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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.

Mots clés :
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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.

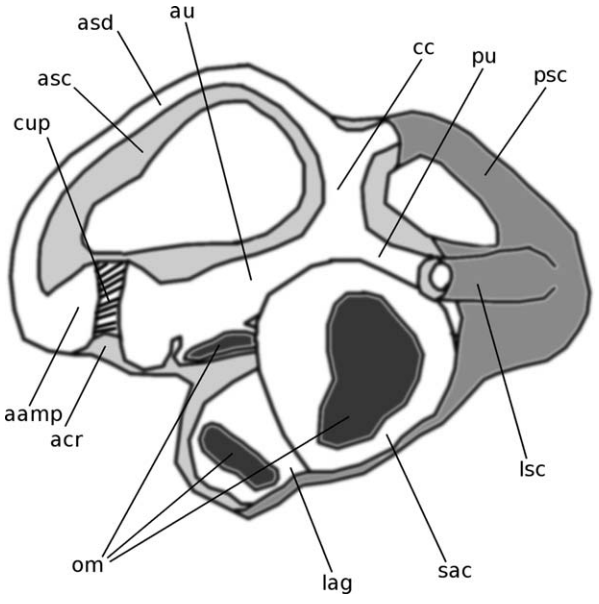

Fig. 1. Lateral view of a schematic labyrinth. The bony labyrinth is in grey. **aamp**: anterior ampulla; **acr**: anterior crista; **asc**: anterior semicircular canal; **asd**: anterior semicircular duct; **au**: anterior utricle; **cc**: common crus; **cup**: cupula; **lag**: lagena; **lsc**: lateral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