Original Investigation

Morphological disparity, conservatism, and integration in the canine lower cervical spine: Insights into mammalian neck function and regionalization

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ABSTRACT

The neck skeleton is constituted as a highly mobile, multi-element and multi-joint kinematic chain. This construction leads to a kinematic redundancy on several levels. The problem of coordinating a large number of joints and muscles is solved by reducing the degrees of freedom to only few preferred motor axes. This is achieved by the regionalization of the cervical spine into three functional compartments. However, the neck skeleton traditionally is only partitioned into two units basing on the derived morphology of the two uppermost vertebrae (atlas and axis). To broaden the understanding of the functional morphology and regionalization of the mammalian neck skeleton, the morphology of the lower cervical vertebrae of a variety of different sized breeds of domestic dogs is compared using 3D geometric morphometrics. The shape analysis reveals significant differences among all lower cervical vertebrae. However, the specific shape of each vertebral level is independent of the actual breed and breed size. The individual vertebrae as well as the whole vertebral proportions are highly integrated. Nevertheless, the mid-cervical vertebrae (C3–C5) are more uniform in their shape whereas the lower ones (C6, C7) have a unique morphology. The tripartition of the cervical spine into functional compartments is confirmed for the neck of dogs. The conserved pattern of level specific vertebral shapes suggests that the morphological and functional tripartition of the cervical spine could be a general trait of all mammalians.

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Introduction

The cervical spine represents a highly mobile, multi-element and multi-joint, open kinematic chain, cantilevering from the trunk (Kummer, 1959; Preuschoft, 1976; Slijper, 1942). Theoretically, it can adopt a huge variety of configurations due to its complex structure and kinematic redundancy with multiple degrees of freedom (DOFs; Aerts et al., 2001; Bizzi et al., 1976; Bout, 1997; Evans, 1939; Keshner et al., 1992, 1997; Keshner, 1994; Pellionisz et al., 1991; Peterson et al., 1989; Van Der Berg, 2000; van der Leeuw et al., 2001a, 2001b; Vidal et al., 1986). However, some authors suggest that anatomical, biomechanical or functional constraints reduce the DOFs of the head–neck system that have to be controlled by the nervous system (Bout, 1997; De Waele et al., 1989; Graf et al., 1995a, 1995b, 1997; Heidweiller et al., 1992; Keshner et al., 1997; van der Leeuw et al., 2001a; Vidal et al., 1988; Zweers et al., 1994), as it was descibed by Bernstein (1947) for complex motor systems. In

mammals, the cervical spine is highly constraint to only seven cervical vertebrae by HOX gene controlled axial patterning during development (Buchholtz et al., 2014; Galis, 1999; Galis et al., 2006; Hautier et al., 2010; Narita and Kuratani, 2005). The partition of the neck skeleton here bases traditionally on the anatomical differences of the first two vertebrae and so divided into upper and lower cervical spine. Whereas the upper part is characterized by the unique morphology of the atlas and axis, the lower part consists of the five other vertebrae, which do not have a derived morphology. In contrast, Graf, Vidal, and colleagues (De Waele et al., 1989; Graf et al., 1995a, 1995b, 1997; Vidal et al., 1986, 1988) proposed an alternative partition of the cervical column into three functional compartments. They recognized a stereotypic resting posture in all mammals with the neck skeleton in a vertical orientation. Changes in gaze in the sagittal plane are restricted to the head–neck junction (Occiput–C1–C2) and the cervico-thoracic junction (C6–C7–Th1), whereas the mid-cervical region does not contribute to movement of the neck.

The uppermost functional compartment is clearly congruent with the anatomically defined upper cervical spine. The medial and lower functional compartments have no anatomically
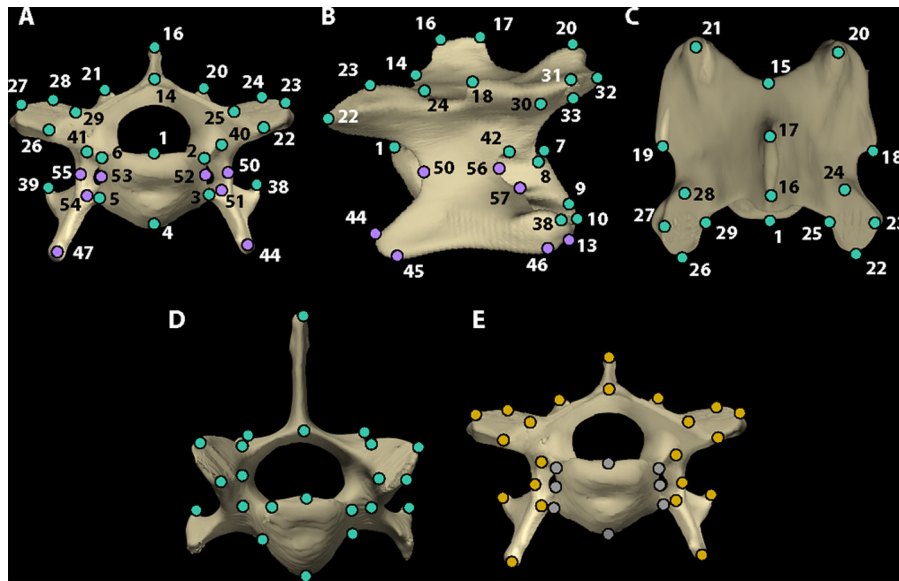
Fig. 1. Landmark configurations. Lower cervical vertebra in (A) cranial, (B) lateral, and (C) dorsal view with the 61 digitized landmarks. The first data set contained all 61 landmarks (green and violet) for C3 to C6. The second data set combined the landmarks of C7 (D) and the first 43 ones of C3 to C6 (green). (E) Modularity hypothesis for the Partial Least Square Analysis of the vertebral body (gray) *vs.* the vertebral arch (orange). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

defined equivalents. The lower cervical vertebrae are traditionally described as very similar and not deviating from the general morphology of a vertebra. This is especially common in veterinary literature but also in human medicine (see the review of Bogduk and Mercer, 2000). Nevertheless, some minor differences among the lower vertebrae were noticed that had already been familiar to Goethe (1817) and Owen (1866). These shape differences included a decreasing body length, an increasing height of the spinous processus, and the extension of the Tuberculum ventrale of C6 (forming the Lamina ventralis). Additionally, unlike the other vertebrae, C7 lacks a costal rudiment and therefore does not possess the Tubercula ventrale or transverse foramina (Fig. 1D). Breit and Künzel (2001, 2002, 2004) were the first that investigated these structures in the context of canine veterinary medicine. They found differences among the vertebral levels and breeds with respect to the shape of the vertebral foramina and the configuration of the articular facets of lower vertical vertebrae (Breit and Künzel, 2001, 2002), relating them to specific rotational abilities of each of the lower cervical vertebra (Breit and Künzel, 2002, 2004).

Here, we evaluate and broaden the understanding of the functional morphology of the mammalian cervical spine in the context of the regionalization proposed by Graf et al. (1995a). We focus on the question if the lower cervical vertebrae are as uniform as frequently described in literature, or if the functional compartmentalization is reflected in their morphological disparity (in the traditional sense of morphological variation/discrimination) as well. We used a variety of different breeds of domestic dogs (*Canis lupus familiaris* or *Canis familiaris*) to study diverse phenotypes and breed sizes within one species, as already recommended by Darwin (1868). The morphology of the lower cervical vertebrae is compared using a 3D geometric morphometric approach. In mammals, it has been has rarely been applied to vertebrae (Chatzigianni and Halazonetis, 2009; Chen et al., 2005; Manfreda et al., 2006) and only once to the serial homologous vertebrae of sirenian cervical spines (Buchholtz et al., 2014). In this study, the canine lower cervical vertebrae are compared to one another in order to see whether their shape patterns relate to their position within the spine or to the breed's size.

Table 1
Breed sample and number of vertebrae.

Breed	Number of individuals	Number of cervical vertebrae
Beagle	3	15
Beauceron	1	5
Berger Blanc Suisse	1	5
Bernese Mountain Dog	1	5
Cane Corso Italiano	1	5
Chihuahua	3	14
Cocker Spaniel	2	10
Collie	1	5
Dachshund	5	23
Doberman Pinscher	2	10
French Bulldog	2	10
German Spitz Klein	2	9
Great Dane	1	5
Labrador	3	15
Magyar Vizsla	1	5
Mastiff	1	4
Miniature Poodle	1	5
Mixed-breed	1	5
Pekingese	1	5
Rottweiler	1	5
Shar Pei	1	5
Shetland Sheepdog	1	5
Sibirian Husky	1	5
Silky Terrier1	1	5
Yorkshire Terrier	2	10
Total	40	195

Material and methods

Sampling design

The overall sample consisted of CT images of 40 adult canine cervical spines (Table 1). The CT scans were obtained from anesthetized patients of the Vetsuisse faculty, University of Bern, Switzerland (Philips Brilliance 16-slice, slice thickness: 1 mm, Matrix 1024, 120 kV/180 mAs, Increment 0.5, Pitch: 0.813, Collimation; 16 × 0.75, Center 800 Window 2000 Filter D). Breed composition was based on the availability of CT data. However, we tried to capture the breed diversity in size (Chihuahua – Great Dane) and skull shape (brachycephal – dolichocephal). As the specimens