Age changes of musculoskeletal stress markers and their inter-period comparisons

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Abstract This study examines the changes with age of 15 musculoskeletal stress markers (MSMs) in the upper and lower limb bones of modern Japanese with documented ages-at-death, on the basis of original scoring criteria corresponding to each advanced stage. The procedure investigated significant differences of mean scores among five age classes at intervals of 10 years from 20 to 69 years for each MSM, and also calculated Pearson's correlation coefficients between MSM scores and age-at-death. These examinations found that most MSMs had significant correlations with aging in both sexes. MSM data of the people from the Yoshigo shell-mound in the Jomon period (Yoshigo Jomon, c. 3000–2300 BP), the Doigahama site in the Yayoi period (Doigahama Yayoi, c. 2100–1800 BP), and modern Japanese were then compared between the 20–39 and 40–59 age categories (younger adult and older adult groups, respectively) for both sexes. Kruskal–Wallis tests found that many MSMs showed significant differences between periods in each age category. Mann–Whitney tests revealed that many MSMs of the prehistoric Yoshigo Jomon and Doigahama Yayoi showed few significant differences, whereas those of many modern Japanese differed significantly. Principal component analysis indicated that the results of a scatter diagram in the younger adult group were considerably different from those of the older adult group. These findings suggest that MSMs are age structured within human populations, but that differences also arise in association with intensity of activity.

Key words: musculoskeletal stress marker (MSM), age changes, modern Japanese, Jomon, Yayoi

Introduction

Musculoskeletal stress markers (MSMs) are osseous changes observed on the muscle attachment portions of bones, especially postcranial limb bones. Enthetic MSMs are divided into two types in terms of muscle attachment morphology: a fibrous type and a fibrocartilaginous type. In the former type, the collagenous tendon attaches directly to the bone, whereas the latter type displays four stages of histological zones in the transition from tendon to bone. Hawkey and Merbs (1995) classified these osseous changes into three categories, i.e. robusticity marker, stress lesion, and ossification exostosis. The robusticity marker is the normal reaction to habitual muscle usage and reflects daily activities that produce rugged markings at the muscle attachment. This marker is observed as a sharp ridge or crest. The stress lesion is defined as a pitting or furrow on the cortical bone. This pattern appears to be activity induced as a result of continual microtrauma at the attachment site. The ossification exostosis is usually due to an abrupt macrotrauma. When a bone avulsion injury occurs, new bone formation may be incorporated into the muscle tissue, and result in an exostosis. These

osseous changes are relatively prevalent in adults after the growth of the skeletal system has been fully completed, and are often considered to reflect physical activities based on daily subsistence or habits during the lifetime of the individual (Hawkey and Merbs, 1995; Chapman, 1997; Churchill and Morris, 1998; Peterson, 1998; Steen and Lane, 1998; al-Oumaoui et al., 2004; Eshed et al., 2004; Molnar, 2006, 2010; Weiss, 2007; Lieverse et al., 2009, 2013; Havelková et al., 2011; Schrader, 2012; Stefanović and Porčić, 2013).

Although Hawkey and Merbs' (1995) method is widely used for scoring MSMs studies, it has some problems. (i) Muscular and ligamentous markers are not distinguished. Muscles are different from ligaments in both embryological origin and anatomical function. Clavicular ligaments in particular cannot be discussed in the same way as muscles. (ii) Some minute changes of muscle attachment are difficult to score in actual materials by macroscopic observation (e.g. scapular markers). (iii) It is doubtful whether all muscles match the defined scores of robusticity marker, stress lesion, and ossification exostosis. Each muscle may need its own definition for proper scoring. (iv) Treatment of difficult-to-score borderline MSMs are not clear (For example, how do researchers record an intermediate score between phase 1 and phase 2?). This method presents a risk of inter- or intra-observer error in respective scorings.

Many researchers have considered the relationships between MSMs and age. Chapman (1997) investigated the relationship between MSM intensity of upper limb bones and

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age category in Pecos Pueblo Native Americans, and found that there were statistically significant differences between young and middle-aged adults in some muscle/ligament insertion features. Wilczak (1998) compared the total area of seven muscle insertions of the humerus in individuals between 20 and 40 years of age based on the Terry/Hamann-Todd collection (20th-century specimens with museum records of death certificates and autopsies). This study revealed that the total insertion area of the muscle was significant greater in 40 year old males than in 20 year old males. Robb (1998) compared MSM scores of the upper and lower limb bones between age categories in an archaeological sample from the Pontecagnano cemetery (7th–3rd century BC) in southern Italy. He suggested that average MSM score exhibits curvilinear change as aging progresses.

Weiss (2003, 2004) investigated the total MSM scores in each of the upper limbs (7 insertion sites) and lower limbs (20 insertion sites) in the skeletal remains of Native British Columbians (3500–1500 BP) and prisoners in Quebec (18th century). The total MSM score correlated with age significantly in both the upper and lower limbs (correlation coefficients: $r = 0.49$ in the upper limbs, $r = 0.61$ in the lower limbs, $P < 0.001$ in both). The research found that older individuals had higher scores and that age was the best overall predictor of MSMs. A similar report also came from the upper limb bone sample of prehistoric Native Americans from Central California (Weiss, 2007). Molnar (2006) and Molnar et al. (2011) studied frequencies of MSM scores in age-specific contexts among Middle Neolithic skeletons from Gotland Island. These studies showed that aging could account to a considerable degree for higher MSM scores.

Whereas the above studies suggest that aging affects MSM scores, most of these analyses were made on the basis of archaeological materials where the correct age-at-death was unknown. Wilczak (1998) used the Terry/Hamann-Todd collection, which is supplied with records of death certificates. However, the analyzed data was derived from only the humerus of a mixed sample of European and African origins. Biological and socioeconomic background is likely to be different between these populations.

Therefore, recent studies have tried to establish relationships between aging and MSM scores in modern skeletal collections with known ages-at-death. Cardoso and Henderson (2010) demonstrated that there was no association between activity and enthesopathies, and that age was the single most significant factor in enthesopathy formation in late-19th- to early-20th-century cemeteries in Portugal. Niinimäki (2011) concluded that age and muscle size were the most powerful factors to explain MSM scores in the upper limbs of early-20th-century Finns. Muscle attachment areas and MSMs exhibited increasing patterns with advancing

age. Milella et al. (2012) investigated postcranial entheses in a large contemporary Italian skeletal series and reported a strong relationship between aging and enthesal changes. Enteseal morphology primarily reflected age, and its association with lifetime activity patterns remained ambiguous.

The current study differs from similar previous attempts by tracking the correlation between age and MSMs, while also exploring differences in MSM expression between populations with different subsistence economies. The work endeavors to provide an enhanced understanding of the development of these features over the human lifespan and of how strain may differentially influence expression. Two hypotheses are tested to achieve this goal: (i) aging is a significant factor for MSM expression in modern Japanese; and (ii) there are significant differences between modern and prehistoric groups in MSM expression when aging is considered.

Materials and Methods

Materials

The modern skeletal materials in this study were anatomical cadaveric specimens of Japanese skeletons. These materials were all adults who lived in the later 19th to early 20th centuries (Table 1). Selected modern Japanese skeletons were identified as to their age-at-death on the basis of body donation records. The subjects were classified into five age classes (20–29, 30–39, 40–49, 50–59, and 60–69 years) and three age stages from ‘younger adult’ (20–39 years), ‘older adult’ (40–59 years), and ‘senile adult’ (60–69 years).

Archaeological skeletal materials were chosen on the basis of sample size (Figure 1, Table 1). For the Jomon period (settled hunter-gatherer society), the Yoshigo shell-mound in Aichi prefecture (Yoshigo Jomon: c. 3000–2300 BP) has one of the largest number of individuals recovered from an archaeological site. For the Yayoi period (the first intensive farming society based on paddy rice), skeletons from the Doigahama site in Yamaguchi prefecture (Doigahama Yayoi: ca. 2100–1800 BP) are the best preserved.

Criteria for scoring MSM

The skeletal elements used in this study are shown in Figure 2 and listed in Table 2. Free parts of the upper and lower limbs (humerus, radius, ulna, femur, patella, tibia, and calcaneus) were observed in this investigation. MSMs were selected based on the following standards: (i) traits originating from skeletal muscles but not ligaments (with the exception of the patellar ligament), (ii) insertions relative to main muscles in motion of the whole body and major joints such as shoulder, elbow, hip, knee, and ankle; (iii) easy to assess by macroscopic observation or palpation, and showing some

Table 1. Skeletal materials used in present study

Period	Sites	Male (<i>n</i>)	Female (<i>n</i>)	Collections
Jomon	Yoshigo shell mound	96	115	Kyoto University Museum Tahara Municipal Museum
Yayoi	Doigahama site	87	66	Kyushu University Museum
Modern	(Kanto and Kinai regions)	224	135	School of Medicine, Chiba University Kyoto University Museum

Figure 1. Geographical locations of the Jomon period Yoshigo shell-mound and the Yayoi period Doigahama site in the used in the present study.

degree of frequency among various populations.

Scoring of each MSM was performed in accordance with advanced stages. Scores were recorded on a scale from 0 to 3, and the scoring criteria are explicitly described in Table 1 and Figure 2. In ambiguous cases, i.e. situations where scores fell between two qualitative values, intermediate scores were assigned (e.g. 1.5 for expressions that fall between 1 and 2).

Comparisons among the Jomon, Yayoi, and modern Japanese

MSM data sets of the Yoshigo Jomon, Doigahama Yayoi, and modern Japanese were divided into the younger adult and older adult groups. The age-at-death of archaeological skeletons was assessed based on cranial sutures, dental attrition, and pubic symphysis surfaces (Lovejoy, 1985; Buikstra and Ubelaker, 1994). Then, each age- and sex-separated group was treated as the further analytical unit. A Kruskal–Wallis test was conducted to find inter-population differences among the Yoshigo Jomon, Doigahama Yayoi, and modern Japanese. Mann–Whitney tests were also carried out between age categories in each population.

Finally, principal component analyses (PCA) among the three groups were conducted in the younger adult and older adult groups, and the age-pooled sample. PCA was employed to further evaluate contributing factors to MSM formation, namely subsistence categories and age groups. Statistical procedures were performed by using SPSS 14.0 for Windows (SPSS Inc.).

Results

Age changes of MSMS in each age class

For the modern Japanese materials, MSM score data were

mixed between right and left sides and divided into five age classes (20–29, 30–39, 40–49, 50–59, and 60–69 years). For each age class, the basic statistics of each MSM were calculated separately for males and females (Table 3, Figure 3).

Kruskal–Wallis tests among the five age classes confirmed significant age differences (Table 3, Figure 3). In the upper limbs, LTC, DT, RT and OL showed significant age changes in both sexes. In the lower limbs, all MSMS exhibited significant age differences. In many of the examined MSMS, the age class of 20–29 years had the lowest score (DT, RT, OL, GT, LT, LA, PB, SL, TT, and CT). While the highest score was observed in the age class of 50–59 years in many MSMS of males (DT, SC, GT, LT, GLT, LA, PB, TT, and CT), most MSM scores were highest in the age class of 60–69 years in females (GTC, LTC, DT, RT, OL, UT, GT, LT, GLT, LA, PB, TT, and CT). A linearly increasing pattern from the lowest to the highest age class was observed in MSMS around the elbow joint (RT: insertion in tendon of biceps brachii; OL: insertion in tendon of triceps brachii), in both males and females.

In 13 MSMS out of 15, Pearson's correlation coefficients between the MSM score and age were statistically significant (Table 4). MSMS that did not show significant correlation with age were GTC and SC in males, and UT and GLT in females. These are upper-limb MSMS. All lower-limb MSMS showed significant correlation.

Comparisons among the Jomon, Yayoi, and modern Japanese

Kruskal–Wallis tests revealed significant population differences of MSM expression among Yoshigo Jomon, Doigahama Yayoi, and modern Japanese (Figure 4 and Table 5). In younger adult males, 9 MSMS differed significantly as did 11 MSMS in older adult males. Among those MSMS, seven (GTC, DT, SC, UT, LT, GLT, and PB) were common between two age groups. Eleven MSMS differed significantly in younger adult females, and in 10 in older adult females. Among those MSMS, seven (GTC, LTC, DT, RT, SC, GT, and CT) were common.

Averaged scores of 15 MSMS are also given in Table 5. Except for older adult males, the score was highest in Yoshigo Jomon. In older adult males, the highest score was observed in modern Japanese.

A Mann–Whitney test was performed to reveal inter-age group difference (Table 6). In Yoshigo Jomon and Doigahama Yayoi, most MSMS did not show significant differences. In contrast, many of the MSMS showed a significant difference between the younger and older adult groups in modern Japanese (in both sexes).

In the scatter diagrams of PCA (Figure 5), the younger adult, older adult, and mixed age group showed different patterns. However, the older adult group showed results that resembled that of the mixed age group.

Discussion

Age changes of MSMS in modern Japanese

In the investigation of modern Japanese, the present study confirmed significant correlations between most MSM scores and age-at-death. Many MSM traits develop in

Figure 2. Schematic explanations of the advanced MSM scoring method used in this study: (a) upper limbs; (b) lower limbs.

Figure 2. (continued)

Table 2. Location of MSMs and corresponding muscles, and criteria for the advanced scores

No.	Element	MSM traits (Abbreviation)	Corresponding muscles	Criteria for scoring MSM			
				Phase 0	Phase 1	Phase 2	Phase 3
1	Humerus	Crest of greater tuberosity (GTC)	Pectoralis major	Normal crest and no depression	Longitudinal irregular depression below 3 mm at inferior level of the crest	Longitudinal irregular depression over 3 mm, below 5 mm at inferior level of the crest	Longitudinal irregular depression over 5 mm at inferior level of the crest
2	Humerus	Crest of lesser tuberosity (LTC)	Teres major Latissimus dorsi	Normal crest and no depression	Longitudinal irregular depression below 3 mm at inferior level of the crest	Longitudinal irregular depression over 3 mm, below 5 mm at inferior level of the crest	Longitudinal irregular depression over 5 mm at inferior level of the crest
3	Humerus	Deltoid tuberosity (DT)	Deltoideus	Unclear tuberosity and lateral outline is almost straight	Slightly developed tuberosity but lateral outline is hardly curved	Developed tuberosity and lateral outline is smoothly curved	Well-developed tuberosity and lateral outline is clearly square
4	Radius	Radial tuberosity (RT)	Tendon of biceps brachii	Tuberosity is not prominent and its outline is flat	Tuberosity is slightly developed and forms a part of medial outline of diaphysis	Outline of tuberosity is prominent and tuberosity surface tilts medially	Whole tuberosity is prominent and tilts medially, enthesophyte is somewhat formed
5	Ulna	Olecranon (OL)	Tendon of triceps brachii	Superior edge of olecranon is smooth and no protuberance	Tendon attachment of olecranon is smoothly developed below 3 mm in height	Tendon attachment of olecranon slightly sharpens over 3 mm, below 5 mm in height	Tendon attachment of olecranon is sharply developed over 5 mm in height
6	Ulna	Supinator crest (SC)	Supinator	Indistinct crest inferior to radial notch and lateral surface is flat	Plain crest inferior to radial notch but lateral surface is still flat	Clear crest inferior to radial notch and the crest projects somewhat to lateral	Crest projects more lateral than outline of radial notch
7	Ulna	Ulnar tuberosity (UT)	Brachialis	Inferior level of coronoid process is flat and tuberosity is hardly prominent	Tuberosity is slightly prominent below 3 mm in height	Tuberosity is clearly developed and forms irregular prominence over 3 mm, below 5 mm in height	Whole tuberosity is developed and forms some enthesophytes
8	Femur	Greater trochanter (GT)	Gluteus medius and minimus	Surface of greater trochanter is smooth and no enthesophytes	Slight enthesophytes on the surface of greater trochanter are confirmed by palpation	Clear enthesophytes below 3 mm in length, on the surface of greater trochanter	Severe enthesophytes over 3 mm in length, on the surface of greater trochanter
9	Femur	Lesser trochanter (LT)	Iliopsoas (Psoas major, Iliacus)	Surface of lesser trochanter is smooth and no enthesophytes	Slight enthesophytes on the surface of lesser trochanter are confirmed by palpation	Clear enthesophytes below 3 mm in length, on the surface of lesser trochanter	Severe enthesophytes over 3 mm in length, on the surface of lesser trochanter
10	Femur	Gluteal tuberosity (GLT)	Gluteus maximus	Surface is smooth and flat, unclear tuberosity	Whole tuberosity is slightly rough but still flat	Tuberosity is rough and projects below 3 mm in height	Whole tuberosity projects over 3 mm in height, occasionally the third trochanter
11	Femur	Linea aspera; lateral and medial lips (LA)	Adductor magnus, longus, and brevis Medial and lateral vastus of quadriceps femoris Short head of biceps femoris	Surface of linea aspera is smooth and both lateral and medial lips are plain, and able to distinguish them	Both lips project slightly as broken lines, lateral lip separates from medial lip	Projection of linea aspera below 3 mm in height, partly one lip is close to other lip	Projection of linea aspera over 3 mm in height, both lips connect and difficult to distinguish them
12	Patella	Patellar base (PB)	Tendon of quadriceps femoris	Superior edge of patellar base is smooth and no enthesophytes	Slight enthesophytes on the superior edge of patellar base is confirmed by palpation	Clear enthesophytes below 3 mm in length, on the superior edge of patellar base	Severe enthesophytes over 3 mm in length, on the superior edge of patellar base
13	Tibia	Soleal line (SL)	Soleus in triceps surae	No soleal line or broken line, posterior surface of tibia is flat	Clear soleal line but no prominence	Clear soleal line and prominent below 3 mm in height	Remarkable soleal line and prominent over 3 mm in height
14	Tibia	Tibial tuberosity (TT)	Patellar ligament attached to quadriceps femoris	Superior edge of tuberosity is smooth and no enthesophytes	Slight enthesophytes on the superior edge are confirmed by palpation	Clear enthesophytes below 3 mm in length, on the superior edge	Severe enthesophytes over 3 mm in length, on the superior edge
15	Calcaneus	Calcaneal tuberosity (CT)	Calcaneal tendon in triceps surae	Posterior of calcaneal tuberosity is smooth and no enthesophytes	Slight enthesophytes on the posterior area of tuberosity are confirmed by palpation	Clear enthesophytes below 3 mm in length, on the posterior area of tuberosity	Severe enthesophytes over 3 mm in length, on the posterior area of tuberosity

Table 3. Basic statistics of each age class in modern Japanese and results of Kruskal–Wallis tests

Male																		
No.	Element	MSMs	20–29 years			30–39 years			40–49 years			50–59 years			60–69 years			Kruskal– Wallis test
			n	M	SD	n	M	SD	n	M	SD	n	M	SD	n	M	SD	
1	Humerus	GTC	37	0.35	0.50	61	0.24	0.46	66	0.08	0.32	43	0.20	0.45	16	0.34	0.47	**
2	Humerus	LTC	37	0.45	0.47	61	0.48	0.56	66	0.67	0.55	43	0.90	0.65	16	0.97	0.50	***
3	Humerus	DT	37	0.65	0.47	61	0.89	0.50	66	1.23	0.56	43	1.63	0.49	16	1.28	0.48	***
4	Radius	RT	36	0.79	0.32	60	1.11	0.44	65	1.19	0.38	43	1.45	0.50	16	1.63	0.65	***
5	Ulna	OL	35	0.16	0.29	59	0.42	0.51	65	0.48	0.50	42	0.55	0.47	16	0.91	0.93	***
6	Ulna	SC	35	0.66	0.51	59	0.63	0.37	65	0.75	0.48	42	0.80	0.44	16	0.56	0.40	ns
7	Ulna	UT	35	0.73	0.41	59	1.03	0.40	65	0.98	0.50	42	0.98	0.45	16	0.97	0.46	*
8	Femur	GT	41	0.06	0.20	58	0.20	0.40	64	0.40	0.48	42	0.85	0.54	14	0.64	0.72	***
9	Femur	LT	41	0.30	0.43	58	0.37	0.48	63	0.63	0.53	42	1.00	0.46	14	0.71	0.61	***
10	Femur	GLT	41	0.45	0.50	58	0.93	0.57	63	1.08	0.56	42	1.10	0.54	14	0.82	0.64	***
11	Femur	LA	41	0.20	0.42	58	0.51	0.46	64	0.83	0.49	42	1.08	0.40	14	0.86	0.36	***
12	Patella	PB	36	0.22	0.37	50	0.22	0.44	59	0.75	0.58	41	1.04	0.66	14	0.36	0.41	***
13	Tibia	SL	40	0.60	0.41	58	0.76	0.41	67	0.89	0.53	43	0.95	0.41	16	1.03	0.62	**
14	Tibia	TT	40	0.38	0.54	58	0.54	0.46	67	0.60	0.45	42	0.81	0.61	16	0.47	0.43	**
15	Calcaneus	CT	34	0.47	0.55	53	0.97	0.58	62	1.15	0.48	39	1.53	0.55	14	1.46	0.41	***

Female

No.	Element	MSMs	20–29 years			30–39 years			40–49 years			50–59 years			Kruskal–Wallis test
			n	M	SD	n	M	SD	n	M	SD	n	M	SD	
1	Humerus	GTC	40	0.00	0.00	28	0.00	0.00	27	0.04	0.13	14	0.00	0.00	ns
2	Humerus	LTC	40	0.54	0.79	28	0.41	0.45	28	0.46	0.65	14	0.50	0.55	**
3	Humerus	DT	40	0.61	0.45	28	0.71	0.25	28	1.05	0.53	14	1.07	0.51	***
4	Radius	RT	40	0.88	0.29	29	0.86	0.26	28	0.88	0.26	14	1.14	0.41	**
5	Ulna	OL	40	0.13	0.27	28	0.18	0.28	29	0.33	0.38	14	0.36	0.36	***
6	Ulna	SC	40	0.50	0.39	29	0.47	0.40	29	0.62	0.37	14	0.75	0.38	ns
7	Ulna	UT	40	0.89	0.52	29	0.83	0.50	29	0.91	0.46	14	0.79	0.38	ns
8	Femur	GT	39	0.09	0.28	29	0.14	0.32	28	0.13	0.29	16	0.53	0.46	***
9	Femur	LT	39	0.18	0.37	28	0.38	0.46	28	0.43	0.47	16	0.38	0.34	**
10	Femur	GLT	39	0.83	0.65	29	0.74	0.70	27	0.57	0.41	16	0.91	0.33	***
11	Femur	LA	39	0.04	0.13	29	0.31	0.43	26	0.48	0.46	16	0.56	0.40	***
12	Patella	PB	35	0.06	0.24	27	0.26	0.47	24	0.46	0.62	16	0.78	0.48	***
13	Tibia	SL	40	0.51	0.40	30	0.65	0.35	31	0.84	0.44	16	1.03	0.43	***
14	Tibia	TT	40	0.13	0.22	29	0.26	0.34	31	0.52	0.54	16	0.38	0.29	***
15	Calcaneus	CT	40	0.30	0.27	26	0.42	0.44	27	0.61	0.38	14	0.93	0.27	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, not significant.

Figure 3. Line graphs of MSM score in each age class: (a) upper limbs; (b) lower limbs.

Figure 3. (continued)

Table 4. Pearson's correlation coefficients between age-at-death and MSM score

No.	Element	MSMs	Male				Female			
			<i>n</i>	<i>R</i>	<i>P</i>		<i>n</i>	<i>R</i>	<i>P</i>	
1	Humerus	GTC	223	-0.0736	0.2738	ns	127	0.2148	0.0153	*
2	Humerus	LTC	223	0.3060	3.E-06	***	128	0.2236	0.0112	*
3	Humerus	DT	223	0.4968	3.E-15	***	128	0.4843	7.E-09	***
4	Radius	RT	220	0.4523	2.E-12	***	129	0.3732	1.E-05	***
5	Ulna	OL	217	0.3108	3.E-06	***	129	0.4191	8.E-07	***
6	Ulna	SC	217	0.0610	0.3712	ns	130	0.1770	0.0440	*
7	Ulna	UT	217	0.1503	0.0268	*	130	0.0401	0.6509	ns
8	Femur	GT	219	0.4560	1.E-12	***	128	0.5168	4.E-10	***
9	Femur	LT	218	0.3937	2.E-09	***	127	0.3214	0.0002	***
10	Femur	GLT	218	0.2638	0.0001	***	127	0.1742	0.0501	ns
11	Femur	LA	219	0.5438	0.E + 00	***	126	0.6925	0.E + 00	***
12	Patella	PB	200	0.3800	3.E-08	***	120	0.6684	1.E-16	***
13	Tibia	SL	224	0.2646	0.0001	***	135	0.3127	0.0002	***
14	Tibia	TT	223	0.1749	0.0089	**	134	0.3535	3.E-05	***
15	Calcaneus	CT	202	0.4921	1.E-13	***	125	0.5838	9.E-13	***

n, sample size; *R*, correlation coefficient; *P*, probability of significant test.

P* < 0.05, *P* < 0.01, ****P* < 0.001; ns, not significant.

response to aging, in particular at 30–59 years of age. The present results support findings in previous studies based on archaeological and contemporary materials that suggest a relationship between MSM expression and age.

Although the scores of many MSMs increased with age, sex differences were observed at higher age stages in several MSMs, especially of the lower limb (DT, GT, LT, GLT, LA, PB, TT, and CT). For these MSMs, the male scores of the age stage of 50–59 years were highest and those of the later age stage (60–69 years) declined. In females, MSM scores increased steadily from the stage of 20–29 years to the stage of 60–69 years. This sex difference is probably related to males retiring from work. Because Japanese males from the late 19th to early 20th centuries retired in their 50 s–60 s, daily muscular activity level and loading of the limb skeleton by labor might have decreased after the stage of 50–59 years and the related MSMs also exhibited lower scores. On the other hand, the continuous increase of MSM scores in senile females may be explained from the view of cortical wasting in the long bones. Wescott and Child (2009) pointed out that MSM expression following immobility was pronounced, despite reduced cross-sectional geometric parameters such as clinical cases with cerebral palsy. Total bone mass of senile females after menopause tends to diminish and, in connection with this, cortical bone also wastes from this period. As a result, cortical wasting in senile females might contribute to stronger MSM expression.

Temporal comparisons

Many MSMs showed significant inter-population differences (9/15 in younger adult males, 11/15 in older adult males, 11/15 in younger adult females, and 10/15 in older adult females) among the Yoshigo Jomon, Doigahama Yayoi, and modern Japanese in each of the younger adult and older adult groups (Table 5).

As for the age-related difference, between the younger adult and older adult groups, most MSMs had no significant differences in the Yoshigo Jomon and Doigahama Yayoi (11/15 in males and 12/15 in females of the Yoshigo Jomon, and 12/15 in males and 9/15 in females of the Doigahama

Yayoi) (Table 6). In contrast, most MSMs of modern Japanese differed significantly between these age groups (13/15 in males, 10/15 in females). Activities performed by younger adults amongst the Yoshigo Jomon and Doigahama Yayoi were likely accentuated compared to those experienced by modern Japanese. It is possible that these prehistoric groups began intensive activity at earlier ages. Okazaki (2007) inferred that Jomon children were already participating in hunting or gathering by adolescence based on allometrical analysis of cross-sectional parameters in juvenile limb bones.

The age differences for modern Japanese were large in both males and females. The physical activities performed by modern younger adults might have been easier than those of older adults due to the reduction of musculoskeletal load by industrialized modern lifestyles. Plus, older adult males of modern Japanese had a number of MSM scores greater than those of the Yoshigo Jomon and Doigahama Yayoi. These modern Japanese lived a longer life than prehistoric groups and delayed the beginning of heavy physical labor until adulthood. Thus, it is probable that cumulative loading promoted MSM expression at the age stage of 40–59 years.

In the two-dimensional plot of PC scores, the configurations of the younger adults (20–39 years) were different from those of the older adults (40–59 years). However, as mentioned above, there were no significant differences in most MSMs between these two age classes in the prehistoric Jomon and Yayoi groups. Therefore, pooling the adult age classes in these prehistoric populations would not be problematic. Modern Japanese, however, had significant differences between the adult age classes, and so modern mixed data should be utilized carefully when it is used as a control group in comparisons of various prehistoric groups.

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Table 5. Basic statistics in each period and results of Kruskal–Wallis tests

Younger adult male

No.	Element	MSMs	Yoshigo Jomon			Doigahama Yayoi			Modern Japanese			Kruskal–Wallis test
			<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD	
1	Humerus	GTC	40	0.95	0.57	17	0.59	0.51	99	0.28	0.47	***
2	Humerus	LTC	41	0.71	0.55	17	0.65	0.49	99	0.47	0.52	*
3	Humerus	DT	44	1.06	0.63	16	0.56	0.44	99	0.80	0.51	**
4	Radius	RT	35	0.96	0.51	15	1.00	0.50	97	0.99	0.44	ns
5	Ulna	OL	39	0.27	0.40	15	0.17	0.36	95	0.32	0.46	ns
6	Ulna	SC	45	1.11	0.60	15	0.47	0.52	95	0.64	0.43	***
7	Ulna	UT	46	0.92	0.40	18	0.53	0.50	95	0.92	0.43	**
8	Femur	GT	37	0.49	0.49	9	0.11	0.33	100	0.14	0.33	***
9	Femur	LT	38	0.37	0.58	13	0.69	0.48	100	0.35	0.46	*
10	Femur	GLT	48	0.45	0.53	14	0.86	0.53	100	0.74	0.59	*
11	Femur	LA	52	0.57	0.53	15	0.63	0.67	100	0.38	0.47	ns
12	Patella	PB	18	0.47	0.43	14	0.57	0.76	87	0.22	0.41	**
13	Tibia	SL	37	0.59	0.43	16	1.03	0.62	99	0.69	0.42	ns
14	Tibia	TT	29	0.74	0.67	12	0.50	0.52	99	0.48	0.50	ns
15	Calcaneus	CT	33	0.97	0.76	12	0.75	0.62	88	0.78	0.62	ns
Average				0.71			0.61			0.55		

Older adult male

No.	Element	MSMs	Yoshigo Jomon			Doigahama Yayoi			Modern Japanese			Kruskal–Wallis test
			<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD	
1	Humerus	GTC	56	1.04	0.48	38	0.82	0.39	110	0.13	0.38	***
2	Humerus	LTC	56	0.66	0.51	38	0.58	0.50	110	0.76	0.60	ns
3	Humerus	DT	59	1.21	0.57	42	0.86	0.40	110	1.39	0.56	***
4	Radius	RT	54	1.06	0.46	40	1.14	0.57	109	1.30	0.45	**
5	Ulna	OL	55	0.17	0.34	34	0.29	0.43	108	0.50	0.49	***
6	Ulna	SC	63	1.07	0.51	36	0.56	0.61	108	0.77	0.46	***
7	Ulna	UT	62	0.90	0.53	38	0.53	0.49	108	0.98	0.48	***
8	Femur	GT	48	0.50	0.56	23	0.48	0.59	107	0.58	0.55	ns
9	Femur	LT	50	0.44	0.51	35	0.80	0.63	106	0.78	0.53	**
10	Femur	GLT	65	0.70	0.59	43	0.98	0.58	106	1.09	0.55	***
11	Femur	LA	66	0.86	0.55	47	0.81	0.66	107	0.93	0.47	ns
12	Patella	PB	36	1.17	0.64	34	0.85	0.69	101	0.87	0.63	*
13	Tibia	SL	59	0.80	0.60	46	1.04	0.46	111	0.91	0.48	*
14	Tibia	TT	45	0.58	0.60	30	0.95	0.50	110	0.69	0.53	**
15	Calcaneus	CT	55	1.35	0.64	30	1.27	0.45	102	1.29	0.54	ns
Average				0.83			0.80			0.86		

Younger adult female

No.	Element	MSMs	Yoshigo Jomon			Doigahama Yayoi			Modern Japanese			Kruskal–Wallis test
			<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD	
1	Humerus	GTC	47	0.99	0.47	27	0.85	0.36	68	0.00	0.00	***
2	Humerus	LTC	50	0.72	0.52	27	0.52	0.49	68	0.49	0.67	*
3	Humerus	DT	53	0.78	0.64	29	0.40	0.34	68	0.65	0.38	**
4	Radius	RT	55	1.16	0.49	22	0.52	0.45	69	0.87	0.28	***
5	Ulna	OL	53	0.10	0.27	24	0.00	0.00	68	0.15	0.27	*
6	Ulna	SC	57	0.98	0.68	27	0.19	0.40	69	0.49	0.39	***
7	Ulna	UT	57	0.93	0.40	26	0.54	0.51	69	0.86	0.51	**
8	Femur	GT	44	0.52	0.59	20	0.15	0.37	68	0.11	0.30	***
9	Femur	LT	45	0.48	0.49	24	0.63	0.49	67	0.26	0.42	**
10	Femur	GLT	60	0.71	0.60	25	0.62	0.53	68	0.79	0.67	ns
11	Femur	LA	64	0.36	0.46	26	0.15	0.37	68	0.15	0.33	*
12	Patella	PB	36	0.25	0.43	18	0.31	0.42	62	0.15	0.37	ns
13	Tibia	SL	60	0.68	0.42	26	0.58	0.27	70	0.57	0.38	ns
14	Tibia	TT	53	0.17	0.36	19	0.32	0.48	69	0.18	0.28	ns
15	Calcaneus	CT	47	0.98	0.68	19	0.55	0.69	66	0.35	0.35	***
Average				0.65			0.42			0.40		

Older adult female

No.	Element	MSMs	Yoshigo Jomon			Doigahama Yayoi			Modern Japanese			Kruskal–Wallis test
			<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD	
1	Humerus	GTC	39	1.11	0.47	24	0.65	0.48	41	0.02	0.11	***
2	Humerus	LTC	34	0.68	0.52	23	0.41	0.49	41	0.48	0.61	*
3	Humerus	DT	41	0.91	0.74	24	0.52	0.31	41	1.07	0.52	***
4	Radius	RT	35	1.23	0.47	23	0.83	0.32	41	0.97	0.34	**
5	Ulna	OL	33	0.25	0.40	22	0.32	0.65	42	0.35	0.37	ns
6	Ulna	SC	41	0.88	0.55	24	0.46	0.51	42	0.68	0.37	*
7	Ulna	UT	41	0.82	0.36	24	0.65	0.48	42	0.85	0.44	ns
8	Femur	GT	33	0.62	0.57	18	0.31	0.46	43	0.31	0.41	*
9	Femur	LT	30	0.61	0.44	22	0.61	0.65	43	0.41	0.42	ns
10	Femur	GLT	40	0.92	0.43	22	0.95	0.43	42	0.73	0.41	*
11	Femur	LA	49	0.48	0.53	22	0.36	0.44	41	0.53	0.43	ns
12	Patella	PB	23	0.61	0.71	15	0.57	0.70	38	0.64	0.59	ns
13	Tibia	SL	36	0.90	0.53	22	0.68	0.25	45	0.91	0.44	*
14	Tibia	TT	21	0.21	0.37	18	0.72	0.43	45	0.46	0.47	***
15	Calcaneus	CT	34	1.39	0.57	19	0.84	0.60	40	0.73	0.37	***
Average				0.77			0.59			0.61		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, not significant.

Figure 4. Bar charts of MSM score of the Jomon, Yayoi, and modern Japanese in each age class: (a) upper limbs; (b) lower limbs.

Figure 4. (continued)

Younger adult (20-39 years)

Older adult (40-59 years)

Mixed age groups (20-59 years)

Figure 5. Scatter diagrams of the Jomon, Yayoi, and modern Japanese based on principal component analysis.

Table 6. Results of Mann–Whitney tests between younger and older adults in each group

No.	Element	MSMs	Yoshigo Jomon		Doigahama Yayoi		Modern Japanese	
			Male	Female	Male	Female	Male	Female
1	Humerus	GTC	ns	ns	ns	ns	**	ns
2	Humerus	LTC	ns	ns	ns	ns	***	ns
3	Humerus	DT	ns	ns	*	ns	***	***
4	Radius	RT	ns	ns	ns	*	***	ns
5	Ulna	OL	ns	*	ns	*	**	**
6	Ulna	SC	ns	ns	ns	*	ns	*
7	Ulna	UT	ns	ns	ns	ns	ns	ns
8	Femur	GT	ns	ns	ns	ns	***	*
9	Femur	LT	ns	ns	ns	ns	***	*
10	Femur	GLT	*	*	ns	**	***	ns
11	Femur	LA	**	ns	ns	*	***	***
12	Patella	PB	***	ns	ns	ns	***	***
13	Tibia	SL	ns	ns	ns	ns	***	***
14	Tibia	TT	ns	ns	*	*	**	***
15	Calcaneus	CL	*	*	*	ns	***	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, not significant.

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