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Variation Units in the Human Permanent Dentition

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The adaptive significance of a certain character should be determined according to intensity of the "functional relationship" (FALCONER, 1960) between the character and fitness. Any morphological character must have a functional relationship with fitness as long as it exists. On the other hand, any arbitrary part of the body can be defined as a character with some function, but can not accomplish its function without every other character which supports it and makes it fill the proper role in a series of the vital activities necessary for survival of an individual. These are also true of human dentition.

DAHLBERG (1945, 1951) suggested that BUTLER's (1939) field hypothesis was applicable to the differential condition in size and shape of the human permanent dentition. The low estimates of heritability or relative genetic variability to the environmental one for the teeth such as the canines and the first molars found in some, not all, of the previous studies (OSBORNE *et al.*, 1958; SOFAER *et al.*, 1971a; ALVESALO and TIGERSTEDT, 1974; POTTER and NANCE, 1976; MIZOGUCHI, 1977; TOWNSEND and BROWN, 1978a, b) do not necessarily support the field hypothesis because a heritability estimate or a correlation coefficient between relatives for a character only shows the proportion of the genetic variance to the phenotypic variance under some simple assumptions and, besides, never presents any information on the stable part of the character determined by the interactions of genes and environment (EDWARDS, 1969; CAVALLI-SFORZA and BODMER, 1971; MIZOGUCHI, 1980). But the low genetic coefficients of variation (LUNDSTRÖM, 1948) for the "key teeth" (DAHLBERG, 1945) within the morphological tooth classes seem to be compatible to the field hypothesis, as do the coefficients of variation in phenotypic size (DAHLBERG, 1945; KIRVESKARI *et al.*, 1978). SOFAER *et al.*, (1971a) showed that the relative variances between the right and left teeth to the tooth size were generally greater in the distal teeth within tooth classes than in the mesial ones. If this tooth asymmetry is due to random environmental factors, the above finding by SOFAER *et al.* implies that the environmental variability of the mesial tooth within each class is also lower relative to its size than that of the distal one. Under simple genetic assumptions, the results mentioned above of LUNDSTRÖM (1948) and SOFAER *et al.* (1971a) are not incompatible with each other nor with the field hypothesis. There is further evidence supporting the differentiation of the human dentition due to morphogenetic fields and the significance of a mesial tooth as a pole within the field. The mesial teeth within morphological tooth classes develop earlier than the distal ones, and between tooth classes the highest correlation coefficients are between the mesial members within the tooth classes (GARN *et al.*, 1965; SOFAER *et al.*, 1971a). It is also known that the amount of dental reduction in size from *Australopithecus* to modern man is less in the mesial teeth within tooth classes than in the distal ones (BRACE, 1967; SAKURA, 1970; SOFAER *et al.*, 1971a). These facts remind us of the greater stability or adaptive significance of the mesial teeth within tooth classes throughout the human evolutionary process. In addition, the possibility of compensatory interaction between adjacent teeth within a morphological tooth class has been shown (GRÜNEBERG, 1965; SOFAER *et al.*, 1971a, b), suggesting the significance of each tooth group existing as a unit. The same can be inferred from the possible existence of the differential variability for the four morphological classes in human permanent dentition revealed by the rotated solution of the factor analysis (LOMBARDI, 1978; MIZOGUCHI, 1980). On the other hand, the problems of adaptive functional differentiation in the primate dentitions have been discussed directly from the viewpoint of interrelationships of the anterior and posterior teeth to the diet (GROVES and NAPIER, 1968; JOLLY, 1970; HYLANDER, 1975; KAY, 1975; GOLDSTEIN *et al.*, 1978; PIRIE, 1978).

Taking all the above into account, it seems likely that each tooth group consisting of a few or several teeth operates as a functional unit (OSBORNE, 1967) and has more significant relationship to fitness than individual teeth. If any tooth group really exists as a functional unit, it will be expected that the teeth belonging to the same tooth group have some common attributes. It goes without saying that the dentition would not function if a set of the maxillary and mandibular dentitions were not completed. This article is an attempt to search what kinds of interrelations can be found between and/or within various tooth groups in the human permanent dentition. It was carried out by the canonical correlation analysis method comparing the maxillary with the mandibular dentition under the assumption that the more significant relations among teeth in adaptive value are those seen simultaneously in both maxillary and mandibular dentitions.

Materials

The materials used were the dental plaster casts of 51 male and 52 female Japanese in Tokyo who were of twelve to fifteen years of age. Their permanent teeth of the central incisors to the second molars on the right side of both jaws were so complete that the mesiodistal crown diameters were measurable on the plaster casts. Measurement was performed by the present author according to FUJITA's (1949) method with a sliding caliper with an accuracy of 0.05 mm. These plaster casts were collected in 1955 by Professor K. HANIHARA of the Department of Anthropology, the University of Tokyo, and are now housed in his institution.

Methods

The factors almost common to the maxillary and mandibular dentitions were extracted by a canonical correlation analysis. Details of the canonical correlation analysis are described by ANDERSON (1958), ASANO (1971), OKUNO *et al.* (1971, 1976), *etc.* In the present study, the variables included in the first variable group, set up in the canonical correlation analysis, were the mesiodistal crown diameters of the maxillary teeth, and the variables in the second variable group were those of the mandibular teeth. The calculation of the canonical correlation analysis was carried out by a HITAC M–200H (VOS 3) computer of the University of Tokyo Computer Centre using CNCRSS program which was coded in FORTRAN by the present author.

Results

The canonical correlation analysis was done on the basis of the sexually segregated data because the significant between-sex differences had been reported in means, variances, and inter-character correlations for the mesiodistal crown diameters of some permanent teeth (MIZOGUCHI, 1980) and were found out also in the present sample (Tables 1 and 2). The result of the canonical correlation analysis is shown in Table 3, where the correlations between mesiodistal diameters and the canonical variates extracted are listed.

The first pair of canonical variates was, on the whole, highly correlated with the

Table 1. Means, Variances and coefficients of variation of the mesiodistal crown diameters.

	Male ($n=51$)			Female ($n=52$)			Sex difference	
	Mean	Var.	C.V.	Mean	Var.	C.V.	F-ratio[1]	t'-value[2]
Maxilla:								
I1	8.64	.2762	6.08	8.43	.2072	5.40	1.33	2.17*
I2	7.12	.2476	6.99	6.83	.3686	8.90	1.49	2.65*
C	8.16	.1216	4.27	7.64	.2504	6.55	2.06*	6.13***
P1	7.47	.1530	5.24	7.27	.1456	5.25	1.05	2.63*
P2	6.96	.1805	6.11	6.80	.1174	5.04	1.54	2.10*
M1	10.59	.2550	4.77	10.19	.1638	3.97	1.56	4.43***
M2	9.77	.3309	5.88	9.59	.1890	4.53	1.75*	1.79
Mandible:								
I1	5.44	.1153	6.24	5.31	.0985	5.91	1.17	2.02*
I2	6.15	.1387	6.06	5.93	.1194	5.82	1.16	3.11**
C	7.19	.1505	5.40	6.66	.1377	5.57	1.09	7.08***
P1	7.40	.2092	6.18	7.10	.1428	5.33	1.47	3.63***
P2	7.26	.1765	5.79	7.03	.1888	6.18	1.07	2.73**
M1	11.54	.1885	3.76	11.13	.1457	3.43	1.29	5.09***
M2	10.85	.4439	6.14	10.40	.2503	4.81	1.77*	3.87***

[1] Two-tailed F-test.

[2] COCHRAN's approximate significance test for the difference between two means with different variances (SNEDECOR and COCHRAN, 1967).

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Table 2. Correlation matrices of the mesiodistal crown diameters in males (upper right half) and in females (lower left half).

	I^1	I^2	C^-	P^1	P^2	M^1	M^2	I_1	I_2	C_-	P_1	P_2	M_1	M_2
I^1		.5387	.5855	.4195	.2151*	.4670	.0661	.7696	.6024	.4085	.3317	.0695	.2102	.0717
I^2	.6400		.3646	.2370	.1283*	.2180	.1124	.4824	.4659	.3032	.2573*	.1978	.1587*	.1197
C^-	.6110	.5585		.6677	.5638	.5385	.2971	.5478	.5584	.7661	.5953	.4646	.4125	.3044
P^1	.5818	.5613	.6478		.6950	.5398	.3306	.3911	.3753	.5992	.7070	.6443	.4179	.3820
P^2	.5578*	.4895*	.5359	.8241		.4242	.4204	.3243	.3517	.4998	.6032	.7047	.4102	.4811
M^1	.4415	.4946	.4151	.5625	.5920		.5131	.4903	.4617	.5909	.4296	.4223	.6516	.3230
M^2	.3073	.3714	.2608	.3026	.3659	.6549		.0945	.0396	.3655	.2567	.4716	.4142	.4609
I_1	.7452	.5636	.5855	.5898	.5866	.4698	.1870		.7332	.5428	.4714	.1694	.3465	.1302
I_2	.6411	.4829	.6461	.6428	.4987	.5236	.2672	.6912		.4819	.3665	.1431	.4052	.2491
C_-	.6086	.6037	.8217	.6075	.5065	.4846	.3152	.5344	.6548		.5899	.5066	.4338	.3136
P_1	.6240	.5811*	.6745	.7455	.6926	.5574	.4743	.5520	.5898	.7448		.7029	.4482	.4153
P_2	.3543	.3285	.4467	.6408	.7293	.5976	.4383	.3657	.3798	.4819	.6342		.5072	.4995
M_1	.4111	.5166*	.4445	.4852	.5649	.7514	.5509	.3901	.4035	.5657	.5441	.5874		.5732
M_2	.4262	.4529	.4707	.4567	.5687	.6035	.5290	.3742	.3975	.5410	.6394	.5673	.6621	

* Correlation coefficients showing the significant between-sex difference at the 5% level, tested by the normal deviates of FISHER's z-statistics (FISHER, 1958; RAO, 1952). However, the approximate chi-square test for significance of difference between two sample correlation matrices (LAWLEY and MAXWELL, 1963) showed no significant between-sex difference ($\chi^2=79.47$, d.f.$=105$, $P\fallingdotseq 0.97$).

Table 3. Correlations of the canonical variates for maxillary and mandibular dentitions with the original variables or mesiodistal crown diameters.

	Canonical variate							
	Male				Female			
	u_1	u_2	u_3	u_4	u_1	u_2	u_3	u_4
Maxilla:								
I1	0.50	0.81	0.06	−0.03	0.79	−0.28	0.04	−0.44
I2	0.44	0.43	0.22	−0.00	0.71	−0.17	−0.26	−0.09
C	0.87	0.15	−0.16	−0.30	0.82	−0.43	−0.00	0.31
P1	0.82	−0.12	0.21	−0.22	0.84	0.07	0.46	0.06
P2	0.78	−0.19	0.45	0.10	0.82	0.35	0.26	−0.13
M1	0.75	0.14	−0.39	0.43	0.76	0.44	−0.32	0.05
M2	0.47	−0.33	0.03	0.62	0.50	0.47	−0.19	0.33
Total contribution (%)	46.5	15.0	6.9	10.4	57.5	11.9	7.0	6.2
Cumulative proportion (%)	46.5	61.6	68.5	78.8	57.5	69.3	76.3	82.5
	v_1	v_2	v_3	v_4	v_1	v_2	v_3	v_4
Mandible:								
I1	0.61	0.77	0.06	0.06	0.79	−0.22	0.01	−0.57
I2	0.64	0.57	−0.04	−0.09	0.78	−0.23	0.13	−0.04
C	0.87	0.02	−0.29	−0.16	0.83	−0.39	−0.12	0.36
P1	0.78	−0.08	0.23	−0.29	0.87	0.02	0.27	0.19
P2	0.76	−0.44	0.36	0.16	0.71	0.48	0.24	0.19
M1	0.65	−0.08	−0.31	0.53	0.73	0.39	−0.49	0.15
M2	0.51	−0.28	0.24	0.40	0.69	0.30	−0.29	0.17
Total contribution (%)	48.7	17.1	6.2	8.3	59.7	10.4	6.9	8.3
Cumulative proportion (%)	48.7	65.8	71.9	80.2	59.7	70.1	76.9	85.3
Canonical correlation[1)]	0.89	0.77	0.63	0.51	0.93	0.74	0.55	0.49

[1)] The canonical correlations of the fourth to the seventh pair in males and of the fifth to the seventh pair in females of canonical variates were found not to be significantly different from zero at the 5% level by BARTLETT's method using WILKS' Λ (ASANO, 1971; RAO, 1952).

diameters of all the teeth examined, and had the highest contribution to the total standardized variance among the canonical variates extracted in both sexes. Therefore, these mutually related canonical variates may be interpreted as factors controlling the general size of the maxillary and mandibular dentitions respectively. The second pair of canonical variates indicates that the group of anterior teeth (I1, I2, C) and that of posterior teeth (P1, P2, M1, M2) vary as opposed to each other. The third pair in females and the fourth pair in males of the canonical variates seem to be related mainly with the posterior teeth, and, within it, to be correlated with the premolar group and the molar group in the opposite directions, especially in females. The fourth pair of the canonical variates in females is likely related with the anterior teeth, and highly correlated with the central incisors and with the canines in the reverse directions.

Discussion

In a canonical correlation analysis, all the sets but a certain one of canonical variates are inevitably correlated positively with some of the original variables and negatively with the other because the sets of canonical variates are so determined that they are orthogonal with one another. It is of importance, however, which original variables are correlated in the same direction with a set of canonical variates. In the present analysis, for example, the mesiodistal diameters of the anterior teeth or those of the posterior teeth showed this kind of characteristic with respect to the second set of canonical variates. The similar differential variation is also recognizable in the results of the principal component analysis of the mesiodistal crown size reported previously (HANIHARA, 1974, 1977), where the second principal component seems to be identified as a factor contrasting the anterior teeth with the posterior ones in both cases of the permanent and the deciduous teeth. But any clear-cut differential variation within the anterior or posterior teeth, as shown here by the third or fourth canonical variates, has not been detected by the principal component analysis.

The four main factors corresponding to the four morphological tooth classes of human permanent dentition, *i.e.* incisor, canine, premolar and molar tooth classes, can be recognized in the rotated solution of the factor analysis or of the principal component analysis as an approximate factor analysis based on the phenotypic correlaton matrix of either mesiodistal or buccolingual diameters (HANIHARA, 1977; LOMBARDI, 1978), or on the genetic correlation matrix of the mesiodistal diameters made through the cross twin analysis (MIZOGUCHI, 1980). It is not necessarily incompatible with the results obtained here. The difference between them is due to the difference in the way of extraction of factors. That is to say, the two tooth groups, anterior and posterior, are recognizable when based on one criterion for factor extraction, but, based on another criterion, the four tooth groups are discernible. Either of them is of no value in biology unless any biological meaning is imposed on such criteria. If the factors causing the greatest covariance in a complex of characters are the most important for adaptation, the factors making up the dichotomous classification for the permanent dentition may be accepted as the most important ones except for the general size factors. The factors related to the anterior and posterior portions of the permanent dentition have also been suggested by the rotated solution of factor analysis in which both mesiodistal and buccolingual diameters are involved (LOMBARDI, 1978; TOWNSEND and BROWN, 1979).

In the primates including hominoids, it is known that frugivores have large incisors and small molars relative to body size, and folivores, on the contrary, have small incisors and large molars (GROVES and NAPIER, 1968; HYLANDER, 1975; KAY, 1975; GOLDSTEIN *et al.*, 1978; PIRIE, 1978). The female primates with relatively large canine base area to body weight tend to be frugivorous, but not to be folivorous (SMITH, 1981). These, together with the results obtained here, seem to suggest that each of the anterior and the posterior portions of human permanent dentition acts as a functional unit (OSBORNE, 1967) beyond the boundaries between the four morphological tooth classes. This partly supports one of JOLLY's (1970) explanations for canine reduction that it is a secondary effect dependent upon the incisal reduction through human evolutionary process.

Even if the existence of the two tooth groups as the most significant functional units is conceivable, it can not be determined by the result of a canonical correlation analysis alone whether the apparently compensatory relationship between the anterior and the posterior tooth groups or within each of the groups means the genuine compensatory relationship or, simply, the partial independence of each other. This problem seems to be concerned with the adaptive significance of such tooth groups at a certain stage of evolution. In the human evolutionary process, at least from Neanderthal stage to modern times, the amount of dental reduction appears to be greater in the anterior teeth than in the posterior ones (BRACE, 1967, 1979; SAKURA, 1970). And, now, the modern man has, together with folivorous gorillas, the smallest incisors relative to their body size among the hominoids (HYLANDER, 1975). This phenomenon, however, does not necessarily imply the less significance in adaptive value of the human anterior teeth in modern times because the smallness of the anterior teeth may have been required for adaptation in the complicated relations with many other characters, in other words, it may be due to the "somatic budget effect" (JOLLY, 1970). In fact, attrition was severer in the anterior teeth than in the posterior ones throughout the late Pleistocene, suggesting the greater functional demands made on the anterior teeth (SMITH, 1977). This never implies that man could not well adapt themselves to their way of life with the small anterior teeth. Therefore, the intensity of the functional relationship (FALCONER, 1960) of a tooth group to fitness should be determined based on another criterion. The relative variabilities like coefficients of variation may roughly be one of such criteria, but it is very difficult to know to what degree they reflect the intensity of functional relationship in the complicated system of characters. Here, therefore, the causes of the superficial compensatory relationships between and within the tooth groups will be inferred indirectly from another evidence.

As regards the anterior and posterior tooth groups, if they have considerably different functions from each other, it seems unlikely that there is any intensive compensatory interrelation in size between them. Thus the contradistinctive relationship between them revealed here is interpreted, at least as a possibility, as a simple reflection of their variabilities partly independent of each other. However, it is unknown which has more significant adaptive value of the anterior and posterior tooth groups.

The contrastive relationships within tooth groups may also be explained by the variabilities of the single teeth relatively independent of each other. However, GRÜNEBERG (1965) observed the fact of the compensatory growth of the later formed molars within the molar tooth row in mice, and SOFAER *et al.* (1971b) suggested the possibility of the similar condition in the maxillary incisor row of human parmanent dentition. If each of the anterior and posterior tooth groups functions as a unit in the human permanent dentitions, the canines or premolars, whose crowns are completed later within each tooth group (Lowrey, 1973), may, in like manner, complement the relevant tooth group as a functional unit through the developmental process. If so, such compensatory development is also interpretable as one of causes for the contrastive relationship between the teeth within a tooth group.

After all, it is likely that the contradistinctive interrelationships between and within the anterior and posterior tooth groups as shown here by the canonical correlation analysis are chiefly due to their variabilities partly independent of each other and, within a tooth group, further due to compensatory interactions.

Finally, it should be emphasized that the above suggestions must be confirmed by the direct and much more sophisticated methods based on the data including the third molars in the future.

Summary and Conclusions

Based on the mesiodistal crown diameters of human permanent teeth except for the third molars, it was found out by the canonical correlation analysis that the contrastive relation between the anterior and the posterior tooth groups seemed to be the most important among all the possible relations in the human permanent dentition except for the correlations due to the general size factors. In conclusion, it is most likely that each of the anterior and posterior tooth groups, rather than the four morphological tooth classes, varies as a unit and is referred to a primary functional unit in the human permanent dentition. The contradistinctive relationships seen between and within the anterior and the posterior tooth groups seem to be mainly reflections of the variabilities partly independent of each other and, partially, of the compensatory interactions among teeth.

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