Divided Hypoglossal Canals in Japanese Macaques

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Received June 19, 1997

Abstract Japanese macaques very often have a divided hypoglossal canal (DHC). Though not statistically significant, the incidence of DHC is lower in dental age class 2 than in other age classes, in males compared to females, and on right sides compared to left sides. The association between the right and left sides is extremely significant ($\chi^2=19.443$), but the phi correlation coefficient (0.312) is not high, suggesting a low heritability estimate. It is suggested that a low heritability estimate within an individual population is not, in itself, an indicator of poor performance of the trait in population comparisons.

Key Words: divided hypoglossal canal, Japanese macaque, bilateral correlation, heritability, population comparison

INTRODUCTION

Divided hypoglossal canal (DHC) is one of the most popular cranial nonmetric characters used for population comparisons. For instance, Dodo (1987), when compiling world-wide population data of DHC, cited more than thirty papers. The prevalence of DHC studies has been brought about by the following reasons. First, DHC is easy to score and the inter-observer errors are negligible (Ishida and Dodo, 1990). Second, the early appearance of DHC suggests that only a small amount of influence comes from external (except for maternal) environment on this trait. Dodo (1980) found DHC in prenatal human skulls (pars lateralis of occipital bones), and O'Rahilly and Müller (1984) found it in early human embryos.

The usefulness of DHC in human population comparisons is without question (Dodo, 1987). However, the generally low incidence of DHC in human populations is preventing the determination of the nature of DHC, especially as regards statistical analyses. In this paper, the meaning of DHC is discussed by using the skulls of the Japanese macaque, which has a very high incidence of DHC (Mouri, 1990; Mouri and Oku, 1997). The significance of heritability estimate of a nonmetric trait for population comparison is also discussed.

MATERIAL AND METHOD

Two hundred skulls of Japanese macaques, housed in Primate Research Institute of Kyoto University, were observed (Table 1). All skulls are from the subspecies of Japan's main islands (*Macaca fuscata fuscata*), and are mostly from captive or reared

Table 1. Sex and dental age of skulls

dental age class	male	female	unknown	total
1 (deciduous dentition)	11	6	2	19
2 (with M1s)	10	9	4	23
3 (with M2s)	33	13	4	50
4 (with M3s)	25	—	0	25
5 (full permanent d.)	35	48	0	83
total	114	76	10	200

animals, or cadavers purchased from animal traders. Since the exact age of the animals was not always known, states of dental eruption in the maxillae were used as substitutes for chronological age (Table 1). Dental age class 4, where upper third molars have fully erupted but upper canines are erupting, is not found in females, since in females canines erupt earlier than third molars. DHC is scored as “present” or scored as “two” or “three,” only when the septum between the divided canals is complete.

RESULTS AND DISCUSSION

1) Morphology of divided hypoglossal canals (DHC) in Japanese macaques

The hypoglossal canal of the Japanese macaque has following characteristics. First, the incidence of DHC is high, DHC occurs even in circum-birth animals (the earliest stage observed in this study), and tripartite DHC, which is very rare in humans, is not rare in Japanese macaques. Cranial incidence of tripartite DHC is 14.0% (28/200), and that of bipartite DHC is 63.0% (126/200). The total incidence of DHC is 77.0% (154/200). However, division of the hypoglossal canal into four or more canals is not yet observed.

Second, the arrangement of the canals of DHC generally follows the cranio-caudal direction of the medulla oblongata in the Japanese macaque, as in fetal and adult humans (Dodo, 1980).

Third, the bony septum of DHC always begins at or near the endorhinal orifice of the hypoglossal canal, and extends variously to the external orifice, but never reach it. No instance of bony septum at the external orifice is yet observed. In other words, the hypoglossal canal of the Japanese macaque very often has separate openings endocranially but always has a single external opening.

Last, in DHC, especially tripartite ones, the diameter of the anterior canal tends to be smaller than that of the posterior canal(s). Sometimes, the most anterior canal of tripartite DHC is very narrow. However, in bipartite DHC, the anterior and posterior canals often have similar diameters.

All quadrupeds have the hypoglossal canal or the nerve, except for amphibians which are thought to have secondarily lost it. This suggests that the hypoglossal canal

or nerve appeared about 400 million years ago (Romer and Parsons, 1977). The evolution of the hypoglossal nerve from the spino-occipital nerves at the posterior end of primitive vertebrate skull is thought to be correlated with the appearance of terrestrial vertebrates, because in the aquatic environment there is little need for a lingua or tongue to manipulate food material (Sarnat and Netsky, 1981). According to Romer and Parsons (1977), in amniotes the hypoglossal nerve usually originates from three pairs of ventral roots of the spino-occipital nerves, which will innervate three pairs of somites, a portion of which later become the occipital bone. In human embryos at stage 12 (21–29 pairs of somites; 3–5 mm; approximately 23 days), there are four pairs of occipital somites, toward the caudal three pairs of which the primordia of the hypoglossal nerve will extend (O’Rahilly and Müller, 1984). The four pairs of occipital somites produce the sclerotomes which will later become the occipital bone (*via* cartilage).

These features of the phylogeny and ontogeny of the hypoglossal nerve and canal are well reflected in the morphology of DHC in the Japanese macaque. For instance, the cranio-caudal arrangement of the canals of DHC agrees with the theory of the evolution of the hypoglossal nerve from a series of spino-occipital nerves. Rather high incidence of tripartite DHC and the absence of a quaternary division suggests the number of pairs of the spino-occipital nerves having participated in the formation of the hypoglossal nerve is three. If we can assume a homology between the hypoglossal canal and the intervertebral foramen, this suggests a homology between the occipital bone and four vertebrae.

Table 2. Incidence of divided hypoglossal canal in sexed age classes (right side)

age class	male	female	unknown	total
1	6/11=54.5%	3/6=50.0%	1/2=50.0%	10/19=52.5%
2	3/10=30.0%	5/9=55.6%	1/4=25.0%	9/23=39.1%
3	17/33=51.5%	11/13=84.6%	3/4=75.0%	31/50=62.0%
4	17/25=68.0%	—	—	17/25=68.0%
5	18/35=51.4%	32/48=66.7%	—	50/83=60.2%
total	61/114=53.5%	51/76=67.1%	5/10=50.0%	117/200=58.5%

Table 3. Incidence of divided hypoglossal canal in sexed age classes (left side)

age class	male	female	unknown	total
1	7/11=63.6%	5/6=83.3%	1/2=50.0%	13/19=68.4%
2	3/10=30.0%	6/9=66.7%	2/4=50.0%	11/23=47.8%
3	21/33=63.6%	10/13=76.9%	3/4=75.0%	34/50=68.0%
4	16/25=64.0%	—	—	16/25=64.0%
5	22/35=62.9%	29/48=60.4%	—	51/83=61.4%
total	69/114=60.5%	50/76=67.1%	6/10=60.0%	125/200=62.5%

2) Incidence of divided hypoglossal canals and influence of age, sex and side

The side incidence of undivided hypoglossal canal is 39.5% (158/400), that of bipartite DHC 51.8% (207/400), and that of tripartite DHC 8.8% (35/400). Hereafter, the bipartite and tripartite DHCs will be combined for the statistical analyses.

Table 2 shows the incidences of DHC on the right side in sexed age classes, and Table 3 shows the incidence of DHC on the left side. On both sides of the skull, there is no significant (at the 5% level) difference of the incidences between the sexed age classes, though age class 2 has a lower incidence.

Since there is no significant difference of the incidences of DHC between the sexed age classes, the statistical test on the difference between males and females is applied to age-combined data. The result is not significant in the right side data (chi-square=3.483), the left side data (chi-square=0.054), or the both side combined data (chi-square=3.402). Though the sex difference of the DHC incidences is not statistically significant, the DHC incidence is larger in females than in males.

The incidence of DHC is higher in the left (62.5%=125/200) than in the right side (58.5%=117/200), but the difference is not significant at the 5% level.

In sum, the DHC incidence in the Japanese macaque is low in the age class 2 (with deciduous dentition but before and just up to the completion of the eruption of maxillary permanent first molars), higher in females than in males, and higher on the left side than on the right side. But these differences are not significant at the 5% level. Predominance of DHC on the left side is already reported for humans (Dodo, 1980) and for pure strains of mouse (Deol, 1955).

3) Bilateral correlation

Of the bilateral association, Table 4 shows chi-square value of 19.443, indicating a extremely high level of significance of the association between the DHC occurrence on the right side and that on the left side, but phi correlation coefficient of 0.312, suggesting a moderate degree of the bilateral correlation.

Since both sides of an individual are assumed to share the same genetic background, they can be considered monozygotic twins with more intensive influences from common environmental factors. Therefore, phi correlation coefficient between

Table 4. Bilateral association of divided hypoglossal canals in Japanese macaques

present on both sides	88/200=44.0%
only on the right side	29/200=14.5%
only on the left side	37/200=18.5%
absent on both sides	46/200=23.0%
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chi-square:	19.443
phi (correlation coefficient):	0.312

right and left sides is thought to be a proportion of total phenotypic variance explained by additive genetic, dominance genetic, common environmental, and other minor variances. Heritability, which is a proportion of the total genetic variance explained by additive genetic variance, is inferred to be lower than a phi correlation coefficient between the sides. In fact, heritability estimate tends to be low; 0.008 for humans (Sjøvold, 1984), 0.14–0.37 for mice (Self and Leamy, 1978). Though, the estimate for rhesus monkey on Cayo Santiago (0.772; Cheverud and Buikstra, 1981) is not low.

It is thought by some that a nonmetric trait with a low heritability estimate (Sjøvold, 1984) or with high frequency of bilateral asymmetry (Trinkaas, 1978) should be excluded for population studies. But, in the studies on pure strains of mice (e.g. Howe and Parsons, 1967), where there is no or limited amount of genetic variance within the strains (then, heritability is zero or near zero), the incidence of nonmetric skeletal traits is claimed to be a good indicator of the genetic diversity among the strains.

Heritability is nothing but a proportion of a total phenotypic variance explained by an additive genetic variance, and is strictly a property of the individual population studied. Therefore, low heritability estimates of a nonmetric trait A in each of compared populations will not deny the genetic nature of the differences in trait A incidences between the populations. This is clearly illustrated by the situation of a pure strain comparison of mice (Howe and Parsons, 1967). Conversely, even if a trait B has a high heritability estimate within each population, the difference of the incidences of trait B between populations may be explained mainly by environmental factors. Although heritability estimates of natural populations, including those of human (Sjøvold, 1984), are valuable, a more pertinent problem for population study is the identification of specific environmental factors in population differences. It is also important to determine whether a hybrid population has an intermediate incidence between those of the parent populations.

CONCLUDING REMARKS

Much higher incidence of the divided hypoglossal canal (DHC) in the Japanese macaque than in the human made it possible to further elucidate the nature of the hypoglossal canal. DHC shows highly significant association between right and left sides (chi-square of 19.443), but the phi correlation coefficient between the sides is low (0.312). The low phi value suggests a low heritability estimate. The argument that a nonmetric trait with a low heritability estimate (Sjøvold, 1984) or with high frequency of bilateral asymmetry (Trinkaas, 1978) should be excluded for population studies is refuted.

ACKNOWLEDGEMENTS

For access to the skulls of Japanese macaques, the author expresses his sincere

thanks to Seiji Hayakawa, Minoru Kinoshita, and Study Material Committee of Primate Research Institute of Kyoto University. Vanessa Hayes of the University of Western Australia kindly revised the English. This study was supported in part by a Grant-in-aid from the Ministry of Education, Science, and Culture (Monbusho) of Japan (no. 62304012).

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