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Cross- and Triple-Ratios of Human Body Parts During Development

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ABSTRACT

Recently developed landmark-based geometric morphometry has been used to depict the morphological development of organisms. In geometry, four landmarks can be mapped to any other four by Möbius transformations, if the cross-ratio of the landmarks is invariant and vice versa. To geometrically analyze the morphological development of the human body, we examined the cross-ratio of three consecutive body parts that are segmented by four landmarks in their configuration. Moreover, we introduced the triple-ratio of five landmarks that segments four consecutive parts (e.g., the shoulder, upper arm, forearm, and hand) and examined their growth patterns. The cross- and triple-ratios of the upper limb and shoulder girdle in fetuses were constant when biomechanical landmarks were used, although the cross-ratio of the upper limb varied when anatomical landmarks were used. The cross-ratios of the lower limbs, trunk, and pelvic girdles in fetuses differed from their corresponding cross-ratios in adults. These results suggest Möbius growth in the fetal upper limb and shoulder girdle but not in the other body parts examined. However, the growth balance of the three contiguous body parts was represented by the developmental change in the cross-ratio. Therefore, the cross- and triple-ratios may be applicable for simple but significant assessments of growth balance or proportion of the body parts. Anat Rec, 00:000–000, 2011. © 2011 Wiley-Liss, Inc.

Key words: cross-ratio; triple-ratio; development; human; limb; Möbius transformation; golden wurf

Petukhov (1989) reported that humans exhibit cross-ratio invariance among different body parts such as the phalanx, arms, legs, and trunk. Cross-ratio invariance between two objects, that is, the arm and leg, indicates that their morphological structures can be transformed into each other by Möbius transformations, which consist of translation, rotation, expansion, and inversion (Needham, 1998). The cross-ratio is defined for four arbitrary points, namely, *p, q, r,* and *s*, as:

Additional Supporting Information may be found in the online version of this article.

Abbreviations: CR = cross-ratio; CRL = crown-rump length; HA = head axis; n = nasion; p = philtrum; sn = subnasale; v = vertex

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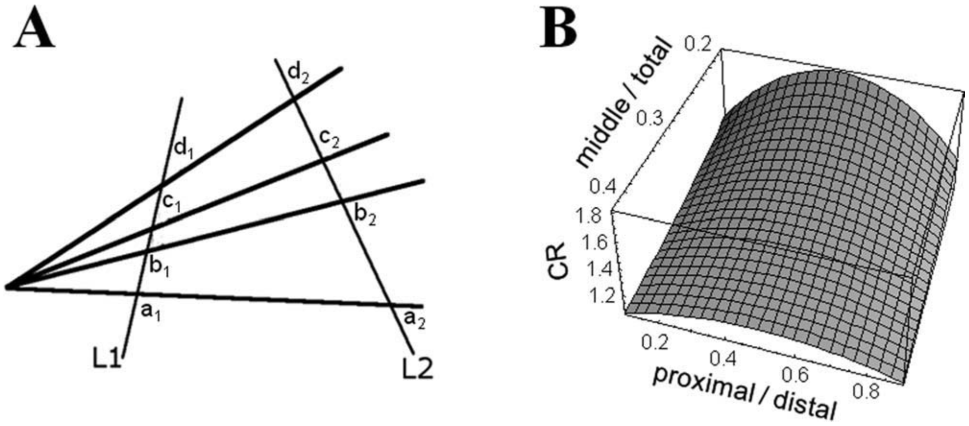

Fig. 1. The cross-ratio invariance and a surface plot of the cross-ratio. **A**: The intersecting lines L1 and L2 have the same cross-ratio, that is, the cross-ratio of a_1, b_1, c_1, and d_1 is equal to that of a_2, b_2, c_2, and d_2. The cross-ratio is invariant for all lines that intersect the four rays. **B**: The smaller the ratio of the middle length to the total length is, the larger the cross-ratio is. The cross-ratio is at a maximum when the proximal and distal lengths are equal, and the middle length is constant.

TABLE 1. Landmarks for textile in men and women in Sweden

	From	To
Upper arm$_{tex}$	Acromiale	Slightly bent elbow
Fore arm$_{tex}$	Slightly bent elbow	Wrist
Hand$_{tex}$	Wrist	Tip of the middle finger
Thigh$_{tex}$	Crotch	Knee joint
Calf$_{tex}$	Knee joint	Ankle
Foot$_{tex}$	Pternion	Acropodion
Head$_{tex}$	Vertex	Suprasternale
Trunk$_{tex}$	Suprasternale	Crotch
Lower limb$_{tex}$	Crotch	Sole

$$\frac{|p-r|\cdot|q-s|}{|q-r|\cdot|p-s|} \qquad (1)$$

As an illustration of the cross-ratio, we quote a very old result, likely by Pappus around the year 320 (Duffin, 1993). Let us consider four non-parallel rays starting at a common point (Fig. 1A). Let L_1 and L_2 be lines intersecting all four rays. Let a_i, b_i, c_i, and d_i be the points at which L_i intersects the rays. The cross-ratio of a_1, b_1, c_1, and d_1 as calculated by Eq. (1) is equal to the cross-ratio of a_2, b_2, c_2, and d_2. The transformation of the intersecting points from L_1 to L_2 is Möbius transformation. By choosing the shoulder, elbow and wrist joints, and the tip of the hand as a_i, b_i, c_i, and d_i, respectively, the growth balance of the upper arm, forearm, and hand can be examined.

Petukhov (1989) claimed that the cross-ratios should be invariant not only among different body parts but also from the fetus to the adult. Furthermore, he claimed that the common value for all these cross-ratios was $\sim\varphi^2/2 \approx 1.31$, termed "the golden wurf," where φ is the golden ratio. However, the measurement methods employed were not described in detail in that article (Petukhov, 1989). In the present study, we measured body parts by using clearly delineated methods during development and applied the cross-ratio to describe the morphological changes of the upper and lower limbs, shoulder and pelvic girdles, and the trunk during human development; subsequently, we prepared standard growth curves of these cross-ratios. Here, we show the availability of cross- and triple-ratios for the description and evaluation of the growth balance or the proportion of any three or four consecutive body parts. Moreover, we show that the invariance of these ratios was limited to the growth of the fetal upper limb.

MATERIALS AND METHODS

Body Measurements in Adults

We used background data for garment sizes from more than 2,000 females and 1,500 males from Sweden aged 13–80 and 13–90 years, respectively. The participants were native Swedes (white Caucasian) except for a minority (about 10%) with non-Swedish parents. The landmarks for textile purposes listed in Table 1 were measured with a Vitus smart body scanner (Vitronic, Wiesbaden, Germany) (Fig. 2A). This study was approved by the Swedish Data Inspection Board. For the Japanese participants, the following were measured using an anthropometer in 15 males and 15 females aged 21–52 years: upper arm, forearm, hand, thigh, calf, and foot lengths; vertex-to-suprasternale, trunk, and trochanteric heights; and biacromial and bitrochanteric breadths (Fig. 2B). The study in Japan was approved by the Ethics Committee of the Shimane University Faculty of Medicine.

All participants volunteered and were informed of the purpose of the study, agreed to the measurements and the use of the data, and signed a consent form.

Body Measurements in Human Embryos, Fetuses, and Infants

To investigate the changes in the cross-ratios of body parts, we used both embryonic and fetal data. We measured normal Japanese embryos whose crown-rump lengths (CRL) were 5.7–27.7 mm (Carnegie stage: 14–23 or ~5–8 weeks of gestational age), normal Japanese fetuses with CRLs of 95–253 mm (4–8 months of

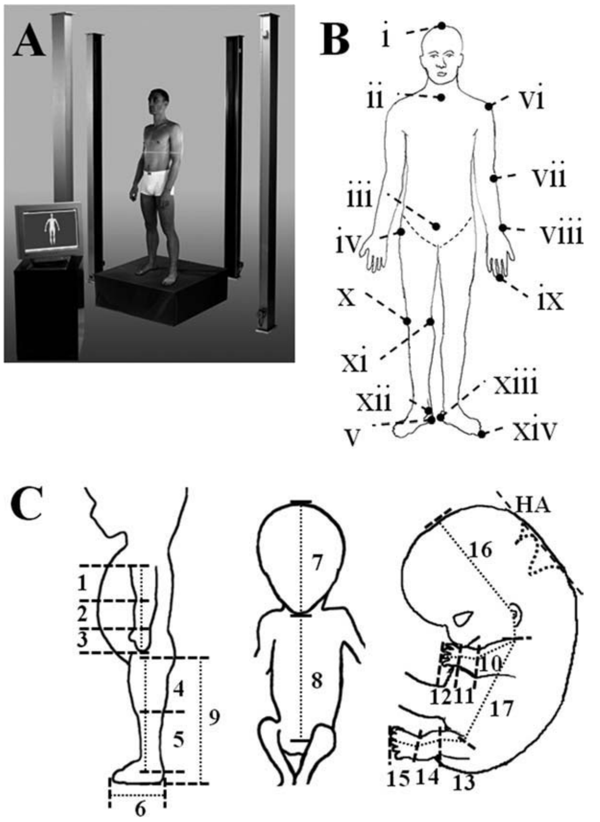

Fig. 2. Measurements in human adults (**A** and **B**), fetuses, and embryos (**C**). The lengths of body parts were measured using (A) a Vitus smart body scanner in Sweden and anthropometers in Japan. B: We measured the height of the head (i: vertex to ii: suprasternale), the length of the trunk (ii–iii: symphysion), the trochanterion height (iv: trochanterion to v: sole), the lengths of the upper arm (vi: acromiale to vii: radiale), forearm (vii–viii: stylion), hand (viii–ix: dactylion), thigh (iv–x: bottom of the epicondylus lateralis), calf (xi–xii: sphyrion), and foot (xiii: pternion to xiv: acropodion), and the biacromial (between vi's) and trochanteric breadths (between iv's). We measured the length of the upper arm (1, 10), forearm (2, 11), hand (3, 12), femur (4, 13), crus (5, 14), foot (6, 15), head-to-cervix (7, 16), trunk (8, 17), and lower limb (9, 13 + 14 + 15) in human fetuses and embryos (C). The head axis (HA) was defined as the line passing tangentially through the two points on the surface ectoderm just above the mesencephalon and the myelencephalon for the embryos; the head height was measured parallel to the HA (C).

gestational age), and an anencephalic fetus (10 months of gestational age). These fetuses are historical specimens and belong to the collection of embryos and fetuses in Kyoto University (Nishimura et al., 1968; Tanaka, 1976; Shiota, 1991; Tanaka, 1991; Otani et al., 2008). In most of these cases, pregnancy was terminated for socioeconomic reasons under the Maternity Protection Law of Japan. Therefore, these fetuses can be considered representative of the normal Japanese intrauterine population. Upon removal, the fetuses were examined for gross external abnormalities, chemically fixed, and were preserved in 10% formalin.

We measured the upper arm, forearm, and hand lengths; the thigh, calf, and foot lengths; the vertex-to-suprasternale, trunk, and trochanteric heights; the biacromial and bitrochanteric breadths in the fetuses (Fig. 2C and Table 1); and the vertex-to-nasion height, nasal height, and philtrum length (Fig. 3A).

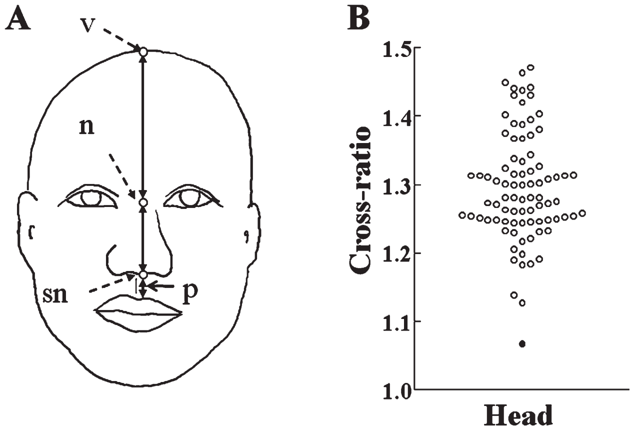

Fig. 3. The difference of the cross-ratio of the head between an anencephalic fetus and normal fetuses. **A**: The cross-ratio of the head was calculated from the heights of the vertex (v)-to-nasion (n), nasion (v)-to-subnasale (sn), and philtrum (p) length. **B**: The cross-ratio of the head was lower in the anencephalic fetus (●) than the normal ones (○).

In embryos, it is not possible to identify the same landmarks as those in fetuses, because bone formation in embryos is incomplete. The landmarks listed in Table 2 were defined to match points of embryos to the corresponding points in fetuses and adults. We defined the head axis as a line passing tangentially through the two points on the surface ectoderm just anterior to the mesencephalon and myelencephalon to measure head height (Fig. 2C).

To examine the developmental changes in the cross-ratio, we used the data of the infant upper limbs from "Japanese Child Body Size Data (2005–2007)" (http://www.hql.jp), which belongs to the Japan Machinery Federation.

Calculation of the Cross-Ratio

We calculated the cross-ratios of the whole body, upper and lower limbs, and shoulder and pelvic girdles by using the anatomical, biomechanical, and textile landmarks specified below, which are segregated using the subscripts $_{\mathrm{a}}$, $_{\mathrm{bm}}$, or $_{\mathrm{tex}}$, respectively.

We calculated the cross-ratios as follows: (1) the cross-ratio of the whole body was calculated using the vertex-to-suprasternale, trunk, and lower limb heights; (2) the cross-ratio of the upper limb was calculated from the upper arm, forearm, and hand lengths; (3) the cross-ratio of the lower limb was calculated from the thigh, calf, and foot lengths; (4) the cross-ratio of the shoulder girdle was calculated from the half-biacromial breadth and the upper arm$_{\mathrm{bm}}$ and forearm$_{\mathrm{bm}}$ lengths; and (5) the cross-ratio of the pelvic girdle was calculated from the half-bitrochanteric breadth, and the thigh and calf lengths. We calculated two different cross-ratios in the lower limb and whole body by using the corresponding anatomical or textile landmarks in the adult (Fig. 2A, Tables 1 and 2). In the upper limb, we calculated three different cross-ratios in both the fetus and adult using the anatomical, biomechanical, and textile landmarks (Fig. 2B, Tables 1 and 2). The anatomical lengths of the

TABLE 2. Landmarks in the body

	Fetus and adult		Embryo	
	From	To	From	To
Upper arm_{bm}	Acromiale	Lateral epicondyle	The most rostral point of the root of the upper limb	Middle point of the elbow
Upper arm_{a}	Acromiale	Radiale		
$\text{Forearm}_{\text{bm}}$	Lateral epicondyle	Stylion	Middle point of the elbow	Middle point of the wrist
$\text{Forearm}_{\text{a}}$	Radiale	Stylion		
Hand	Stylion	Dactylion	Middle point of the wrist	Tip of the upper limb bud
Thigh	Trochanterion	Knee joint	The most rostral point of the root of the lower limb	Middle point of the knee
Calf	Knee joint	Sphyrion	Middle point of the knee	Middle point of the ankle
Foot	Pternion	Acropodion	Middle point of the ankle	Tip of the lower limb bud
Head	Vertex	Suprasternale	Head height + ear-shoulder length	
Trunk	Suprasternale	Symphysion	The most rostral point of the root of the upper limb	The most rostral point of the root of the lower limb
Lower limb	Trochanterion	Sole	The most rostral point of the root of the lower limb	The tip of the lower limb

upper arm and forearm were measured by the following landmarks: acromiale, radiale, and stylion (Zatsiorsky, 2002). In the upper limbs_{bm}, the epicondyle was used as the landmark instead of the radiale, because the epicondyle is the approximate elbow joint (Zatsiorsky, 1998; Stokdijk et al., 1999; Anglin and Wyss, 2000; Venture et al., 2006; Table 2). Some of these lengths correspond to the upper arm and forearm lengths that were measured in the human embryos (Fig. 2). We defined a new ratio (see Supporting Information) for the upper limb and shoulder girdle; this ratio was termed as the "triple-ratio of five landmarks" to quantify the relationship between the lengths of four consecutive limb sections. The triple-ratio was defined for the five arbitrary points *p, q, r, s,* and *t* as the following:

$$\frac{|p-r|\cdot|q-s|\cdot|r-t|}{|q-r|\cdot|r-s|\cdot|p-t|}\quad \text{(see Supporting Information).}$$

For the upper limb, we denoted this triple-ratio as the triple-ratio of the upper limb_{tri}, which was calculated using the half-bitrochanteric breadth and the upper arm_{bm}, $\text{forearm}_{\text{bm}}$, and hand lengths. Note that there is a Möbius invariance of the triple-ratio, which is similar to that of the cross-ratio (see Appendix). If the cross-ratios of the upper limb_{bm} and shoulder girdle, and the triple-ratio of the upper limb_{tri} were invariant during development, the growth of the upper limb_{bm} and shoulder could then be described by a Möbius transformation (see Supporting Information).

The correlation between the cross-ratio of the upper limb and age was examined by regression analysis. We also examined the cross-ratios of the whole body, upper and lower limbs, and shoulder and pelvic girdles between sexes by using Student's t-tests. We plotted standard growth curves for the embryonic and fetal cross-ratios of the whole body, upper and lower limbs, and shoulder and pelvic girdles with a 95% confidence interval around each curve, as calculated by regression analysis. We examined the difference in the cross-ratios between fetuses and adults by using Mann–Whitney U-tests, because some data did not have a normalized distribution.

Relationship Between the Cross-Ratio and the Proportion of Body Parts

We examined the relationship between the cross-ratio and the proportion of body parts during the prenatal period. The differences in the ratios of the first, second, or third part to the total length of the three contiguous parts were examined between the fetuses and adults by using the Kruskal–Wallis test, because many data did not have a normalized distribution. $P < 0.05$ was considered significant in statistical analyses.

RESULTS

Characteristics of the Cross-Ratio

To obtain a better understanding of the cross-ratio, let us examine the surface in Fig. 1B, which illustrates the cross-ratio of the consecutive lengths by the relative length of the middle part (e.g., forearm length/total upper limb length) and the relative length of the proximal part (e.g., the upper arm) to the distal part (e.g., the hand). The shorter the relative length of the middle part (e.g., forearm) is or the more the lengths of the proximal (e.g., upper arm) and distal (e.g., hand) parts are similar, the higher the cross-ratio is as calculated by taking the partial derivatives of the separate lengths in the cross-ratio (Fig. 1B).

Low Cross-Ratio of the Head in an Anencephalic Fetus

The cross-ratio of the head was lower in an anencephalic fetus, which had a smaller height of the vertex-to-nasion, than in the normal fetuses (Fig. 3B).

Cross-Ratios in Adults

ANOVA revealed a significant relationship between these cross-ratios and age in both males and females. However, there was a small difference (<0.015)

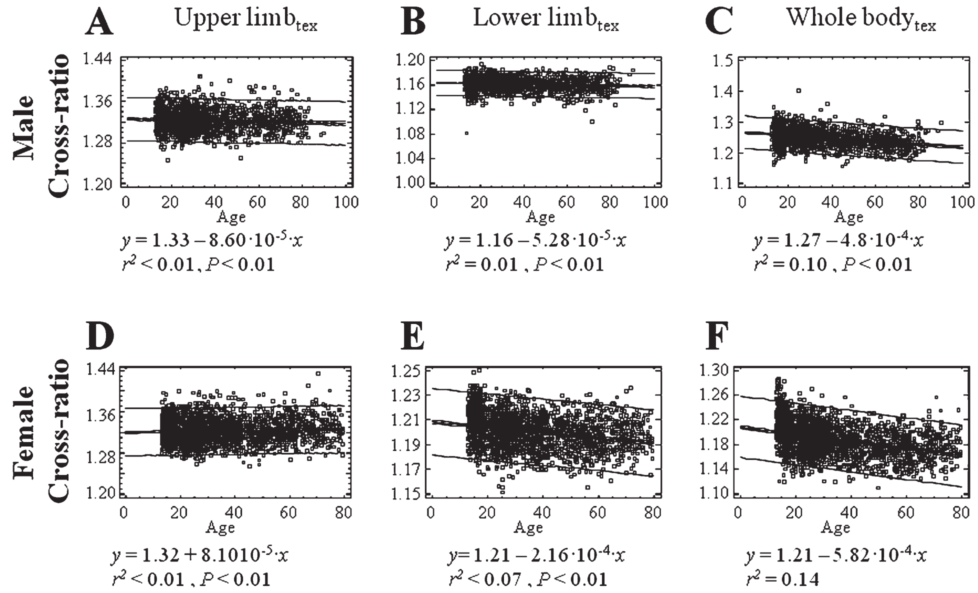

Fig. 4. Relationship between the cross-ratios (*y*) of body parts for textile and age (*x*) in the adolescents and adults in Sweden. There was a small difference (<0.015) between adolescents and older adults in the cross-ratio of the upper (**A** and **D**) and lower (**B** and **E**) limbs according to a regression analysis in both males and females, whereas the difference in the cross-ratio of the whole body was 0.04 between them (**C** and **F**). The cross-ratio of the upper limb$_{tex}$, lower limb$_{tex}$, and whole body$_{tex}$ were 1.32 (0.02), 1.16 (0.01), and 1.25 (0.03) for males (A, B, and C), and 1.32 (0.02), 1.20 (0.01), and 1.19 (0.03) for females (D, E, and F). ANOVA revealed significant relationships between the cross-ratios and age ($P < 0.01$), except for that of the whole body in females. Males: A–C, Females: D–F.

TABLE 3. The cross- and triple-ratios of the body portions in Japanese people

		Male	Female
Upper limb$_{bm}$	Adult	1.29 (0.01), N = 9	1.29 (0.02), N = 5
Upper limb$_{a}$	Adult	1.31 (0.01), N = 15	1.32 (0.03), N = 15
Lower limb	Adult	1.28 (0.02), N = 15	1.28 (0.02), N = 15
Shoulder girdle	Adult*	1.24 (0.01), N = 18	1.23 (0.02), N = 16
	Fetus	1.25 (0.05), N = 57	1.24 (0.04), N = 33
Pelvic girdle	Adult	1.14 (0.01), N = 15	1.15 (0.02), N = 15
Whole body	Adult	1.32 (0.02), N = 15	1.33 (0.03), N = 15
Upper limb$_{tri}$	Adult	1.72 (0.04), N = 9	1.71 (0.02), N = 5

Value = Mean (SD).
*$P < 0.05$.

according to the regression equation of the upper and lower limbs. This small deviation from a constant value can be described as a linear function with respect to age (Fig. 4). The cross-ratio of the whole body$_{tex}$ largely decreased with age (Fig. 4C,F).

No significant difference was observed in the cross-ratios of the upper limb$_{bm}$, upper limb$_{a}$, lower limb, pelvic girdle, or whole body between the Japanese adult male and female groups. In addition, there was no significant difference in the triple-ratio of the upper limb$_{tri}$ between these two groups (Table 3), although there was a significant difference in the shoulder girdle according to the Student's *t*-test ($P < 0.05$; Table 3).

Developmental Changes in the Cross- and Triple-Ratios from Human Embryos to Adults

We calculated the cross-ratios of the upper and lower limbs, shoulder and pelvic girdles, and whole body in human embryos and fetuses (Fig. 5). Large variances were observed in the cross-ratios of the upper and lower limbs, and shoulder and pelvic girdles of human embryos whose CRLs were less than 23 mm (Fig. 5B,C). The cross-ratio of the whole body increased during the embryonic period (Fig. 6A). Regression analysis revealed that the standard growth curve of the cross-ratio of the whole body in the embryos could be approximated by a basic trigonometric function (Fig. 6A, Table 4). In the fetus, there was no significant difference in the cross-ratio of the shoulder girdle (Table 3), whole body, upper and lower limbs, pelvic girdle, or the triple-ratio of the upper limb (data not shown) between males and females.

Regression analysis revealed no significant correlation between the cross-ratio and CRL in the upper limb$_{bm}$; however, there was a significant correlation between the cross-ratio and CRL in the upper limb$_{a}$. The cross-ratio of the upper limb$_{a}$ increased linearly with the increase in CRL during the fetal period (Fig. 6C, Table 4), and decreased with age during childhood after birth toward the adult value (1.32; Fig. 5D). The cross-ratios of the shoulder girdle [Mean (SD); 1.24 (0.04)] (Fig. 6D, Table 4) and the upper limb$_{bm}$ [1.31 (0.04)] (Fig. 5C, Table 4) were invariant during the fetal period. The triple-ratio of the upper limb$_{tri}$ was constant [1.76 (0.08)] (Fig. 7A) in addition to the constancy observed in the cross-ratio of the upper limb$_{bm}$ and shoulder girdle during the fetal period. However, this triple-ratio was not close to the golden triple (1.89), which corresponds to the golden ratio (see Supporting Information). The cross-ratios of

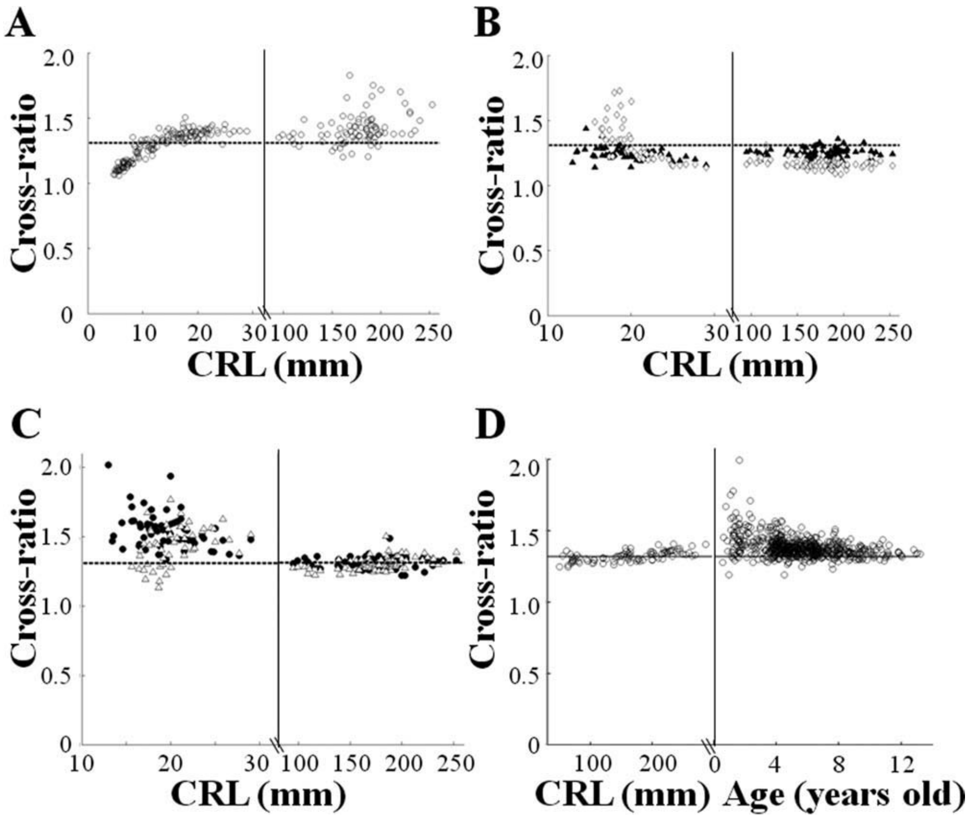

Fig. 5. Developmental changes in the cross-ratios of body parts. **A**: The cross-ratio of the whole body (○) increased during the embryonic period. **B**: The cross-ratio of the shoulder girdle (▲) decreased during the embryonic period; however, it was constant during the fetal period. The cross-ratio of the pelvic girdle (◇) decreased during the prenatal period. **C**: The cross-ratio of the upper limb$_{bm}$ (●) and lower limb (Δ) had a large variance during the embryonic period. The cross-ratio of the upper limb$_{bm}$ was constant and close to the golden wurf during the fetal period. **D**: The cross-ratio of the upper limb$_{a}$ increased during the fetal period and decreased in childhood such that it reached the adult cross-ratio (1.32). The dotted horizontal line shows the golden wurf in panels A–C, and the solid horizontal line in D shows the adult cross-ratio of the upper limb$_{a}$.

the upper limb$_{bm}$ (Fig. 8D) and the triple-ratio of the upper limb$_{tri}$ (Fig. 7B) were significantly higher in fetuses than in adults.

There was a significant correlation between the fetal age and the cross-ratios of the upper limb$_{a}$, lower limb, pelvic girdle, and the whole body (Table 4). With the increase in CRL (x), the cross-ratio (y) of the whole body increased in a manner similar to that of the lower limb, but the cross-ratio of the pelvic girdle decreased during the fetal period (Table 4). Robust regression has been found to be more stable with respect to outliers in the data set (Rousseeuw and Leroy, 1987) than regression using the least squares method. By using robust regression, we observed a relationship between fetal CRL or child age and the cross-ratios of the upper limb$_{a}$ in childhood, the whole body, lower limb, and pelvic girdle (Figs. 5D, 6B,E,F, and Table 4) during the fetal period. The cross-ratios of the whole body, lower limb, and pelvic girdle were higher in fetuses than those in adults (Fig. 8A–C).

The Proportion of Body Parts

Kruskal–Wallis tests revealed significant differences in the ratios of body parts to the total length in the whole body ($P < 0.01$), upper limb$_{bm}$ ($P < 0.01$), lower limbs ($P < 0.01$), and pelvic girdle ($P < 0.01$) between the fetuses and adults (Table 5). Regarding the shoulder girdle, Kruskal–Wallis tests revealed a significant difference in the ratios of the half-biacromial breadth, a, the upper arm, b, and forearm lengths, c, to total length between the fetuses and adult females, and between the adult males and females (Table 5). In addition, the ratios of the half-biacromial breadth (a) and the upper arm (b) to total length in the shoulder girdle were significantly lower and higher, respectively, in adult females than those in fetuses or adult males ($P < 0.05$; Table 5).

DISCUSSION

Möbius Growth of the Body Parts

Petukhov (1989) preliminarily calculated the cross-ratios of the upper-part–torso–lower-part, the shoulder–forearm–wrist, and the hip–shin–foot. He reports all these values to be around 1.31, and that the cross-ratios from the fetuses to adults are invariant; he terms this value "the golden wurf." In the present study, with the exception of the upper limb$_{bm}$ during the fetal period, we obtained different results for the cross-ratio values.

The cross-ratios of the upper limb$_{bm}$ and shoulder girdle, and the triple-ratio of the upper limb$_{tri}$ were

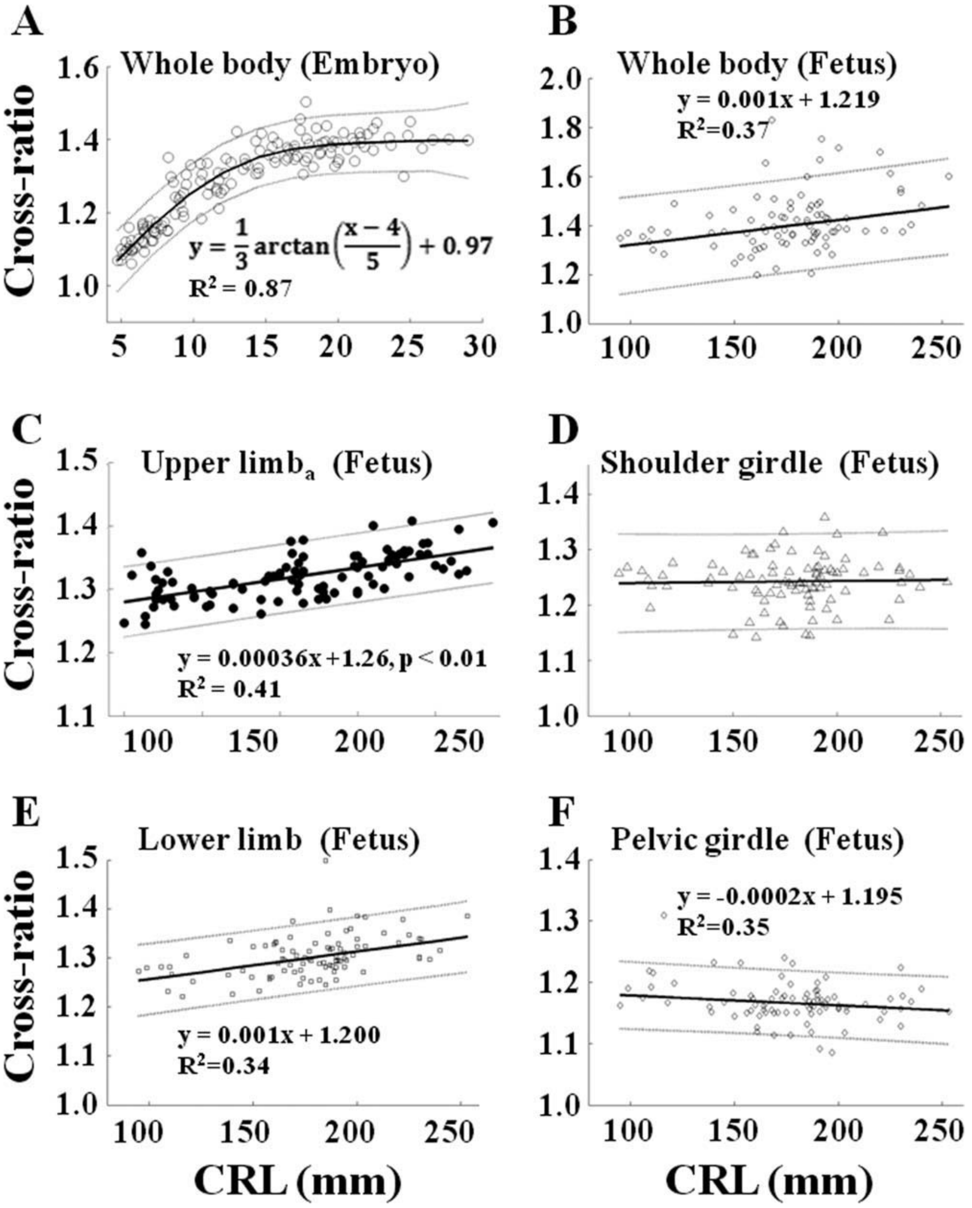

Fig. 6. Regression analysis of the cross-ratio in the prenatal period. Regression analysis revealed that the standard growth curve of the cross-ratio of the whole body in the embryo (**A**) was approximated by a trigonometric function; however, the cross-ratio of the whole body in the fetus increased linearly (**B**). The cross-ratios of the upper limb$_a$ (**C**) increased linearly, whereas the shoulder girdle (**D**) was invariant [1.24 (0.04)] in the fetus. The cross-ratio of the lower limb (**E**) increased, while that of the pelvic girdle (**F**) decreased during the fetal period. Dotted lines show 95% confidence intervals.

constant during the fetal period. These results may indicate that the morphological growth of the upper limb$_{bm}$ and shoulder girdle can be described using a sequence of Möbius functions during the fetal period and we can say that the upper limb$_{bm}$ and shoulder girdle exhibit Möbius growth (see Supporting Information). The five landmarks (the dactylion, stylion, epicondyle, acromion, and the bisector of the distance between the acromions) could be mapped by a Möbius transformation between different gestational ages (see Supporting Information).

In contrast, the cross-ratio of the upper limb$_a$ continues to change throughout the fetal period and in childhood. The upper arm, forearm, and hand lengths in the upper limb$_a$ correspond to the anatomical lengths; the anatomical lengths of the upper arm and forearm are approximate to the humeral and radial lengths, respectively (Zatsiorsky, 2002). The developmental change in the cross-ratio of the upper limb$_a$ suggests that the anatomical growth of the upper limb is more complicated than Möbius growth alone; this is in contrast to the statement by Petukhov (1989).

TABLE 4. Regression analysis of the cross-ratio during development

	Age	Regression equation of cross ratio	*P*	r^2
Upper limb$_{bm}$	Fetus	–	0.908	–
Upper limb$_{a}$	Fetus	$y = 3.60 \times 10^{-4}x + 1.26$	<0.01	0.41
		$y = 3.69 \times 10^{-4}x + 1.26^{\dagger}$		$0.38^{\dagger}$
	Childhood	$y = 0.20e^{-0.24x} + 1.30e^{0.002x\dagger}$		0.17
		$y = 0.10e^{-0.27x} + 1.35e^{-0.001x\dagger}$		$0.49^{\dagger}$
Shoulder girdle	Fetus	–	0.808	–
Lower limb	Fetus	$y = 6.01 \times 10^{-4}\,x + 1.20$	<0.01	0.20
		$y = 5.65 \times 10^{-4}\,x + 1.20^{\dagger}$		$0.34^{\dagger}$
Pelvic girdle	Fetus	$y = -2.76 \times 10^{-4}\,x + 1.22$	0.01	0.08
		$y = -1.60 \times 10^{-4}\,x + 1.20^{\dagger}$		$0.35^{\dagger}$
Whole body	Embryo	$y = \frac{1}{3}\arctan(\frac{x-4}{5}) + 0.97$		0.87
	Fetus	$y = 1.21 \times 10^{-3}\,x + 1.20$	<0.01	0.11
		$y = 1.02 \times 10^{-3}\,x + 1.22^{\dagger}$		$0.37^{\dagger}$

x, CRL in the fetus and embryo or age in childhood; *y*, cross-ratio; –, non-calculated;
†, The values in the robust linear regression.

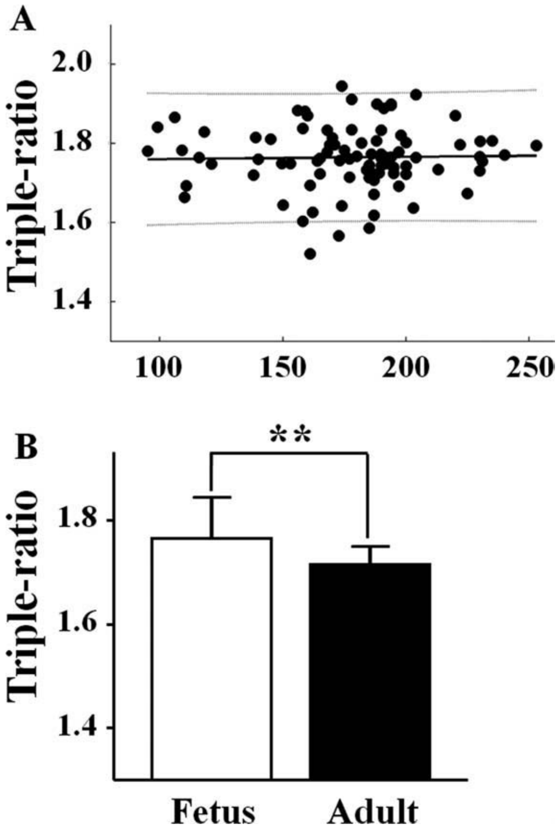

Fig. 7. Developmental change in the triple-ratio of the upper limb$_{tri}$. This ratio was calculated by the half width of the shoulder girdle and the lengths of the upper arm, forearm, and hand. **A**: Regression analysis revealed that the triple-ratio was constant during the fetal period. Dotted lines show 95% confidence intervals. **B**: The triple-ratio was significantly larger in fetuses than in adults. $^{**}P < 0.01$.

Differences in the Cross-Ratio Between Developmental Stages or Sexes

We observed a significant difference in the cross-ratio of the shoulder girdle between males and females in adults but not in fetuses (Table 3). This ratio was significantly higher in fetuses than in female adults, indicating that lateral growth from the mid-sagittal plane in the shoulder girdle is cross-ratio invariant during the fetal period but not after birth. In adults, the ratio of the half-biacromial breadth to the upper arm$_{bm}$ was significantly higher in males [0.703 (0.039)] than in females [0.658 (0.038)] (Student's *t*-test, $P < 0.01$). The higher cross-ratio of the shoulder girdle in males than in females led by the relatively larger shoulder breadth in the upper limb in males, suggests that the shoulder girdle structure is optimized to draw more arm and shoulder power in males than in females after infancy. This hypothesis is corroborated by the following reports: female weight lifters have larger biacromial breadths than non-athlete women (Devi, 2006), and one repetition of maximum bench-press strength is significantly correlated with the biacromial breadth in 57 females who had not undergone any muscular strength training for at least three months (Cummings and Finn, 1998); Malina and Zavaleta (1976) reported that the index calculated by the equation [3 × biacromial breadth – bicristal breadth] is greater in female shot putters and javelin and discus throwers than in female runners and non-athletes as well as being greater in non-athlete males than in non-athlete females.

Changes in the Cross-Ratio Corresponding to Changes in the Proportion of Body Parts

The cross-ratios of the whole body, shoulder, and pelvic girdles and lower limb were higher in fetuses than in adults in our study. These results suggest that at least one of the following two situations occurs: (1) the relative length of the middle part is shorter in fetuses than in adults or (2) the lengths of the proximal and distal parts are more similar in fetuses than in adults, as observed when taking partial derivatives of separate lengths in the cross-ratio (Fig. 1B).

According to fact (1), the large growth of the upper arm after birth may contribute to the low cross-ratio of the shoulder girdle in adults. Similarly, the large growth of the thigh may contribute to the low cross-ratio of the pelvic girdle in adults. With regard to the lower limb or whole body, the low cross-ratio in adults may be due to the dramatic decrease in the ratio of the foot or head length to the total lower-limb length or stature, respectively, in accordance with fact (2).

Thus, the upper limb, lower limb, shoulder girdle, pelvic girdle, and whole body grow disproportionally such that the cross-ratio decreases with respect to Möbius transformations after birth.

Evaluation of the Growth Balance of the Whole Body in the Organogenetic Period

The standard growth curve of the cross-ratio of the whole body was well approximated by a trigonometric function, and its regression coefficient was 0.88. The proportion of the vertex-to-suprasternale, trunk, or lower limb height varied dramatically in the embryonic stages; their cross-ratios may reflect these changes. These results suggest that the growth of body parts in the embryonic period cannot be described by Möbius transformations. The embryo has a relative large head in the early stages, and the lower limb bud appears only at Carnegie stage 13 (O'Rahilly and Müller, 2001a). The ratios of the head and trunk heights to lower limb height decreased noticeably during the embryonic period, suggesting that the lower limb grows more rapidly than the head and trunk. Because of this dramatic proportional change, the growth of body parts in the organogenetic period is too complicated to be analyzed; however, the examination of cross-ratios can be a simple way to evaluate this growth. In fact, we can examine the cross-ratio number of the whole body with its standard curve in two-dimensional space despite the dramatic changes in four variables, namely, the vertex-to-suprasternale, trunk, and lower limb heights, and CRL. Morphological growth profiles in the embryonic period have been previously described and evaluated using mostly non-metric surface structures (O'Rahilly and Müller, 2001b), with the exception of a few metric studies (Tanaka, 1976, 1991; Otani et al., 2008). The cross-ratios may be a useful parameter for metric description and evaluation of complicated morphogenesis. The confidence interval of the standard curve of this cross-ratio is easily determinable unlike multidimensional regression analysis, because this curve is one-dimensional. This suggests that the growth balance of body parts can be compared easily between individuals by using the cross-ratio. An abnormal balance of body growth may be detected by using this simple statistical method.

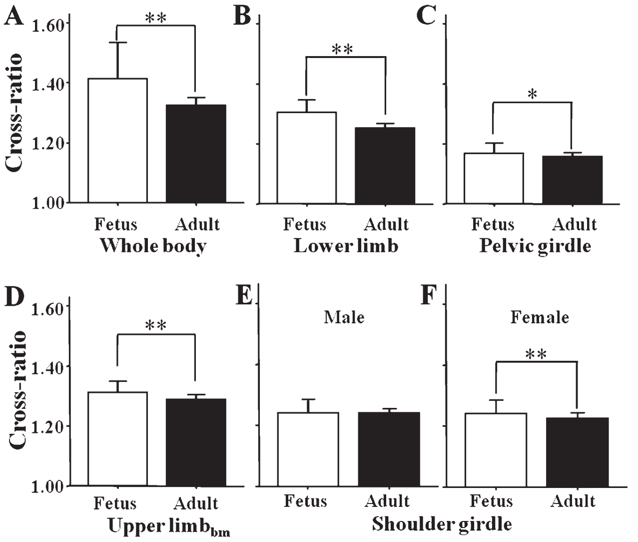

Fig. 8. Comparison of the cross-ratio of body parts between human fetuses and adults. The cross-ratios of the whole body (**A**), lower limb (**B**), pelvic girdle (**C**), and upper limb$_{bm}$ (**D**) were significantly larger in fetuses than those in adults. In the shoulder girdle, the cross-ratio was significantly larger in fetuses than that in female adults (**E**) but not male adults (**F**). $^{*}P < 0.05$, $^{**}P < 0.01$.

Detection of Growth Imbalance of the Body Parts Using the Cross-Ratio

The length or ratio of two lengths of body parts is often compared in clinical diagnoses (e.g., head vs. abdomen circumference). Morphology is diagnosed as abnormal if the (relative) length is below the 5th or above the 95th percentile of the normal distribution. However, in addition to the (relative) length of a given part, the combined balance of the parts is important for the assessment of morphological development. Since we found a relatively low cross-ratio of the head in an anencephalic fetus, the imbalance of body parts can be detected by the cross-ratio (Fig. 3B). In Chiari malformation, the cerebellar tonsils, inferior vermis, pons, and medulla oblongata are displaced through the foramen magnum into the cervical vertebral canal (Kinsman and Johnston, 2007). Therefore, it might be possible to diagnose disorders such as Chiari malformation by using the cross- or triple-ratios if we define proper landmarks in the brain including the cerebellum and medulla oblongata.

TABLE 5. The ratios of the body parts to the total length

		a	*b*	*c*
Upper limb$_{bm}$	Fetus	0.389 (0.025)	0.339 (0.018)	0.272 (0.023)
	Adult	0.393 (0.010)	0.350 (0.008)**	0.257 (0.011)**
Shoulder girdle	Fetus	0.276 (0.031)	0.387 (0.030)	0.337 (0.018)
	Adult male	0.271 (0.011)	0.386 (0.008)	0.343 (0.008)*
	Adult female	0.261 (0.009)**,§§	0.397 (0.014)*,§	0.342 (0.013)
Lower limb	Fetus	0.371 (0.023)	0.347 (0.023)	0.282 (0.018)
	Adult	0.411 (0.017)**	0.352 (0.012)	0.237 (0.009)**
Pelvic girdle	Fetus	0.178 (0.022)	0.425 (0.028)	0.397 (0.024)
	Adult	0.167 (0.012)**	0.449 (0.018)**	0.376 (0.015)**
Whole body	Fetus	0.317 (0.047)	0.301 (0.040)	0.381 (0.029)
	Adult	0.192 (0.009)**	0.301 (0.014)	0.507 (0.016)**

Value = Mean (SD). $^{*}P < 0.05$, $^{**}P < 0.01$ in comparison with the fetal ratio by Kruskal–Wallis *U* test. $^{\S}P < 0.05$, $^{\S\S}P < 0.01$ in comparison with the adult male ratio by Kruskal–Wallis test.

Age-Related Changes in the Cross-Ratio

The small magnitude of change observed in the cross-ratio of the upper and lower $\text{limbs}_{\text{tex}}$ by regression analysis suggests that these cross-ratios are nearly constant across all ages and/or generations after adolescence. The difference in the cross-ratio of the whole body_{tex} in males was ~0.03 between 20- and 80-year-old people. Deformities of the vertebrae and vertebral discs lead to high cross-ratios due to the shortening of the middle part of the body (i.e., the trunk; Fig. 1B). A lower cross-ratio of the whole body_{tex} in the older generation than in the younger one suggests that the age-related change in the cross-ratio depends on the change in body proportions over the generations of the last 70 years rather than on the aging of the vertebral column described above.

Geometric Morphometry and the Cross- and Triple-Ratios

Isometric and allometric methods are used for assessing morphological development of humans (Jones et al., 1986). Although growth curves using one parameter (e.g., body weight, femoral length, or head circumference) are described by these methods, the relative and geometric growth rates among body parts have not been examined. Multivariate statistical analyses with linear distance measurements began to be used to describe patterns of shape variation among groups in the 1960s and 1970s (Adams et al., 2004). Multivariate analyses can reveal differences or similarities in the growth patterns among body parts (e.g., organ sizes; Udagawa et al., 2010). However, it is difficult to make a growth curve that describes the growth balance of body parts and assess it quantitatively or geometrically. Recently developed landmark-based methods such as generalized Procrustes analysis have revealed morphological variations and differences in body parts such as the skull, scapulae, and femurs among vertebrates (Bookstein, 1996; Slice, 2007). Ontogenic morphological differences can be quantified by these methods, in which non-shape variation is eliminated, and the variables representing the shape are compared between objects (Bookstein, 1996; Adams et al., 2004). However, it is difficult to examine the relationship between the proportions of body parts by using these landmark-based methods in contrast to using the cross- or triple-ratios. Recently, the multidimensional growth curve among body parts was developed statistically (Naito et al., 2010). A combination of the cross-ratio and the multidimensional growth curve can examine the proportions of more than three body parts in a simple and precise manner.

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