



Functional analyses of the primate upper cervical vertebral column



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ABSTRACT

Recent work has highlighted functional correlations between direct measures of head and neck posture and primate cervical bony morphology. Primates with more horizontal necks exhibit middle and lower cervical vertebral features that indicate increased mechanical advantage for deep nuchal musculature and mechanisms for column curvature formation and maintenance. How features of the C1 and C2 reflect quantified measures of posture have yet to be examined. This study incorporates bony morphology from the upper cervical levels from 20 extant primate species in order to investigate further how posture correlates with cervical vertebrae morphology. Results from phylogenetic generalized least-squares analyses indicate that few vertebral features exhibit a significant relationship with posture when accounting for differences in size. When size-adjusted traits were correlated with posture, vertebral variation had a stronger relationship with neck posture than head posture variables. Two C1 traits—relative posterior arch length and superior facet curvature—were correlated with neck posture variables. Relative posterior arch length exhibits a positive relationship with neck posture, while superior articular facet curvature demonstrates a negative relationship, such that as the neck becomes more horizontal, the greater the facet curvature. Four C2 features were also correlated with neck posture: relative pedicle and lamina lengths, relative superior facet orientation, and dens orientation. Relative pedicle and lamina lengths become craniocaudally longer as the neck becomes more horizontal. Relative C2 superior facet orientation and dens orientation exhibit negative correlations with posture, such that as the neck becomes more horizontal, the superior facet becomes more caudally inclined and the dens more dorsally inclined. These results produce a similar functional signal observed in the middle and lower cervical spine. Modeling the cervical vertebrae of more pronograde taxa within a sigmoidal spinal column model is further discussed and may prove useful in refining and testing future hypotheses of primate cervical mechanics.

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1. Introduction

Previous research has identified skeletal correlates of positional behavior in both the thoracic and lumbar regions of the primate vertebral column (e.g., Schultz, 1930; Slijper, 1946; Pal and Routal, 1986; Ward, 1991, 1993; Shapiro, 1995, 2007; Johnson and Shapiro, 1998; Shapiro and Simons, 2002; Meyer, 2005; Shapiro et al., 2005; Russo, 2010), but much less is known about primate cervical vertebrae functional morphology (Toerien, 1961; Mercer, 1999; Manfreda et al., 2006; Nalley, 2013). This is surprising given that the neck—acting as the bridge between the head and trunk—performs several biomechanical roles related to posture

and locomotion, including directing and stabilizing head movement and providing a bony platform for the soft tissues of the pectoral girdle and upper limb (Schultz, 1942; Swindler and Wood, 1973; Kapandji, 1974; Dean, 1982; Mercer and Bogduk, 2001).

Although a rich literature in the biomechanical and medical fields provides experimental evidence linking function with form in the human cervical spine (e.g., Compere et al., 1959; Penning, 1968; Holness et al., 1984; White and Panjabi, 1990; Milne, 1991; Yoshida et al., 1992; Panjabi et al., 1993; Whyne et al., 1998; Bogduk and Mercer, 2000; Mercer and Bogduk, 2001; Yoganandan et al., 2001; Panzer and Cronin, 2009; Womack et al., 2011; DeWit and Cronin, 2012), nonhuman primate comparisons have been limited in terms of the species examined and the development of a rigorous functional framework for interpreting variation (Vidal et al., 1986; Dickman et al., 1994; Tominaga et al., 1995; Graf et al., 1995a,b; Elias et al., 2005; Meyer, 2005). Furthermore, most comparative

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functional investigations into primate cervical vertebrae have used simple behavioral categories (Ankel, 1972; Mercer, 1999; Meyer, 2005; Manfreda et al., 2006; Nalley, 2013). Although the use of these categories is often necessary, they omit potentially important variation in positional behavior, locomotor repertoires, and their biomechanical requirements (White et al., 2015). For example, the locomotor category “knuckle-walking” is commonly used to describe both gorillas and chimpanzees (Gebo, 1996; Hunt et al., 1996); however, these primates maintain different neck orientations during knuckle-walking bouts ($\sim 56.4^\circ$ vs. $\sim 81.5^\circ$ relative to the gravity vertical, respectively. Also see Table 1) (Strait and Ross, 1999). The value of using quantified measures of positional behavior is underscored by our recent analysis (Nalley and Grider-Potter, 2015) demonstrating that features of the subaxial cervical spine (C3–C7) are correlated with quantified measures of head and neck angles across primates. In this study, we adopt a similar approach to investigate the relationship between features of the upper part of the cervical column (atlas, C1; axis, C2).

Comparative studies focusing on upper cervical vertebrae morphology suggest that primates tend to separate taxonomically, but some variation that may be attributable to differences in positional behavior has been reported (Ankel, 1965, 1970, 1972; Coroner and Latimer, 1991; Manfreda et al., 2006; Mitteroecker et al., 2007; Grider-Potter and Hallgren, 2013). For example, in comparison to recent humans, nonhuman primate atlanto-occipital joints have been described as “more deeply concave” or as exhibiting a greater degree of curvature (Aiello and Dean, 1990: 217; Dickman et al., 1994; Tominaga et al., 1995; Grider-Potter and

Hallgren, 2013). Research conducted by Coroner and Latimer (1991) quantified occipital condyle curvature in *Homo*, *Pan*, *Gorilla*, and *Australopithecus afarensis*, and found that *A. afarensis* grouped with *Pan* and *Gorilla* rather than with *Homo* (see also Nalley, 2008; Grider-Potter and Hallgren, 2013). Although this result is unexpected based on the postcranial evidence indicating that *A. afarensis* was a humanlike biped and was presumably more similar to humans in its positional behavior than to African apes (e.g., McHenry, 1986; Stern, 2000; Ward, 2002; Kimbel and Deleuzene, 2009), the assumption that this early hominin used neck postures that were humanlike (i.e., vertical) requires further examination. Notably, several additional apelike craniocervical features have been documented in *A. afarensis*, including a posteriorly inclined foramen magnum (Kimbel and Rak, 2010), relatively robust cervical pedicle and lamina dimensions (Nalley, 2013; Meyer, 2016), relatively large dorsal pillar proportions (Meyer et al., 2017) and the relatively long, dorsally oriented spinous process of a lower (likely a C6) cervical vertebra (Lovejoy et al., 1982; Nalley, 2013; Arlegi et al., 2017; Meyer et al., 2017). The functional implications of these morphologies with regard to head and neck posture remain untested.

Manfreda et al. (2006) and Mitteroecker et al. (2007) examined the relationship between locomotor pattern and overall C1 and C2 shape across anthropoids and found that species vary along a postural gradient, ranging from pronograde to orthograde torso postures. Behavioral values were calculated as the number of bouts of differing locomotor activities (e.g., vertical climbing, brachiation, quadrupedalism) taken from Gebo (1996). Their results indicate

Table 1
Comparative sample listed alphabetically within family and then species.

Family	Species	Male (n)	Female (n)	Combined (n)	Neck ^a inclination angle (NI)	Head-neck ^a angle (HNA)	Orbital ^b kyphosis angle (AOA)
Primary sample							
Atelidae	<i>Alouatta seniculus</i>	2	0	2	107.7	86.5	196.0
	<i>Ateles fusciceps</i>	9	6	15	62.8	51.6	170.2
	<i>Ateles geoffroyi</i>	1	4	5	50.4	49.3	165.0
Cebidae	<i>Sajapua apella</i>	8	8	16	61.1	48.1	166.2
	<i>Chlorocebus aethiops</i>	10	8	18	58.4	40.7	163.9
Cercopitheciidae	<i>Colobus guereza</i>	10	7	17	71.0	45.3	170.2
	<i>Erythrocebus patas</i>	4	3	7	53.6	41.3	154.1
	<i>Macaca fuscata</i>	3	2	5	51.6	49.8	152.4
	<i>Gorilla gorilla</i>	6	5	11	56.4	37.8	165.0
	<i>Homo sapiens</i>	10	10	20	17.9	8.6	122.0
Hominidae	<i>Pan troglodytes</i>	10	9	19	81.5	57.9	161.0
	<i>Pongo pygmaeus</i>	11	10	21	55.0	37.8	166.7
	<i>Hylobates lar</i>	1	1	2	47.0	45.3	162.7
	<i>Symphalangus syndactylus</i>	1	5	6	49.7	61.3	174.8
Lemuridae	<i>Lemur catta</i>	7	4	11	88.7	83.7	178.8
	<i>Varecia variegata</i>	2	6	8	91.7	85.4	178.2
Total		95	88	183			
C1 SFC analyses sample ^c							
Cebidae	<i>Saimiri sciureus</i>	2	1	3	48.7	37.8	–
Cercopitheciidae	<i>Chlorocebus aethiops</i>	1	0	1	58.4	40.7	163.9
	<i>Macaca fascicularis</i>	0	2	2	62.0	51.0	–
	<i>Papio hamadryas</i>	5	4	9	58.4	39.0	142.1
	<i>Papio ursinus</i>	1	2	3	61.9	50.4	–
	<i>Gorilla gorilla</i>	4	5	9	56.4	37.8	165.0
Hominidae	<i>Homo sapiens</i>	5	5	10	17.9	8.6	122.0
	<i>Pan troglodytes</i>	5	5	10	81.5	57.9	161.0
	<i>Pongo pygmaeus</i>	3	2	5	55.0	37.8	166.7
	<i>Hylobates lar</i>	3	2	5	47.0	45.3	162.7
Lemuridae	<i>Symphalangus syndactylus</i>	1	0	1	49.7	61.3	174.8
	<i>Lemur catta</i>	3	3	6	88.7	83.7	178.8
Total		33	31	64			

All angular data in degrees.

^a Data taken from Strait and Ross (1999). Each value represents an average for both sexes when present and locomotor behavior most commonly sampled.

^b Data collected from Ravosa (1988) and Ross (1993).

^c Many specimens are unique individuals from the primary sample.

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