



Modularity of the anthropoid dentition: Implications for the evolution of the hominin canine honing complex



Lucas K. Delezene

Department of Anthropology, University of Arkansas, Fayetteville, AR 72701, USA

ARTICLE INFO

Article history:

Received 5 May 2013

Accepted 3 July 2015

Available online 11 August 2015

Keywords:

Morphological integration

Constraint

Canine reduction

Australopithecus

ABSTRACT

In most anthropoid primates, the maxillary canine, mandibular canine, and mesial mandibular premolar form a functional complex that hones the canines. Characters in functional complexes are predicted to covary genetically, which constrains their evolutionary independence. As a result of substantial changes to canine and honing premolar size and shape, hominins are characterized by the apomorphic loss of canine honing. In early hominins, changes in canine and 'honing' premolar size and shape appear to have been uncoordinated, which is unexpected if there is strong genetic covariation coupling these teeth. Using the pattern and magnitude of phenotypic dental size covariation in extant anthropoids, results of this study indicate that certain dimensions of the anthropoid honing complex are characterized by strong size covariation within species and that canine and honing premolar size have evolved in a coordinated manner in both males and females, which undermines arguments that the complex is selectively important only in males. Further, there is no evidence for negative or strong positive covariance between canine and either incisor or postcanine size. If patterns of phenotypic covariation reflect genetic covariation, this suggests that canine reduction was unlikely to have been a dependent change associated with the development of postcanine megadontia or incisor reduction.

© 2015 Published by Elsevier Ltd.

1. Introduction

The canine honing complex is a nearly ubiquitous functional complex in the nonhuman anthropoid dentition. During early hominin evolution, the canines and honing premolar were altered in size and shape, which resulted in the loss of functional canine honing and a shift to apically-dominated canine wear. Fossils attributed to *Ardipithecus* and the earliest species of *Australopithecus* suggest that maxillary canine height reduction preceded mandibular canine height reduction, that substantial reduction in canine heights preceded reduction in their basal sizes, and that the P₃ retained morphological relicts of its honing past long after the maxillary canine was reduced and the function of canine honing was lost (Haile-Selassie, 2001; Haile-Selassie et al., 2004, 2009; Semaw et al., 2005; Kimbel and Delezene, 2009; Suwa et al., 2009; Ward et al., 2010; Delezene and Kimbel, 2011; Manthi et al., 2012). Thus, the fossil record currently points to a mosaic transformation of the hominin 'honing' complex (Ward et al., 2010; Manthi et al., 2012). As the canines and honing premolar form a functional

complex in extant anthropoids, a hypothesis of morphological integration predicts that the size and shape of these teeth should covary as a result of genetic and/or developmental factors and that they should have evolved in a coordinated manner (e.g., Wagner et al., 2007; Klingenberg, 2008). Therefore, their evolutionary independence in early hominins indicates that either the elements of the complex are not coupled genetically in extant nonhuman anthropoids or that selection was particularly strong on only some aspects of the complex and acted upon genetic variance not shared among all dimensions of the canines and mesial mandibular premolar.

In most nonhuman anthropoid primates, canines are used in visual threat displays and occasionally as weapons, especially during intraspecific conflicts (e.g., Walker, 1984; McGraw et al., 2002; Leigh et al., 2008; Galbany et al., 2015). Many anthropoid primates have tall, projecting canines; however, canine size varies between sexes and among species. Anthropoid species characterized by high intensity and frequency of agonism have larger relative canine size than species with less frequent and less intense agonism (Kay et al., 1988; Plavcan and van Schaik, 1992; Plavcan, 1993, 1998, 2001; Thoren et al., 2006). This pattern holds in both males and females (Plavcan et al., 1995); however, since male–male

E-mail address: delezene@uark.edu.

competition for mates results in greater variance in reproductive success than female competition for resources, selection is stronger for large, hypertrophied male canines (Plavcan et al., 1995).

In addition to crown height, other aspects of anthropoid canines suggest that selection has shaped their use as weapons. For example, though many male (and some female) canine crowns are quite tall, they are as resistant to bending stresses as are carnivore canines, which is perhaps an adaptation to resist breakage during conflicts involving the canines (Plavcan and Ruff, 2008). Additionally, as it slides against the labial face of the maxillary canine (C^1) during occlusion, the mandibular canine (C_1) is honed along its distal face. At the same time, occlusion between the distolingual surface of the C^1 and the mesiobuccal surface of the mesial-most mandibular premolar (P_2 in platyrrhines, P_3 in catarrhines) hones the C^1 , sharpening its distal crest from the apex towards the cervix of the tooth (Zingesser, 1969; Walker, 1984).

The honing premolar, be it P_3 or P_2 , is specialized for its function as a honing device and is morphologically distinct from more distal premolars, which Greenfield and Washburn (1992) describe as premolar heteromorphy. Though the honing premolars may not be homologous in platyrrhines and catarrhines, they share a suite of anatomical features that reflects their function as a hone for the C^1 . Generally, the honing premolar is unicuspid and the single cusp, the protoconid, is taller than on the more distal premolar(s). In addition, catarrhines have a mesiobuccal root that is partly covered by an enamel extension that forms the honing surface. The tall, centrally-placed protoconid, elongated mesial face, and inferior projection of enamel create a broad sloping surface that hones the C^1 (e.g., Zingesser, 1969).

Models predict that natural selection shapes genetic covariation to be strong among characters in functional complexes and to be weak between characters in different complexes (e.g., Cheverud, 1989, 1996; Wagner et al., 2007); such functionally and genetically coupled traits are said to be ‘integrated’ (Olson and Miller, 1958; Chernoff and Magwene, 1999). Genetic covariation is reflected within populations as phenotypic covariation. As a result, patterns of phenotypic covariation are predicted to reflect functional modularity so that the phenotype is divisible into variational ‘modules,’ which are “set[s] of covarying traits that vary relatively independently of other such sets of traits” (Wagner et al., 2007: 921; Wagner, 1996; Wagner and Altenberg, 1996; Klingenberg, 2008). Since the honing premolar and canines work together to complete the function of honing, a hypothesis of integration predicts that phenotypic covariation should exist within species for the elements of the canine honing complex.

The pattern of genetic variance and covariance among a series of characters is summarized by the genetic variance-covariance matrix (the **G**-matrix or, simply, **G**). Typically, **G** is estimated in pedigreed populations with large sample sizes; therefore, it is difficult to estimate in wild populations where familial relationships are uncertain (e.g., de Oliveira et al., 2009). As a result, estimates of **G** in primates have been limited to a few laboratory populations (e.g., *Papio* sp. at the Southwest National Primate Research Center [SNPRC]) (e.g., Hlusko and Mahaney, 2007a,b, 2009 Koh et al., 2010). Due to limitations in the estimation of **G**, the phenotypic variance-covariance matrix (**P**-matrix or **P**) is often used to estimate **G** in non-pedigreed samples (Cheverud, 1988a). For a wide assortment of traits and in diverse taxa, this substitution has been shown to be valid (e.g., Cheverud, 1988a; Roff, 1995; Waitt and Levin, 1998). Indeed, when dental size **P**-matrices estimated from wild-shot cercopithecoid samples were compared to the **G**-matrix of SNPRC *Papio*, both Hlusko and Mahaney (2007a) and Grieco et al. (2013) found that **P** and **G** were similar. Since **P** is affected by both genetic and environmental influences, it is desirable for the effect of the environment to be minimal. The relative effect of

additive genotypic and environmental variance on the phenotypic variance of a character is defined as its narrow-sense heritability (h^2); as h^2 approaches 1, the effect of the environment on variance is minimized. Overall, estimates of h^2 for dental size in humans and nonhuman primates are relatively high. For linear measures of dental size in *Homo sapiens*, h^2 estimates generally range from 0.6 to 0.8 (e.g., Townsend and Brown, 1978; Townsend et al., 2006), which is similar to h^2 estimates for linear and areal dimensions of the dentition in SNPRC baboons (Hlusko et al., 2002, 2011; Hlusko and Mahaney, 2007a,b). In fact, for 68 dimensions of the SNPRC baboon dentition, Hlusko et al. (2011) report an average h^2 of 0.56 after the effects of age and sex are taken into account. Thus, for the samples and elements that have been considered, primate dental size h^2 has been shown to be high.

Genetic covariation is an evolutionary constraint (Maynard Smith et al., 1985) that limits the ability of characters to evolve independently (e.g., Klingenberg, 2010; Marroig and Cheverud, 2010). In the most extreme case where characters are perfectly correlated, they must change states simultaneously when selection acts on either of them. For characters that are highly correlated but that retain some independent variance, selection tends to pull them along the major axis of covariation (termed the ‘line of least evolutionary resistance’; Schluter, 1996; Marroig and Cheverud, 2010). For genetically-coupled characters, phenotypic correlations observed among species are in part an extension of the genetic relationship that exists within species (e.g., Lande, 1979; Cheverud, 1982, 1988b, 1989, 1996).

If fitness is affected by the interaction of characters that are genetically uncorrelated, then, to maintain functional equivalence during evolutionary change, the characters must independently respond to selection. This is referred to as ‘selective covariance.’ In this case, unlike what is observed with characters that strongly covary genetically, no pattern of phenotypic covariation is expected within species even though one exists among species (e.g., Armbruster and Schwaegerle, 1996). Therefore, selection that has acted upon genetically correlated and uncorrelated traits can result in significant among-species phenotypic correlation; however, it is possible to distinguish between the two processes if both the within- and among-species patterns of covariation are examined.

Few studies have examined the hypothesis that the canine honing complex is a variational module in anthropoid primates. Both Cochard (1981) and Grieco et al. (2013) included canine basal dimensions in their examinations of cercopithecoid dental size covariation. Cochard examined *Colobus badius* males and females separately and found similar patterns of covariation. Within each arch, the observed ranges ($r^2 = 0.00–0.46$ for females; $r^2 = 0.03–0.48$ for males) and averages ($r^2 = 0.19$ for females; $r^2 = 0.15$ for males) between the canines and all other dental dimensions are similar in both sexes. Between the C^1 and C_1 bases, Cochard found covariation that ranged from $r^2 = 0.05–0.35$ and no significant differences between males and females. Grieco et al. (2013) estimated **P** for maxillary dental size in six cercopithecoid taxa and also compared these **P**-matrices to estimates of **P** and **G** in SNPRC baboons. They found that **P** is similar among samples and similar to **G** in the SNPRC sample. Among all samples, phenotypic covariation between canine and incisor size ($r^2 = 0.02–0.62$, average $r^2 = 0.21$) and canine and postcanine size ($r^2 = 0.00–0.64$, average $r^2 = 0.16$) are similar. Observed covariation between the length and width of the maxillary canine, though, is stronger ($r^2 = 0.13–0.90$; average $r^2 = 0.53$). The Cochard and Grieco et al. studies suggest that the pattern of covariation is similar among cercopithecoids, is similar in males and females, and that canine basal size covaries with the size of teeth outside the complex, though generally at a lower absolute value than between the basal dimensions of the canines. However,

Download English Version:

<https://daneshyari.com/en/article/4555989>

Download Persian Version:

<https://daneshyari.com/article/4555989>

[Daneshyari.com](https://daneshyari.com)