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ORIGINAL ARTICLE

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Plasma insulin-like growth factor-I, testosterone and morphological changes in the growth of captive agile gibbons (*Hylobates agilis*) from birth to adolescence

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Abstract We examined growth changes in concentrations of plasma insulin-like growth factor-1 (IGF-1) and testosterone, and somatometric parameters in two captive male agile gibbons from birth to about 4 years of age, to examine the evolution of growth patterns in primates. Plasma IGF-1 concentrations in agile gibbons generally increased with age with values ranging from 200 to 1,100 ng/ml. The growth profiles in plasma IGF-1 in the gibbons were similar to those reported for chimpanzees. The highest concentrations of plasma testosterone (230 and 296 ng/dl) were observed within the first 0.3 years from birth, then the concentrations rapidly decreased and fluctuated below 100 ng/dl. Continuously higher IGF-1 concentrations were observed after 2.6 and 3.5 years of age. The profiles of plasma testosterone in these gibbons also resembled those of other primates including humans. However, their plasma testosterone levels in both neonate and adult stages (60 ng/dl) were lower than those reported for macaques and chimpanzees of respective stages. The obtained growth profiles of plasma IGF-1 and testosterone suggest that the adolescent phase starts around 2.6 or 3.5 years of age in male agile gibbons. The growth trend in many morphological parameters including body weight showed a linear increase without a significant growth spurt at approximately the onset of puberty. Head length and first digit length had reached a plateau during the study period. Brachial index, which indicates the relative length of forearm to upper arm, significantly increased gradually through the growth period. This result indicates that forearm becomes relatively longer than the upper arm with growth, which may be an evolutionary adaptation for brachiation.

Keywords Gibbon · Growth · Insulin-like growth factor-1 · Somatometry · Testosterone

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Introduction

Despite the importance of somatic growth data in gibbons, existing literature on the evolution of the growth pattern in primates is limited. Exceptional studies were made on dental eruption by Smith et al. (1994) and on body weight by Sawina and Orpachowa (1981), Linke (1988), Araki et al. (1989), and Leigh and Shea (1995).

To compare the growth profiles in primates, it is most important to define the age at reproductive maturation as one of the essential time-markers in the life-cycle. In primates, somatic maturation and reproductive maturation are not always concurrent (Smith 1992). This is why the adolescent phase of growth is inserted between juvenile and adult phases in higher primates (Bogin 1999). Puberty is the growth phenomenon marking the onset of the adolescent phase in higher primates. However, literature on reproductive maturation of gibbons in particular is meager at best, with the exception of a report dealing with the age of sexual maturation in captive gibbons by Geissmann (1991). Re-evaluating the previous studies dealing with reproduction in *Hylobates*, he concluded that gibbons, both wild and captive, usually become sexually mature between 6 and 8 years of age. It is not certain, however, that this age corresponds either to that at the onset or to that at the completion of sexual maturation.

Both somatometric and physiological data are necessary to determine the adolescent phase in gibbons. This is because gibbons do not show such remarkable morphological changes with reproductive maturation like macaques or chimpanzees (e.g., swelling of sexual

skin). Our previous study revealed a close functional relationship between insulin-like growth factor-1 (IGF-1) and skeletal growth in Japanese macaques (*Macaca fuscata*) (Suzuki et al. 2000). We also confirmed that the adolescent phase of the macaque males begins in the summer at 3 years of age, as shown from the profiles of IGF-1 and testosterone secretion (Suzuki et al. 2000). Plasma IGF-1 has been identified as one important hormone that maintains somatic growth in primates (Copeland et al. 1982, 1984, 1985; Humbel 1984; Wilson et al. 1984; Martin 1985; Wilson 1986). Gonadal steroids have been analyzed to determine the sexual maturation or reproductive potential of macaques (Nigi et al. 1980; Wilson et al. 1984, 1986), baboons (Copeland et al. 1984), chimpanzees (*Pan troglodytes*) (Copeland et al. 1985), and humans (Martin 1985).

In the present report, we made a longitudinal study of endocrinological and morphological parameters relating to the growth of two male agile gibbons (*Hylobates agilis*) from birth to adolescence. We traced the progress of reproductive maturation via the profiles of plasma IGF-1 and testosterone. To clarify the characteristics of somatic growth, we used somatometry on linear dimensions and body weight. We also analyzed the age-related changes in the limb indices, such as brachial index and intermembral index, as gibbons apparently have the largest indices among non-human primates (Napier and Napier 1967) for the adaptation to brachiation.

Methods

This study was approved by the Animal Welfare and Animal Care Committee of the Primate Research Institute, Kyoto University. Routine care of gibbons and experiments were performed in accordance with guidelines of the Institute.

Animals and rearing conditions

Two male agile gibbons (Ha3 and Ha4) used in this study were born in 1998 and 1999 respectively, and were reared at the Primate Research Institute. They were siblings from Ha1 (father) and Ha2 (mother). They were artificially nursed, since their mother failed to suckle them. They were first reared in incubators: the elder (Ha3) for 7 months from birth and the younger (Ha4) for 9 months from birth. Subsequently, both were reared indoor in individual cages, constructed of stainless steel frames 0.85 m high with 0.6 m^2 floor space or 1.50 m high with 0.975 m^2 in a room with a temperature range between 25 and 30°C; Ha3 and Ha4 spent 27 months and 17 months in these cages, respectively, after birth. Then they were reared together with their mother in an indoor group cage, which was framed stainless steel 2.5 m high with 11.27 m^2 floor space. They were nursed with a commercially available formula-milk (Meiji Dairies, Tokyo, Japan). Weaning (i.e., eating ordinary diets described below) began at 0.3 years of age in both gibbons and terminated at 2.0 and 1.2 years of age for Ha3 and Ha4, respectively. Both were fed commercial monkey-chow (Oriental Yeast Co., Tokyo, Japan) daily with a supplement of fruits and vegetables (bananas, apples, grapes, persimmon, sweet potatoes and cabbage).

A pair of adult white-handed gibbons (*Hylobates lar*), Hl9 (female) and Hl10 (male), were also used in the present study. They were cared for under the same conditions, i.e., in an indoor group cage, framed stainless steel 2.5 m high with 11.27 m^2 floor space. All adult gibbons were born in the wild and their case histories prior to introduction to our facilities are unclear. They were older than 26 years of age at the period of examination.

Blood sampling

Until the two gibbons reached 1 year of age, 0.5 ml blood samples were taken with syringes containing 1% sodium heparin once or twice a month without anesthesia. When they were between 1 and 2 years of age, 1.0 ml blood samples were drawn once or twice a month under anesthesia. After 2 years of age, blood collection was performed simultaneously with somatometry once a month under anesthesia. They were anesthetized by an intramuscular injection of ketamine-hydrochloride (1.25 mg/kg body weight; Sankyo, Tokyo, Japan) and medetomidine-hydrochloride (0.05 mg/kg body weight; Meiji Seika Kaisha, Tokyo, Japan). All procedures were carried out between 1330 and 1400 hours. They were not fed before blood sampling and/or somatometry. Blood samples were drawn once from the four adult gibbons under anesthesia in the same manner as the two immature gibbons. Plasma samples were stored at −30°C until assayed for IGF-1 and testosterone.

Somatometry

Two immature subject gibbons were measured somatometrically from 2.2 to 3.8 years of age on Ha3 and 1.2 to 2.8 years of age on Ha4 once a month. Body weight was measured simultaneously with blood sampling from 0 to 3.8 years of age on Ha3 and to 2.8 years of age on Ha4. A total of 27 somatometric parameters, which are classified into head, face, trunk, and limb groups, listed in Table 1, were measured with instruments used for humans. The obtained data (mm) omit the figures below the first decimal place. The measurement method of Martin and Saller (1957) incorporating the modifications of Iwamoto (1971) was followed.

Two limb indices, namely, brachial index and intermembral index, were calculated from measurement of limb segments as follows (Martin and Saller 1957; Ashley-Montagu 1960):

Brachial index (%) = Forearm length × 100/Upper arm length, and Intermembral index (%) = (Upper arm length + Forearm length) × 100 / (Thigh length + Leg length).

Hormone assays

Plasma IGF-1 and testosterone were measured with the enzyme immunoassay (EIA) kit for human IGF-1 (R&D Systems, Minneapolis, USA) and with the radioimmunoassay (RIA) kit (Testosterone 'Eiken', Eiken Chemical Co., Tokyo, Japan) for humans, respectively, after extraction. Detailed procedures have been reported previously (Suzuki et al. 2000). All samples were determined in duplicate. The ranges of the assays were 32.5–2,000 pg/ml for IGF-1 and 0.125–4 ng/ml for testosterone. Inter- and intra-assay coefficients of variation were less than 10% and 12% for IGF-1 and testosterone, respectively.

Data analyses

The plasma IGF-1 concentrations measured with EIA in this study were transformed by a linear regression formula for comparison with those in our previous reports determined with RIA (Suzuki et al. 2000, 2001). This linear regression formula was calculated from the values obtained both by EIA and RIA using the same control samples. The formula for transformation was as follows:

$$\text{IGF} - 1 \text{ concentration (RIA)} = \text{IGF} - 1 \text{ concentration (EIA)} \times 2.784 \quad (r^2 = 1.0)$$

Peaks in the plasma IGF-1 profiles are defined as follows: marked elevation (denoted by arrowheads in Fig. 1) which is higher

Table 1 Summary of somatometric data of male agile gibbons from birth to adolescent phase. Somatometric parameters were adopted from Martin and Saller (1957). Numbers in parentheses correspond to those used by these authors. Three additional limb-related paremeters, namely, foot breadth, 1st toe length, and 3rd toe length, were chosen from Iwamoto (1971). All data, excluding body weight, are expressed in mm. Body weight is expressed in grams

Gibbon	Ha3					Ha4				
Age (year)	2.21	2.54	3.03	3.53	3.75	1.23	1.56	2.05	2.55	2.77
Somatometric parameter										
(A) Head										
Head length (1)	81	81	82	83	83	80	81	83	84	83
Head breadth (3)	70	71	71	74	73	64	65	67	68	67
Head height (15)	89	87	87	89	87	–	91	95	98	97
(B) Face										
Bizygomatic breadth (6)	63	65	67	69	71	54	57	60	61	63
Bigonial breadth (8)	44	43	46	43	44	38	39	42	43	43
Facial height (18)	43	44	44	47	47	40	42	44	46	46
Upper facial height (20)	26	27	27	30	31	24	26	27	29	26
(C) Trunk										
Sitting height (23)	383	395	405	421	425	350	–	399	411	419
Anterior trunk length (27(1a))	235	238	253	265	264	205	223	240	249	258
Bi-acromial breadth (35)	137	118	109	132	133	103	102	101	121	101
Chest breadth (36)	95	96	99	108	110	85	89	96	100	105
Chest depth (37)	86	86	84	85	89	66	71	75	82	83
Bi-iliac breadth (40)	87	90	94	94	97	74	77	81	88	87
Bitrochanteric breadth (42)	100	102	108	115	115	85	89	100	105	110
Chest girth (61)	318	330	346	358	359	280	296	316	337	343
(D) Limbs										
Upper arm length (47)	178	189	193	206	205	159	173	193	201	213
Forearm length (48)	196	201	211	225	233	163	180	197	223	225
Hand length (49)	141	151	157	162	165	128	141	148	158	162
Hand breadth (52)	35	36	35	39	38	31	33	36	36	36
First digit length (51a)	–	34	36	33	31	30	29	33	36	34
Third digit length (51)	83	85	89	90	91	76	78	85	92	91
Thigh length (55(1))	169	178	185	192	197	148	160	172	187	193
Leg length (56a)	144	155	160	169	170	125	138	156	169	165
Foot length (58)	133	137	141	146	147	119	128	136	144	146
Foot breadth	29	29	29	31	33	27	29	29	31	32
First toe length	33	33	35	34	36	30	34	36	36	38
Third toe length	57	65	59	62	61	52	56	60	64	63
Body weight (71)	3,400	3,730	4,010	4,580	4,720	2,320	2,800	3,320	3,900	3,940

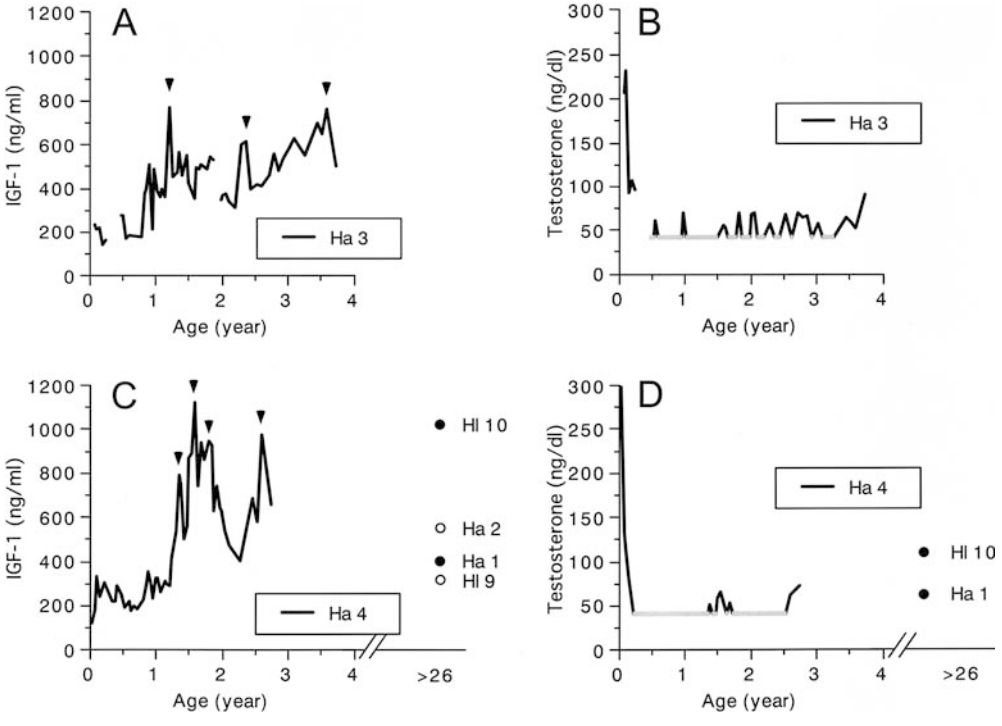

Fig. 1A–D Age-related changes in plasma IGF-1 and testosterone levels in captive-born male agile gibbons. **A** Change in plasma IGF-1 in Ha3. **B** Change in plasma testosterone in Ha3. **C** Change in plasma IGF-1 in Ha4. **D** Change in plasma testosterone in Ha4. The data for adult gibbons are indicated at the >26 year point in **C** and **D**. Ha1, adult male agile gibbon; Ha2, adult female agile gibbon; Ha3, elder captive-born agile gibbon; Ha4, younger captive-born gibbon; Hl9, adult female white-handed gibbon; Ha10, adult male white-handed gibbon. *Arrowheads* indicate identified peaks of plasma IGF-1 level

than mean by 1 SD, and an increase having more than 1 SD unit from the nadir point of the graph. To determine the tendency of the age-related changes in limb proportions, simple regression was calculated with a method of least squares between index and age. All statistical analyses were performed by Excel (Microsoft, Tokyo, Japan) and DeltaGraph (Japan Poladegital Co., Tokyo, Japan). To compare the growth profiles of body weight among apes, body weight (g or kg) was transformed to relative weight (%) of adult weight (RWA). The mean body weight (5.83 kg) of adult male agile gibbons (Jungers 1984) was used to calculate the RWA values.

Results

Changes in the concentrations of plasma IGF-1 and testosterone

Plasma IGF-1 concentrations in both Ha3 and Ha4 generally increased with age with values ranging from 200 to 1,100 ng/ml (Fig. 1A, C). Profiles of plasma IGF-1 concentrations revealed three peaks in Ha3, and four peaks in Ha4. These peaks were seen at 1.2 (765 ng/ml), 2.3 (611 ng/ml), and 3.6 (756 ng/ml)years of age in Ha3, and at 1.4 (784 ng/ml), 1.6 (1,113 ng/ml), 1.8 (940 ng/ml) and 2.6 (969 ng/m)years of age in Ha4. The plasma IGF-1 concentrations of their parents, Ha1 and Ha2, and a pair of white-handed gibbons, Hl10 and Hl9, were 388 ng/ml, 526 ng/ml, 1,004 ng/ml, and 295 ng/ml, respectively.

Plasma testosterone concentrations in immature male gibbons ranged between an undetectable level (lower than 50 ng/dl) and 300 ng/dl (Fig. 1B, D). The highest concentrations of plasma testosterone, 230 ng/dl in Ha3 and 296 ng/dl in Ha4, were observed during the first 0.3 and 0.2 years, respectively, from birth. These neonatal concentrations are 2- or 3-fold higher than those in adult males (Ha1, 60 ng/dl; Hl10, 105 ng/dl). After 0.3 years of age, the concentrations in Ha3 and Ha4 rapidly decreased and fluctuated below 100 ng/dl. The first increase in plasma testosterone after 0.3 years of age was detected at 0.6 years in Ha3 (59.1 ng/dl) and at 1.4 years in Ha4 (50.5 ng/dl). The noticeable frequent peaks in the concentration of plasma testosterone were detected after 1.9 years in Ha3. In contrast, only one peak was detected at 1.6 years of age in Ha4. At other ages examined plasma testosterone concentrations were not detectable. Continuously higher concentrations were observed after 3.5 and 2.6 years of age in Ha3 and Ha4, respectively.

Age changes in body weight

Growth in body weight of the two agile gibbons was almost identical (Fig. 2A) and showed an almost linear increase. In Ha3, body weight increased from 622 g (10.7% of RWA) at 0.1 years, 1,890 g (32.4% of RWA) at 1.0 year, to 4,720 g (81.0% of RWA) at 3.8 years of age. In Ha4, body weight increased from 520 g (8.9% of RWA), 2,000 g (17.5% of RWA), to 3,940 g (67.6% of RWA), at 0.1, 1.0 and 2.8 years of age, respectively.

Growth in linear dimensions

The somatometric values of 27 parameters at the selected ages are shown in Table 1. Many of the measured parameters showed a linear increase between the first and fourth year in Ha3 and Ha4. Though the growth

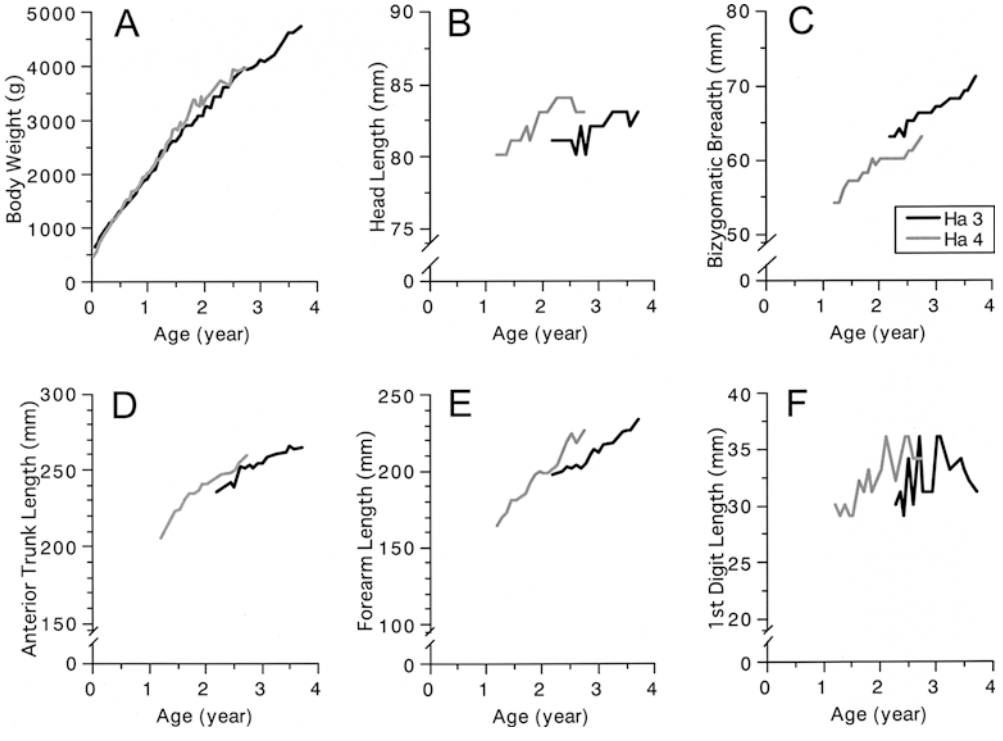

Fig. 2A–F Changes in body weight and five body parameters in captive-born male agile gibbons during the growth period. *Black solid line* indicates Ha3 and *gray solid line* indicates Ha4 in all six (**A–F**) panels. **A** Change in body weight; **B** change in head length; **C** change in bizygomatic breadth; **D** change in anterior trunk length; **E** change in upper arm length; and **F** change in first digit length. Ha3, elder gibbon; Ha4, younger gibbon

pattern of the two gibbons adhered to the above *general pattern*, few parameters had reached a plateau during the study period.

The somatometric parameters were arranged into four groups: (A) head-related, (B) face-related, (C) trunk-related, and (D) limb-related. Growth patterns in each of these groups are briefly noted below:

A. Head-related parameters: growth of parameters in this group, except head length, exhibited the general pattern with a linear increase. Head length reached a plateau at 3.3 years of age in Ha3 and at 2.3 years of age in Ha4 (Fig. 2B). Comparing parameters between both gibbons at the same age, head breadth in Ha3 was greater than Ha4, head length in Ha3 was smaller than Ha4, and head height in Ha3 and Ha4 was the same.
B. Face-related parameters: all parameters belonging to this group increased linearly. Comparing parameters between both gibbons at the same age, bizygomatic breadth in Ha3 was greater than that in Ha4 (Fig. 2C), upper facial height in Ha3 was smaller than that in Ha4, and the remaining two parameters in Ha3 were similar to those in Ha4.
C. Trunk-related parameters: growth of these body components, except bi-acromial breadth, exhibited a linear increase. In contrast, growth in bi-acromial breadth was negligible. Bi-iliac breadth in Ha3 was greater than that in Ha4, chest depth in both gibbons was the same, and the remaining four parameters in Ha3 were smaller than those in Ha4 (Fig. 2D).
D. Limb-related parameters: growth measured by these parameters, except the length of first digit, exhibited the general pattern mentioned above with a linear increase (Fig. 2E). Increase in the length of the first digit stopped by 2.0–2.5 years of age (Fig. 2F). All limb-related parameters, except the first digit length and hand breadth, in Ha3 were smaller than those in Ha4. Length of the first digit and hand breadth in both gibbons were the same.

Age changes in limb proportions

Brachial index (BrI) increased gradually during the growth period studied (both linear regression analyses had statistically significant correlation coefficients, $P < 0.05$). Linear regression formulae (Fig. 3A) were as follows: for Ha3, BrI = 2.74×Age (year) + 101.27, and for Ha4, BrI = 2.75×Age (year) + 98.65.

Intermembral index (IntI) in Ha3 was stable during the examined period. Although that in Ha4 showed an increase, the correlation coefficient of this linear regression was not statistically significant (Fig. 3B). The mean and standard deviation of intermembral index was 118.3 ± 1.8% in Ha3. Linear regression formula for Ha4 was as follows: IntI = 1.70×Age (year) + 116.62.

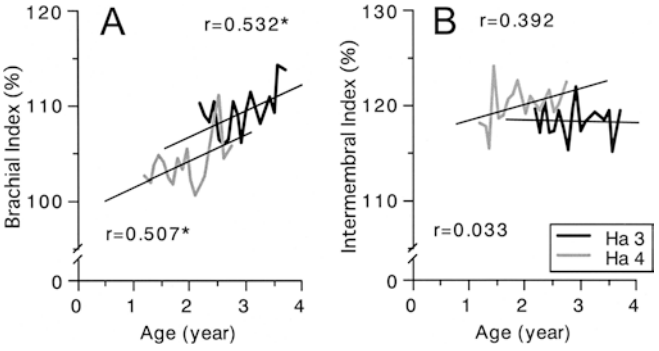

Fig. 3A, B Changes in limb indices in captive-born male agile gibbons. *Black solid line* indicates Ha3 and *gray solid line* indicates Ha4 in both panels. **A** Change in brachial index with linear regression curve; **B** change in intermembral index with linear regression curve. *Asterisk* indicates significant correlation coefficients at $P < 0.05$

Discussion

Plasma IGF-1 and testosterone profiles with growth

The plasma IGF-1 concentrations in gibbons Ha3 and Ha4 varied between 200 and 1,100 ng/ml during the observed growth phase. In adult gibbons, Ha1, Ha2, Hl10 and Hl9, the concentrations were 388 ng/ml, 526 ng/ml, 1,004 ng/ml and 295 ng/ml, respectively (Fig. 1A, C). The mean concentration of plasma IGF-1 in captive adult gibbons, which were classified as the white-handed gibbon group, was 383.13 ± 38.3 ng/ml in females and 344.4 ± 52.4 ng/ml in males with a maximum of 699.3 ng/ml in one male (Suzuki et al. 2001). The plasma IGF-1 levels in the four adult gibbons measured in this study fall within the range of the previous report in gibbons and humans (Sanayama et al. 1984; Tachibana et al. 1993, 1994). Peaks of plasma IGF-1 levels in this study were found in the juvenile and adolescent period, starting from 1 to 1.5 years of age. The highest plasma IGF-1 levels in gibbons, 700 ng/ml or more, was 2- to 3-fold higher than the mean level of all measured IGF-1 levels in each individual. Maximum plasma IGF-1 level of adolescents was nearly 2-fold higher than that in adult male chimpanzees (Copeland et al. 1985; Suzuki et al. 2001) and human males (Sanayama et al. 1984; Tachibana et al. 1993, 1994). Since the growth-related changes in plasma IGF-1 in agile gibbons resemble those of chimpanzees and humans, we may infer that plasma IGF-1 levels in agile gibbons decreases up to 50% after sexual maturation.

Growth profile of the plasma IGF-1 level in the gibbons Fig. 1A, C showed some marked peaks with an interval of about 1 year. These peaks are suggestive of the seasonality of IGF-1 secretion. In addition to the developmental increase, longitudinal data of plasma IGF-1 have shown seasonal fluctuation in adolescent male Japanese macaques (Suzuki et al. 2000). Thus, additional research is necessary to determine the seasonality of plasma IGF-1 concentrations.

Plasma testosterone levels in neonate gibbons determined in this study appear lower than those in neonate macaques (Plant and Zorub 1982; Meusy-Dessolle and Dang 1985; Plant 1985; Suzuki et al., unpublished data) and chimpanzees (Copeland et al. 1985; Marson et al. 1991) but higher than those in humans (Forest et al. 1974). Furthermore, the levels in adolescent or adult gibbons also appear lower than those in macaques (Plant and Zorub 1982; Meusy-Dessolle and Dang 1985; Plant 1985; Suzuki et al. 2000), chimpanzees (Copeland et al. 1985; Marson et al. 1991) and humans (Martin 1985) of corresponding growth stages. Three reasons may account for the lower concentration of plasma testosterone detected in gibbons. Firstly, there is the physiological occurrence of a circadian fluctuation of this hormone. Plasma testosterone levels at night show 2- to 3-fold higher values than those in the daytime in adult male rhesus macaques (*Macaca mulatta*) (Plant and Zorub 1982), and the range of plasma testosterone levels is 200–1,000 ng/dl during a 24-h period with peak amplitudes in the morning in humans (Martin 1985). If one believes that gibbons should also exhibit a circadian fluctuation of testosterone levels such as in macaques or humans, it is reasonable to observe lower concentrations of the hormone in the samples collected in the afternoon. Secondly, testosterone levels can also vary depending on the prevailing social structure of a particular primate species. Macaques and chimpanzees live in multi-male and multi-female units. Contrastingly, gibbons live in a one-male and one-female unit. Thus the difference in reproductive strategy may influence the secretion of reproductive hormones. Thirdly, the lower levels of plasma testosterone in adolescent gibbons may be an outcome of incomplete development of gonadal organs. Testicular function and testis size achieve full maturity during several years from the onset of the adolescent phase in male Japanese macaques (Nigi et al. 1980; Matsubayashi and Mochizuki 1982). Testosterone levels of the first peak were generally less than a half of those for the subsequent year and later on during the adolescent phase in Japanese macaques (Nigi et al. 1980; Suzuki et al. 2000). Thus additional observations of fluctuations in testosterone concentration during the growth phase are needed to confirm these tendencies.

We found the highest concentration of plasma testosterone in neonatal agile gibbons before 0.2 or 0.3 years of age in this study (Fig. 1B, D). High concentrations of plasma testosterone during the first several months of life have been previously reported in rhesus macaques (Plant and Zorub 1982; Meusy-Dessolle and Dang 1985; Plant 1985), Japanese macaques (Suzuki et al., unpublished data), chimpanzees, as well as humans (Forest et al. 1974; Winter et al. 1975). Thus, this is a common feature among catarrhines. It has been suggested that higher concentrations of plasma testosterone during the neonatal period are essential for the development of external genital organs in non-human primates as well as in humans (Katharina et al. 2000).

After the neonatal period, the highest concentrations of this hormone, which were apparently higher than the levels of the sporadic increases, were 89 ng/dl at 3.8 years of age in Ha3 and 70 ng/dl at 2.8 years of age in Ha4. These concentrations are comparable to those of adult gibbons (Ha1, 60 ng/dl; Hl10, 105 ng/dl).

The onset of the sexual maturation process or adolescent phase in agile gibbons

As described above, the growth profiles of plasma IGF-1 and testosterone in agile gibbons were similar to those in other primate species, e.g., Japanese macaques or chimpanzees. Plasma IGF-1 concentrations in agile gibbons generally increased with age with some marked peaks (Fig. 1A, C). On the other hand, plasma testosterone concentrations increased to the adult level at 3.5 years of age in Ha3 (Fig. 1B) and 2.6 years of age in Ha4 (Fig. 1D). However, the onset of puberty cannot be determined only by the growth profile of plasma testosterone.

Our previous study (Suzuki et al. 2000) of male Japanese macaques revealed that the plasma IGF-1 level starts to increase around 1 year earlier than the plasma testosterone level in the later juvenile phase. The state of reproductive maturity is confirmed by the prominent development of the testes. The relationship between the growth profiles of these hormones during periadolescent phase in Japanese macaques is considered to be held in agile gibbons. Thus the onset of adolescent phase in agile gibbons, although not easily confirmed by testicular development, can be determined in the same manner as in Japanese macaques. The onset of puberty in the subject agile gibbons occurred at 2.6 or 3.5 years. These ages are younger than those (4.5 year of age) reported in white-handed gibbons by external observation (Roonwall and Mohnot 1977). However, it has to be noted that the onset of adolescent phase in gibbons is somewhat difficult to determine by external observation. This is because gibbons show no such external signs of sexual maturation (e.g., swelling of sexual skin) as observed in macaques and/or chimpanzees.

Growth profiles of body weight

One-year-old agile gibbons used in this study weighed 1,890 g and 2,000 g. These values are somewhat lower than those reported for artificially-nursed white-handed gibbons (Araki et al. 1989) and a mother/artificially nursed white-handed gibbon (Sawina and Orpachowa 1981), but similar to those of mother/artificially nursed gibbons [White-handed gibbon × Javan gibbon (H. moloch)) (Linke 1988)].

As mentioned above, the two gibbons studied were considered to have reached the adolescent phase during the experimental period. Body weight in Ha3 and Ha4 reached 76.2% and 66.4% of RWA, respectively, at the

onset of the adolescent phase. In male captive chimpanzees, onset of adolescence has been determined to be 6 years from birth, based on the profiles of plasma IGF-1 and testosterone (Copeland et al. 1985; Marson et al. 1991). The adolescent onset phase in human males has been determined as 11.5 years of age (Kimura 1979; Sanayama et al. 1984; Martin 1985; Tachibana et al. 1993, 1994), based on the same procedure used for chimpanzees. At the adolescent onset phase, the body weight reaches about 60% (range: 56.5–63.9%) of RWA in human males (Kimura 1979) and approximately 42% of RWA in male chimpanzees (Copeland et al. 1985; Marson et al. 1991) and male Japanese macaques (Hamada 1994). Growth changes in body weight at the onset of adolescence in agile gibbons are similar to and a little faster than those in humans, and are obviously faster than those in chimpanzees and Japanese macaques. In contrast, in the latter two species body weight increases remarkably after the onset of puberty. Differences in growth patterns may be closely related with differences in social structure or reproductive strategy, as already mentioned above. Further comparative studies are necessary.

Profiles of growth in linear dimensions

Many of the 27 somatometric parameters showed a *general pattern*, as indicated by a linear increase in 4 years after birth in male agile gibbons. However, head length and the length of the first digit had reached a plateau within this period. Comparison of growth profiles of somatometric parameters suggests either that Ha4 grows faster than Ha3 or that Ha4 will be bigger than Ha3 at the end of the growing phase. The conclusion drawn from endocrinological analyses suggests the former.

Age-related changes of limb proportions in gibbons attract interest because of their locomotor behavior (brachiation). The brachial index increased gradually with growth in both Ha3 and Ha4. This result indicates that the forearm becomes relatively longer than the upper arm with growth, which may be related to an evolutionary adaptation for brachiation. However, the intermembral index did not show consistent age changes between subjects.

Adolescent spurt in somatic growth

Watts and Gavan (1982) observed that the adolescent spurt in primates was an incremental phenomenon rather than all-or-nothing in nature. However, later reports showed that primate species possessing larger sexual dimorphism in size and/or weight exhibit an apparent adolescent spurt (Coelho 1985; Shohoji and Sasaki 1985; Watts 1985). In contrast, primates with little or no sexual dimorphism in size and/or weight may show almost no adolescent spurt (Yoshida 1994). Therefore, contrary to the observations of Watts and Gavan (1982), it is reasonable to suggest that an adolescent spurt cannot be observed in agile gibbons, because the white-handed gibbon group species are devoid of sexual dimorphism in physical characteristics (Napier and Napier 1967). Leigh and Shea (1995) showed no acceleration in body weight growth in two species of gibbons (*Hylobates lar* and *H. syndactylus*). However, to confirm this hypothesis it is necessary to analyze precisely not only longitudinal data of body weight growth but also the data of growth changes in length and size by using velocity curves for each individual's data.

Conclusion

By tracing the profiles of plasma IGF-1 and testosterone, we determined the puberty onset to be around 2.6 and 3.5 years of age in two male agile gibbons, and these gibbons were found to be in the adolescent phase during the experimental period. However, the necessity for follow-up observations of these two gibbons to elucidate the growth characteristics in this species more precisely cannot be underestimated.

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