their true values that could be obtained from a membranous labyrinth in an extant specimen. Studies are now underway to measure the range of variation obtained from the two, membranous and bony labyrinth.

4.2. Specific problems encountered with the use of fossilised specimens

To perform a valid analysis of the SCFS, the vectorial structure must answer to some criteria. The magnitudes of the vectors of homologous semicircular canals must be the same and their directions must be symmetrical relative to the sagittal plane. Different sources of errors can lead to violate these criteria in fossil specimens. They are: (1) the deformation of the structure of the semicircular canal system; (2) the loss of parts of canals or of entire labyrinths due to a bad preservation of the otic capsule; and (3) the difficulty to accurately reconstruct the labyrinth based on datasets which show a poor density contrast.

In most fossil amniotes the labyrinths are often protected against deformation by the solidly built otic capsule. Dislocation and relative displacement of the bones of the braincase, however, often occur, leading to an asymmetric placement of the two labyrinths to each other. When the two labyrinths are intact, how well they overlay in lateral view will give us an indication of the quality of preservation and of the quality of the reconstruction. This is an easy way to readily see if the semicircular canal system of a fossil specimen has been deformed and if the reconstruction has been correctly done. Moreover, the analysis of the magnitude of the vectors resulting from the reconstruction of fossil semicircular canal systems and the analysis of the angles between these vectors can help us to estimate quantitatively the accuracy of the SCFS. The angular relationship between the three ipsilateral semicircular canals of a labyrinth inform us about the deformation of the labyrinth. If the angular relationship between ipsilateral semicircular canals of the right labyrinth is the same as the angular relationship between ipsilateral semicircular canals of the left labyrinth, this means that the labyrinths are not deformed. However, even if the labyrinths are not deformed, the structure of the semicircular canal system can be deformed if the bones of the braincase experience some displacement and deformation. The angular relationship between the functional pairs of vertical semicircular canals can help us to quantify the deformation of the semicircular canal system. If the angle between the right anterior semicircular canal and the left posterior semicircular canal is the same as the angle between the left anterior semicircular canal and the right posterior semicircular canal, this generally means that there is no deformation of the semicircular canal system. It should be noted that a simple translation of one labyrinth in space does not affect the SCFS, but a rotation of one labyrinth does. Finally, the comparison of the angular relationships between the ipsilateral semicircular canals of the two labyrinths and the comparison of the magnitudes of the sensitivity vectors between the homologous semicircular canals informs us about the quality of the virtual reconstruction. Similar angular relationships of ipsilateral canals and similar magnitudes for the vectors of homologous semicircular canals indicate an accurate reconstruction of the semicircular canal system.

If a complete and non-deformed semicircular canal system cannot be reconstructed, it is, however, possible to estimate the SCFS. The SCFS can be estimated if there is information about: (1) the sensitivity vector of at least one anterior semicircular canal; (2) the sensitivity vector of at least one posterior semicircular canal; (3) the sensitivity vector of at least one lateral semicircular canal; and (4) the position of the bilateral symmetry plane. When the semicircular canal system is deformed, we need a different estimation for the angular relationship between each labyrinth, or part of labyrinth, and the bilateral symmetry plane. If the above criteria are satisfied, it is then possible to reconstruct the SCFS by mirroring each vector of a pair of homologous semicircular canals relative to the respective bilateral symmetry plane in order to reconstruct the missing vector of the pair. This method can then be applied in the case of missing semicircular canals, deformation of labyrinths or semicircular canal systems and heterogeneity in the quality of reconstruction between the right and the left labyrinths. This method, however, implies an increase in the number of hypotheses and is then less precise than the computation of the SCFS based on a complete and non-deformed semicircular canal system.

4.3. Implications of some morphofunctional parameters on inferred behaviours

Semicircular canal functioning can be described by six morphofunctional parameters which consist of: (1) the axes of maximal response; (2) the sensitivity along these axes; (3) the maximal gain (ratio between cupula bending and impulse rotation); (4) the natural frequencies of head rotation where these gains occur; and (5) the upper and (6) lower corner frequencies which constrain the range of head rotation effectively detected by the system (Howland and Masci, 1973; Jones and Spells, 1963; Mayne, 1950; Muller, 1999; Muller and Verhagen, 2002a; Oman et al., 1987; Rabbitt, 1999; Rabbitt et al., 2004; Squires, 2004; ten Kate et al., 1970; van Egmond et al., 1949). With all six parameters the semicircular canal system's response dynamic and intensity can be described fully for any given rotational stimulus. Information drawn from the bony labyrinth alone makes it possible to calculate the axes of maximal response, the natural frequencies, and to estimate the sensitivities of the canals and lower corner frequencies. Information of upper corner frequencies and maximal gains, however, can only be obtained from the membranous labyrinth.

It is noteworthy to mention here that, for a same body mass, more agile taxa possess longer semicircular canals (Sipla, 2007; Spoor, 2003; Spoor et al., 2007). In general, however, increased body mass and therefore slower head rotations, are associated with an increase in semicircular canal length (Howland and Masci, 1973; Jones and Spells, 1963; Muller, 1999; Spoor et al., 2007). These two trends seem to contradict each other. Why are longer semicircular canals found in slow and agile taxa (Muller, 1999; Yang and Hullar, 2007)? Longer semicircular canals involve a decrease in natural and lower frequency, but also an increase in sensitivity due to an increased area enclosed by the semicircular canals (Howland and Masci, 1973; Jones and Spells, 1963; Muller, 1999). Biomechanical sensitivity can be measured as the endolymph volume displacement for a unit rotational velocity (Muller, 1999, 2000; Muller and Verhagen, 2002a) and seems to be directly linked with afferent nervous sensitivity (Curthoys et al., 1977; Yang and Hullar, 2007 but see Hullar, 2006). An increased sensitivity allows for a more precise resolution of differences in angular head movement, which is a considerable advantage for agile taxa (Clarke, 2005; Spoor, 2003). Several hypotheses can explain the above contradiction. If the total area of the cupula surface increases with the body mass faster than does the mean cross-section area of the slender part of the semicircular duct, the sensitivity factor will decrease with the body mass. Under this assumption, more massive, slower moving taxa can detect slower movements due to their increased semicircular canal length, which in return leads to a decrease of the lower corner frequency without increasing the sensitivity. Another way to make sense of this contradiction is to assume that sensitivity is not the optimized parameter in agile taxa. Therefore if baseline sensitivity is sufficient, an increase in semicircular canal length may go hand in hand with a decrease in semicircular duct cross-section area. In return, an increase of the upper corner frequency is expected, allowing these taxa to detect faster movements. Since most of the studies which deal with the link between the semicircular canals and behaviours are based on bony labyrinth morphology (Spoor, 2003), little can be proven of the latter hypotheses. It would therefore be interesting to obtain information of the membranous labyrinth of agile taxa to see if they present a decrease in semicircular duct cross-section area along with an increase in semicircular canal length. At the same time, it would be interesting to observe if the sensitivity factor decreases with the body mass. Linking behaviour and morphological parameters is never straightforward and each case needs to be considered independently.

4.4. Effect of the bilateral symmetry on the semicircular canals system and its functioning

Bilateral symmetry applies some constraints on the system's response. Any change in one side of the head is mirrored in the other side. Thus, for all rotations around axes included in the sagittal plane (i.e. roll, yaw and all intermediate rotations), the response of each canal of one labyrinth will be the exact opposite of the homologous canal of the other labyrinth. This can be seen at the level of the bilateral symmetry plane where each projection of a vector of a pair of homologous semicircular canals possesses the same magnitude and direction than the projection of the other one, but shows an opposite sense (see Fig. 7B). Thus, for any rotation around an axis included in this plane, the global response of each pair of homologous semicircular canals will be zero, and this will result in a zero global response of the whole system for such rotations. The only natural axis which can show a non-zero global response is the pitch axis because the vectors of sensitivity of the semicircular canals are not constrained by symmetry along this axis.

Bilateral symmetry also constrains the configuration of the vectors of sensitivity of the semicircular canals in space. In the reference system of the labyrinth, each component of the vectors of the SCFS shows the signs presented in Table 1. We can see in this table that the sense of the vectors of the vertical semicircular canals can only vary along the dorsoventral axis, whereas the sense of the vectors of the lateral semicircular canals can only vary along the lateral axis.

There are only two possibilities to modify the sensitivity of the semicircular canal system: one can either change the orientation of the vectors and/or change their magnitude. A problem posed is the increasing of the sensitivity along a natural axis without modifying its value along the other two. A solution to this problem is to modify both the orientation and magnitude of the vectors of a pair of homologous semicircular canals. If only one parameter is modified, e.g., orientation or magnitude, already the sensitivity along two main axes of rotation will be slightly modified. The same sensitivity along an axis of rotation can be achieved by different orientation and magnitude of the semicircular canals vectors. However, few deviations of orientation seem to modify the sensitivity much more than the increase in magnitude (Yang and Hullar, 2007).

Table 1
Possible signs of the components of the vectors of the SCFS in the labyrinth reference system.
Tableau 1
Signes possibles des composantes des vecteurs du SCFS dans le système de référence du labyrinthe.

	Front	Left	Top
Right anterior vector	+	+	+/−
Left anterior vector	−	+	−/+
Right posterior vector	+	−	+/−
Left posterior vector	−	−	−/+
Right lateral vector	0	+/−	−
Left lateral vector	0	+/−	+

In summary, we have proposed a method based on central streamlines extraction of three-dimensional triangulated surface meshes of the labyrinth in order to extract the semicircular canal system functional structure and to study it through three main analyses. The use of central streamlines is not a novelty, but was previously applied to analyse the dynamic response of the semicircular canal system to particular rotations (Ifediba et al., 2007; Rabbitt, 1999), or to study intraspecific morphological variation of the labyrinth (Bradshaw et al., 2010). This is, however, the first time that the SCFS is used to compare and infer vestibular capacities of extant and extinct taxa.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2010.07.012.

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