Journal of Anatomy

J. Anat. (2009) **215**, pp373–382

doi: 10.1111/j.1469-7580.2009.01125.x

Dimensions of forelimb muscles in orangutans and chimpanzees

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Abstract

Eight forelimbs of three orangutans and four chimpanzees were dissected and the muscle mass, fascicle length and physiological cross-sectional area (PCSA) of all forelimb muscles were systematically recorded to explore possible interspecies variation in muscle dimensions. Muscle mass and PCSA were divided by the total mass and total PCSA of the entire forelimb muscles for normalization. The results indicate that the mass and PCSA ratios of the monoarticular elbow flexors (*M. brachialis* and *M. brachioradialis*) are significantly larger in orangutans. In contrast, the mass ratios of the biarticular muscles in the upper arm (the short head of *M. biceps brachii* and the long head of *M. triceps brachii*) are significantly larger in chimpanzees. For the rotator cuff muscles, the force-generating capacity of *M. subscapularis* is significantly larger in orangutans, whereas the opposite rotator cuff muscle, *M. infraspinatus*, is larger in chimpanzees. These differences in forelimb muscle dimensions of the two species may reflect functional specialization for their different positional and locomotor behaviors.

Key words locomotion; *Pongo*; *Pan*; physiological cross-sectional area; positional behavior.

Introduction

Orangutans and chimpanzees are generally regarded as adapted to climbing and suspension in an arboreal environment due to their common morphological features associated with suspension, including a broad thorax, dorsally placed scapulae and long forelimbs (Aiello & Dean, 1990; Larson, 1993; Rose, 1993; Fleagle, 1999). However, positional and locomotor behaviors of the two large-bodied great apes are actually known to differ substantially. Orangutans are fundamentally quadrumanous climbers in the rain forest canopy, and they seldom walk on the ground. Indeed, field researchers have suggested that females and young orangutans spend almost all of their lives in trees and never descend to the forest floor (MacKinnon, 1974; Cant, 1987; Delgado & van Schaik, 2000; Thorpe & Crompton, 2005, 2006). Exceptions are the larger male orangutans in Borneo, which spend about 20% of their total travel time on the ground to move between trees (Rodman, 1979). However, chimpanzees travel between feeding trees mainly on the ground by knuckle-walking. Chimpanzees spend nearly 90% of their total travel time on the ground (Doran, 1992), and knuckle-walking accounts for 90% of all locomotor modes (Hunt, 1992). Consequently, the arboreal locomotor repertoire of orangutans is much more versatile than that of chimpanzees (Thorpe & Crompton, 2006). When comparing arboreal locomotion between the two species, in orangutans, the frequency of suspensory locomotion accounts for 39% of traveling and feeding, followed by vertical climbing (25%) and quadrupedal walking (18%) (Thorpe & Crompton, 2006); in chimpanzees, vertical climbing (50%) is the predominant locomotion because they approach food sources from the ground, followed by quadrupedal walking (31%) in trees (Hunt, 1992). In vertical climbing, orangutans exhibit relatively longer cycle duration and longer stride length than African apes (Isler & Thorpe, 2003; Isler, 2005), indicating slow and cautious arboreal climbing in orangutans.

Such marked contrasts in positional and locomotor behaviors between orangutans and chimpanzees are actually reflected in their forelimb skeletal morphology. For instance, the scapula of orangutans possesses a relatively larger infraspinous fossa (Roberts, 1974), a lower angulated spine (Young, 2003, 2008) and a shortened coracoid and acromion (Ciochon & Corruccini, 1977) than that of chimpanzees to allow enhanced shoulder joint mobility. The ulna of orangutans also appears to be longer (Drapeau

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Accepted for publication *5 June 2009*

Table 1 General specimen data

	O1	O2	O3	C1	C2	C3	C4
Species	Ppa*Ppp	Ppa?	Ppa	Pt	Pt	Pt	Pt
Sex	M	M	F	M	M	M	F
Age at death (years)	18	10	40	27	Approx. 35	Approx. 27	11
Body weight at death (kg)	–	78.6	48.8	–	–	46.5	30.2
Cause of death	CV	Unknown	Ge	Unknown	ID	Unknown	DD
Preservation	70% alc.	70% alc.	Frozen	Frozen	Frozen	Frozen	Frozen
Side	Right	Left	Left	Left and right	Right	Left	Left
Upper arm length (cm)	38.8	32.1	29.6	27.9	26.2	30.8	26.6
Forearm length (cm)	39.8	31.4	30.9	27.7	25.4	26.3	24.8
Total muscle mass of forelimb (g)	5677.4	4948.9	752.6	4008.5	3127.1	2918.8	1946.8

Ppa, *Pongo pygmaeus abelii*; Ppa*Ppp, *Pongo pygmaeus abelii*pygmaeus*; Pt, *Pan troglodytes*. O3 data are cited from a previous study (Oishi et al. 2008). CV, cardiovascular disease; Ge, geromarasmus; ID, infectious disease; DD, digestive disease. 70% alc., 70% alcohol. Upper arm length, distance from greater tubercle to lateral epicondyle of humerus; forearm length, distance from head to styloid process of radius. In C1 the right and left values were averaged.

& Ward, 2007) and has a relatively shorter olecranon process (Drapeau, 2004) for longer reach with full extension of the elbow. The proximal and middle phalanges of orangutans are more curved (Susman, 1979) than those of chimpanzees. These morphological features of orangutans suggest that the orangutan is more specialized for arboreal life. However, it has been suggested that humeral head torsion is relatively larger in chimpanzees, permitting the elbow to rotate on a parasagittal plane (Larson, 1988, 1996). In addition, dorsiflexion of the wrist joint and extension of the metacarpophalangeal joints are mechanically restricted in chimpanzees due to the projected dorsal margin of the distal radius and the heads of the metacarpals (Tuttle, 1967, 1969; Susman, 1979; Richmond & Strait, 2000), implying that the skeletal architecture of the chimpanzee is more specialized for terrestrial knuckle-walking.

Because locomotor capabilities are determined by the structure and function of both skeletal and muscular systems, one could expect that such differences in the positional and locomotor behaviors in orangutans and chimpanzees would also be reflected in their muscle morphology. To date, however, very few reports have described the forelimb muscle morphology of the chimpanzee (Thorpe et al. 1999; Ogihara et al. 2005; Carlson, 2006) and orangutan (Payne, 2001; Oishi et al. 2008), although the muscle morphology of the hindlimb of these species has been more completely described (Thorpe et al. 1999; Payne, 2001; Payne et al. 2006). Recently, we had additional opportunities to dissect several orangutans and chimpanzees. Therefore, this study aimed to provide complete quantitative data on the forelimb muscles of these species. Interspecies variations in the muscle dimensions of orangutans and chimpanzees are then explored, and possible functional relationships with their positional and locomotor behaviors are discussed.

Materials and methods

Eight forelimbs of three orangutans and four chimpanzees were dissected. Three adult orangutan specimens (O1, O2 and O3) were obtained for dissection from Yagiyama Zoological Garden, the Primate Research Institute, Kyoto University, and Higashiyama Zoo and Botanical Garden, respectively. Four adult chimpanzee specimens (C1, C2, C3 and C4) were donated to the Primate Research Institute, Kyoto University or the National Science Museum (Tokyo, Japan) from Chausuyama Zoo, Nogeyama Zoo, Yamajiboku and Tama Zoological Park, respectively. General specimen data are presented in Table 1. Two orangutan specimens (O1 and O2) had been preserved in alcohol after death. The chimpanzee specimens were all stored frozen until dissection. The data of the female fresh orangutan specimen (O3) were taken from our previous study (Oishi et al. 2008) and are included here for interspecies comparisons.

During dissection, the muscles listed in Table 2 were exposed and removed from the forelimb bones. The muscle belly (between the proximal ends of the most proximal and distal ends of the fibers of the muscles) and the external tendon were separated at the belly–tendon junction, and muscle belly mass (= mass) was measured using an electronic balance. Each muscle belly was immersed in 10% formalin and then in water overnight. Muscle fiber length (= fascicle length) was measured at three to six places dissected in varying locations within the muscle belly using calipers, and the mean value was calculated. In fixed specimens (O1 and O2), muscle mass was based on the wet weight of the fixed muscles, which were weighed after immersion in water overnight. The physiological cross-sectional area (PCSA) was calculated by dividing muscle volume by fascicle length. Muscle volume was obtained by dividing muscle mass by muscle density (1.0597 g cm^{-3}) (Mendez & Keys, 1960). The PCSA is proportional to the force-generating capacity of the muscle (Close, 1972; Zajac, 1992; MacIntosh et al. 2006). The pennation angle (the angle between the direction of the muscle fibers and the tendon) was not included in the calculation of PCSA because it was difficult in the two-dimensional muscle model to correctly measure the angle of the three-dimensional fascicle within a muscle. Moreover, the muscle moment arms

Table 2A Morphometric data for the muscles of the forelimb in the orangutans

		O1			O2			O3		
	Abbreviation	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)
Teres major	TMa	189.1	14.36	12.4	176.7	20.18	8.3	26.6	2.15	11.7
Teres minor	TMi	47.7	6.90	6.5	55.3	10.63	4.9	6.8	1.34	4.8
Deltoideus, pars clavicularis	DC	190.5	16.20	11.1	169.4	13.26	12.1	21.3	2.39	8.4
Deltoideus, pars acromialis	DA	398.2	47.14	8.0	288.0	33.39	8.1	51.1	6.93	7.0
Deltoideus, pars scapularis	DS	104.6	11.08	8.9	100.2	11.80	8.0	12.9	1.21	10.0
Supraspinatus	Sp	202.4	33.32	5.7	121.8	18.71	6.1	14.1	3.81	3.5
Infraspinatus	If	254.3	25.95	9.2	250.3	32.15	7.3	33.9	4.77	6.7
Subscapularis	Sb	449.4	52.63	8.1	353.8	57.29	5.8	50.7	10.04	4.8
Biceps brachii, caput longum	BL	164.6	9.26	16.8	147.6	10.16	13.7	17.8	1.71	9.9
Biceps brachii, caput breve	BS	110.3	5.20	20.0	134.9	7.37	17.3	20.1	1.50	12.7
Coracobrachialis medius	CoM	78.5	13.67	5.4	74.0	13.50	5.2	12.4	2.59	4.5
Coracobrachialis longus	CoL	–	–	–	–	–	–	–	–	–
Brachialis	B	412.7	28.90	13.5	449.4	35.79	11.8	57.1	7.37	7.3
Dorsoepitrochlearis	DE	50.4	4.92	9.7	65.4	7.88	7.8	5.9	0.53	10.5
Triceps brachii, caput longum	TLo	172.2	19.50	8.3	141.8	16.28	8.2	22.3	2.15	9.8
Triceps brachii, caput laterale	TLa	235.7	23.04	9.7	179.9	18.62	9.1	25.4	2.87	8.3
Triceps brachii, caput mediale	TMe	325.5	32.80	9.4	199.6	23.47	8.0	31.7	4.22	7.1
Anconeus	AL	17.1	5.28	3.0	13.1	6.37	1.9	1.0	0.26	3.5
Brachioradialis	Br	379.5	14.36	24.9	438.9	18.93	21.9	61.6	4.22	13.8
Extensor carpi radialis longus	ECRL	46.4	4.08	10.7	64.8	4.62	13.2	10.0	1.36	7.0
Extensor carpi radialis brevis	ECRB	87.6	8.74	9.5	75.5	9.50	7.5	11.8	1.92	5.8
Extensor digitorum 2	EDC2	27.3	2.33	11.1	26.7	3.27	7.7	5.5	0.70	7.5
Extensor digitorum 3	EDC3	32.8	2.97	10.4	26.9	3.14	8.1	4.1	0.76	5.1
Extensor digitorum 4	EDC4	26.7	2.40	10.5	19.8	2.52	7.4	2.9	0.48	5.7
Extensor digitorum 5	EDC5	29.0	2.53	10.8	18.5	2.51	6.9	8.8	0.93	8.9
Extensor indicis 2	EI2	12.2	1.24	9.3	7.4	0.99	7.1	2.6	0.35	7.1
Extensor indicis 3	EI3	13.8	1.59	8.2	7.2	1.15	5.9	4.0	0.58	6.5
Extensor digiti minimi 4	EDM4	7.6	0.85	8.5	10.4	1.63	6.0	1.8	0.23	7.2
Extensor digiti minimi 5	EDM5	8.3	0.90	8.7	10.3	1.35	7.2	2.7	0.31	8.3
Extensor carpi ulnaris	ECU	76.5	9.28	7.8	70.8	12.51	5.3	10.7	1.77	5.7
Supinator	Spn	105.3	21.94	4.5	88.3	23.02	3.6	11.1	4.18	2.5
Abductor pollicis longus	APL	68.7	8.33	7.8	57.9	12.63	4.3	11.9	3.13	3.6
Extensor pollicis longus	EPL	15.5	1.64	8.9	13.6	1.74	7.4	2.2	0.37	5.6
Pronator teres, caput humerale	PTh	80.4	12.03	6.3	60.7	10.01	5.7	7.4	1.49	4.7
Pronator teres, caput ulnare	PTu	20.5	4.16	4.7	18.6	4.14	4.2	7.3	1.86	3.7
Flexor carpi radialis	FCR	124.1	12.95	9.0	103.0	18.35	5.3	17.8	2.76	6.1
Palmaris longus	PL	42.8	4.62	8.8	32.4	5.65	5.4	4.1	0.54	7.2
Flexor carpi ulnaris	FCU	118.8	12.36	9.1	84.7	16.88	4.7	13.7	2.01	6.4
Flexor digitorum superficialis 2	FDS2	50.5	7.73	6.2	47.7	12.25	3.7	6.5	0.80	7.7
Flexor digitorum superficialis 3	FDS3	84.9	9.35	8.6	68.1	11.47	5.6	10.7	1.07	9.4
Flexor digitorum superficialis 4	FDS4	71.9	6.89	9.8	57.7	9.38	5.8	5.7	0.61	8.9
Flexor digitorum superficialis 5	FDS5	28.6	3.17	8.5	26.5	4.92	5.1	2.8	0.32	8.3
Flexor digitorum profundus 2	FDP2	111.4	7.38	14.2	70.4	9.03	7.4	16.0	1.49	10.2
Flexor digitorum profundus, caput accessorium	FDPa	–	–	–	–	–	–	3.8	0.41	8.7
Flexor digitorum profundus 3	FDP3	132.1	8.17	15.3	114.2	12.51	8.6	29.2	2.44	11.3
Flexor digitorum profundus 4	FDP4	134.3	7.77	16.3	102.4	10.08	9.6	18.3	1.79	9.6
Flexor digitorum profundus 5	FDP5	83.3	4.75	16.5	73.5	7.71	9.0	10.2	1.00	9.6
Pronator quadratus	PQ	16.9	6.67	2.4	11.8	5.02	2.2	3.1	1.22	2.4
Abductor pollicis brevis	APB	13.5	2.80	4.5	15.9	3.80	4.0	2.2	0.58	3.6
Flexor pollicis brevis	FPB	12.7	3.65	3.3	12.2	3.95	2.9	0.9	0.61	1.5
Opponens pollicis	OP	4.0	1.46	2.6	5.9	1.92	2.9	1.0	0.42	2.3
Adductor pollicis	AP	32.2	6.57	4.6	32.0	7.58	4.0	1.2	0.48	2.4
Abductor digiti minimi	ADM	13.7	2.79	4.6	17.9	5.39	3.1	2.4	0.61	3.7
Flexor digiti minimi brevis	FDMB	10.0	1.99	4.8	6.0	1.77	3.2	1.1	0.32	3.4

Table 2A *Continued*

		O1			O2			O3		
	Abbreviation	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)
Opponens digiti minimi	ODM	6.3	3.43	1.7	6.7	4.18	1.5	0.7	0.66	1.0
Dorsal interosseus 1	DI1	39.7	7.98	4.7	39.3	10.39	3.6	6.7	2.36	2.7
Dorsal interosseus 2	DI2	21.3	6.07	3.3	21.9	8.19	2.5	4.7	1.74	2.6
Dorsal interosseus 3	DI3	15.6	4.69	3.1	13.1	5.01	2.5	1.8	0.66	2.5
Dorsal interosseus 4	DI4	16.3	5.49	2.8	15.0	5.27	2.7	2.2	0.89	2.4
Palmar interosseus 1	PI1	11.5	2.65	4.1	8.3	3.34	2.3	2.2	0.65	3.2
Palmar interosseus 2	PI2	6.0	1.66	3.4	6.5	2.31	2.6	2.0	0.58	3.3
Palmar interosseus 3	PI3	9.0	2.27	3.7	5.4	2.15	2.3	1.7	0.49	3.2
Lumbricalis 1	L1	6.0	0.54	10.6	3.5	0.41	8.1	0.6	0.06	9.3
Lumbricalis 2	L2	8.6	0.78	10.3	4.1	0.46	8.5	0.8	0.08	10.0
Lumbricalis 3	L3	6.7	0.63	10.1	3.7	0.33	10.8	0.7	0.07	9.4
Lumbricalis 4	L4	3.9	0.36	10.3	2.2	0.21	9.9	0.3	0.04	6.6

In the orangutan *M. extensor indicis* was partially separated into two bundles, and inserted into both the second and third digits; *M. extensor digiti minimi* also consisted of two partially-separated bundles inserted into the fourth and fifth digits; in one orangutan (O3) *M. flexor digitorum profundus* had a weak bundle as an accessory head, which arose from a capsule in the elbow joint and the coracoid process of the ulna with *M. flexor digitorum superficialis*. These noted differences are consistent with previous reports (Sonntag, 1924; Sullivan & Osgood, 1927; Oishi et al. 2008). The mass of the fixed specimens (O1 and O2) was based on the wet weight of the fixed muscles, which were weighed after immersion in water overnight. For O3 data see previous study (Oishi et al. 2008). PCSA, physiological cross-sectional area; FL, fascicle length.

Table 2B Morphometric data for the muscles of the forelimb in the chimpanzees

	C1			C2			C3			C4		
Abbreviation	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)
TMa	292.8	21.66	12.8	162.7	11.21	13.7	149.1	10.57	13.3	98.5	7.32	12.7
TMi	45.1	8.18	5.2	24.7	4.01	5.8	34.1	6.58	4.9	20.5	3.14	6.2
DC	118.6	12.10	9.2	79.6	6.55	11.5	67.3	5.92	10.7	50.9	5.14	9.3
DA	222.9	33.97	6.2	225.3	29.86	7.1	216.4	32.90	6.2	116.0	19.08	5.7
DS	88.1	7.47	11.2	61.5	4.39	13.2	56.8	4.45	12.1	38.5	3.29	11.0
Sp	113.7	26.60	4.1	77.9	17.45	4.2	107.5	22.53	4.5	52.6	13.09	3.8
If	233.2	30.73	7.2	178.8	21.45	7.9	180.9	29.15	5.9	110.3	16.35	6.4
Sb	303.0	46.07	6.2	195.5	27.68	6.7	207.9	25.64	7.7	154.9	25.10	5.8
BL	137.8	10.95	11.8	78.4	4.92	15.0	104.4	6.75	14.6	62.2	5.60	10.5
BS	191.1	14.22	12.7	139.3	8.11	16.2	87.2	4.06	20.3	77.1	5.86	12.4
CoM	58.8	12.15	4.6	52.8	8.08	6.2	36.0	5.83	5.8	30.5	5.35	5.4
CoL	–	–	–	–	–	–	29.3	4.49	6.2	–	–	–
B	247.9	28.91	8.1	151.2	13.92	10.3	136.1	11.96	10.7	106.4	12.90	7.8
DE	51.2	5.10	9.4	45.4	3.18	13.5	24.2	1.81	12.6	22.7	1.81	11.9
TLo	155.9	19.86	7.4	168.6	13.96	11.4	180.8	18.11	9.4	92.0	9.61	9.0
TLa	161.1	22.87	6.7	143.9	13.31	10.2	222.2	22.35	9.4	85.2	9.84	8.2
TMe	218.6	35.10	5.9	264.1	28.67	8.7	132.7	17.21	7.3	126.9	16.97	7.1
AL	12.3	3.18	3.7	11.1	2.89	3.6	8.0	1.88	4.0	5.8	1.50	3.6
Br	151.4	8.58	16.7	85.2	3.55	22.7	82.3	3.42	22.7	78.6	4.31	17.2
ECRL	35.4	4.26	7.9	47.1	3.54	12.5	43.5	3.81	10.8	18.5	2.24	7.8
ECRB	38.2	6.78	5.3	39.8	5.48	6.9	45.8	6.95	6.2	23.2	4.08	5.4
EDC2	21.1	2.63	7.6	19.4	2.00	9.1	10.4	1.17	8.4	10.6	1.37	7.3
EDC3	27.0	2.86	8.9	20.0	1.91	9.9	23.8	2.41	9.3	14.8	1.66	8.4
EDC4	23.8	2.83	7.9	22.2	2.43	8.6	14.5	1.68	8.1	10.5	1.27	7.8
EDC5	7.7	0.99	7.3	5.0	0.50	9.4	5.9	0.71	7.8	1.6	0.19	8.0
EI2	4.7	0.71	6.2	12.8	1.52	8.0	4.0	0.55	6.8	3.1	0.52	5.7
EI3	–	–	–	–	–	–	–	–	–	–	–	–

Table 2B *Continued*

	C1			C2			C3			C4		
Abbreviation	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)	Mass (g)	PCSA (cm^2)	FL (cm)
EDM4	–	–	–	–	–	–	–	–	–	–	–	–
EDM5	11.5	1.70	6.3	6.6	0.96	6.5	6.2	0.92	6.4	7.2	0.98	6.9
ECU	28.1	5.73	4.6	25.9	4.66	5.2	31.0	6.49	4.5	19.0	3.21	5.6
Spn	73.9	22.28	3.1	64.6	17.50	3.5	49.7	14.86	3.2	36.9	12.60	2.8
APL	47.4	11.68	3.8	39.2	9.81	3.8	35.1	7.40	4.5	32.3	8.69	3.5
EPL	7.9	1.46	5.2	7.3	1.26	5.5	3.8	0.75	4.8	5.0	0.86	5.4
PTh	67.3	11.86	5.4	51.2	11.14	4.3	29.8	4.34	6.5	28.1	6.71	3.9
PTu	4.3	0.97	4.1	–	–	–	13.1	3.65	3.4	–	–	–
FCR	99.2	15.66	6.0	96.1	12.82	7.1	50.7	8.20	5.8	47.4	6.84	6.5
PL	11.0	2.33	4.5	6.6	1.43	4.4	7.9	1.23	6.1	3.0	0.76	3.8
FCU	74.2	16.47	4.3	74.4	13.67	5.1	67.6	13.24	4.8	36.9	8.12	4.3
FDS2	36.9	12.87	2.7	31.0	6.97	4.2	25.7	5.03	4.8	16.6	4.27	3.7
FDS3	77.4	12.46	5.9	52.8	5.98	8.3	57.6	6.87	7.9	45.0	7.24	5.9
FDS4	33.7	5.98	5.2	37.7	4.09	8.7	57.3	6.45	8.4	30.6	5.58	5.2
FDS5	38.7	7.43	4.8	12.9	1.99	6.1	8.8	1.27	6.5	11.2	2.59	4.1
FDP2	70.7	10.45	6.4	35.0	3.90	8.5	37.6	4.41	8.1	26.6	3.36	7.5
FDPa	–	–	–	–	–	–	–	–	–	–	–	–
FDP3	77.1	9.03	8.1	55.4	4.87	10.7	56.8	5.49	9.8	47.8	5.36	8.4
FDP4	89.6	11.78	7.2	56.8	6.13	8.7	53.4	5.45	9.2	38.6	4.96	7.3
FDP5	57.0	9.20	5.9	36.0	4.79	7.1	26.5	3.51	7.1	30.0	4.92	5.8
PQ	12.9	7.82	1.6	14.8	5.05	2.8	10.4	4.63	2.1	8.6	3.78	2.1
APB	10.1	3.56	2.7	6.4	1.88	3.2	3.1	1.06	2.8	4.0	1.21	3.1
FPB	6.1	2.69	2.1	1.9	0.66	2.7	2.9	1.02	2.7	1.9	0.64	2.8
OP	2.0	1.34	1.5	5.1	1.99	2.4	3.4	1.74	1.9	2.9	1.12	2.4
AP	15.4	4.58	3.2	10.9	3.18	3.2	9.5	2.63	3.4	6.5	2.04	3.0
ADM	11.6	4.84	2.3	12.8	4.42	2.7	8.3	2.42	3.2	6.6	2.49	2.5
FDMB	1.6	0.63	2.4	2.5	0.73	3.2	1.5	0.49	2.9	1.8	0.60	2.9
ODM	3.7	3.05	1.1	3.2	3.18	1.0	3.4	2.56	1.2	2.2	1.15	1.8
DI1	19.7	8.46	2.2	16.8	7.12	2.2	12.5	5.19	2.3	8.1	3.91	2.0
DI2	13.8	7.10	1.8	8.0	4.67	1.6	7.9	3.14	2.4	6.7	3.32	1.9
DI3	9.3	4.73	1.9	7.9	4.21	1.8	5.3	2.20	2.3	4.2	2.49	1.6
DI4	9.3	5.29	1.7	8.0	3.60	2.1	5.5	1.93	2.7	5.5	2.88	1.8
PI1	5.9	2.58	2.2	10.4	3.50	2.8	3.5	1.08	3.1	3.0	1.29	2.2
PI2	5.4	2.69	1.9	6.2	1.93	3.0	3.4	0.89	3.6	3.2	1.40	2.1
PI3	5.8	2.69	1.9	4.3	2.48	1.6	3.0	1.19	2.4	2.2	1.21	1.7
L1	2.5	0.28	8.5	2.5	0.30	8.0	1.7	0.22	7.2	1.5	0.17	8.2
L2	2.2	0.20	10.3	2.2	0.21	10.1	2.0	0.21	8.7	1.6	0.18	8.7
L3	2.0	0.19	9.9	0.9	0.09	9.2	1.5	0.16	9.1	1.8	0.19	9.0
L4	1.8	0.18	9.5	1.2	0.10	11.2	0.5	0.05	9.4	0.8	0.09	9.0

In two chimpanzees (C1 and C3) *M. pronator teres* had a bundle as an ulnar head. One chimpanzee (C3) possessed *M. coracobrachialis brevis* and *M. coracobrachialis longus*. The former was inserted into the middle of the humerus and the latter into the medial epicondyle of the humerus. These noted differences are consistent with previous reports (Sullivan & Osgood, 1927). In C1 left and right values were averaged. Muscle name abbreviations are as detailed in Table 2A. PCSA, physiological cross-sectional area; FL, fascicle length.

were not measured in this study because such measurements are technically difficult without an experimental setup as in Payne (2001). For C1, both right and left forelimbs were dissected; hence, the right and left values were averaged to obtain the data listed in Table 2.

The mass of each muscle was divided by the total muscle mass of the forelimb to calculate the mass ratio. The PCSA ratio was also calculated in the same way. The muscle parameters were not normalized by body mass as in Payne (2001) because the body mass was not available for every specimen used in the present study. Each mean fascicle length was normalized by dividing by upper arm length (Table 1) because Drapeau & Ward (2007) indicated that humeral length is fairly conservative in orangutans and chimpanzees, although the ulna of orangutans is relatively longer than that of African apes. The normalized fascicle was calculated as the weighted harmonic mean (i.e. the significance of each individual fascicle length weight by the muscle mass) (Alexander et al. 1981). These normalizations allow comparisons of muscle dimensions between the orangutan and chimpanzee. The significance of differences in the mean mass ratios and PCSA ratios between the two species was examined by the nonparametric U-test ($P < 0.05$) using SPSS 11.0J (SPSS, Chicago, IL, USA). The coefficient of variation was calculated for each muscle to assess variability.

Results

The measured muscle mass, PCSA and fascicle length of all forelimb muscles are presented in Table 2. For each individual, mean ratios (± standard deviation) of measured to species-average muscle mass, PCSA and fascicle length were computed for comparisons. The mean ratios of muscle mass were 1.50 (± 0.18), 1.28 (± 0.18) and 0.22 (± 0.09) for O1, O2 and O3, respectively, and 1.33 (± 0.26), 1.09 (± 0.25), 0.91 (± 0.21) and 0.67 (± 0.13) for C1, C2, C3 and C4, respectively, suggesting that, in both species, male muscles were absolutely larger than those of females (O3 and C4) and the muscles of O3 were particularly small. The mean PCSA ratios were 1.30 (± 0.21), 1.44 (± 0.21) and 0.25 (± 0.10) for O1, O2 and O3, respectively, and 1.44 (± 0.27), 0.99 (± 0.23), 0.85 (± 0.22) and 0.71 (± 0.14) for C1, C2, C3 and C4, respectively, showing similar tendencies as those for muscle mass. The mean fascicle length ratios were 1.18 (± 0.11), 0.92 (± 0.14) and 0.90 (± 0.16) for O1, O2 and O3, respectively, and 0.91 (± 0.10), 1.08 (± 0.10), 1.07 (± 0.11) and 0.94 (± 0.11) for C1, C2, C3 and C4, respectively. Unlike mass and PCSA, both species showed a small degree of sex-related variation in fascicle length.

Comparisons of the mean mass and PCSA ratios in the orangutans and chimpanzees are presented in Table 3. The means of the coefficients of variation were 0.21 and 0.24 for the mass ratios and PCSA ratios, respectively, in the orangutan and 0.21 and 0.23, respectively, in the chimpanzee, indicating that some inter-individual differences actually exist in both species.

We confirmed that the muscle dimensions of the forelimb were essentially similar in both species, as shown in Table 3. However, the statistical analyses showed that there were some significant differences in the mass and PCSA ratios between the orangutans and chimpanzees. The mass and PCSA ratios of the elbow flexors (*M. brachialis* and *M. brachioradialis*) were larger in the orangutans, indicating that the orangutans are equipped with larger monoarticular elbow flexors (Table 3). In contrast, the mass ratios of the biarticular muscles in the upper arm (the short head of *M. biceps brachii* and long head of *M. triceps brachii*) and *M. teres major* were larger in the chimpanzees. For the rotator cuff muscles, the PCSA ratio of *M. subscapularis* was significantly larger in the orangutans, whereas that of *M. infraspinatus* was larger in the chimpanzees. The PCSA ratios of the wrist and digital II–V extensors tended to be larger in the orangutans, whereas those of the flexors were larger in the chimpanzees, although they were not significantly different. In the intrinsic hand muscles, the mass ratios of the interosseous muscles and the PCSA ratios of the lumbrical muscles were significantly larger in the orangutans.

When the fascicle length was normalized by the upper arm length, the fascicles of the shoulder retractor and digital II–V extensor muscles were longer in the chimpanzees, whereas those of the interosseous muscle were longer in the orangutans (Table 3). Although the differences between the two species were not significant, the digital II–V flexors were slightly longer in the orangutans than in the chimpanzees.

Discussion

The present study presents the complete set of muscle parameters for both the orangutan and chimpanzee based on multiple individuals, allowing comparative evaluation of the biomechanical capacity of the forelimb muscles in the two species. In our previous report on the orangutan's muscle dimensions based on a single individual (O3) (Oishi et al. 2008), we suggested that orangutans tend to possess larger PCSA (i.e. force-generating capacity) in the elbow flexors, notably *M. brachioradialis*, and smaller PCSA in the wrist and the digital II–V flexor muscles than chimpanzees. In this study, such tendencies were confirmed in a larger number of specimens (Table 3).

As preliminarily suggested by our previous study (Oishi et al. 2008) and clearly confirmed by the present study, the monoarticular elbow flexor muscles, *M. brachialis* and *M. brachioradialis*, were much larger in the orangutans than in the chimpanzees (Table 3). This tendency was also observed by Payne (2001). We attributed this morphological specialization to arboreal locomotion, such as vertical climbing, and torso-orthograde suspensory locomotion because the elbow flexors are important for weight suspension and progression in trees (see Oishi et al. 2008). In particular, Thorpe & Crompton (2006) suggested, based on their complete orangutan positional behavior dataset, that it is the presence of pronograde suspensory posture and locomotion that distinguishes the orangutan from the African apes. Such differences in locomotion might be functionally aligned to the above morphological specialization in the elbow muscles.

Furthermore, the present study demonstrated that the brachial biarticular muscles, namely the long head of *M. triceps brachii* and the short head of *M. biceps brachii*, had relatively smaller mass ratios in the orangutans than in the chimpanzees (Table 3). Electromyographic studies of forelimb muscles during knuckle-walking in chimpanzees suggested that the *M. triceps brachii* is active during the stance phase to retract the humerus while maintaining the elbow joint in extension for vaulting the body over it (Tuttle et al. 1983). Although this activity was reported to be modest during horizontal knuckle-walking in an experimental setting, the activity tended to be much increased in the natural environments, as the electromyographic activity increases when the chimpanzees walk up and down a slope (Tuttle et al. 1983). Therefore, the large *M. triceps*

Table 3 Comparisons of forelimb mass and physiological cross-sectional area (PCSA) ratios between the orangutan and chimpanzee

	Mass ratio (%)		PCSA ratio (%)		FL/upper arm length	
	Orangutan (SD)	Chimpanzee (SD)	Orangutan (SD)	Chimpanzee (SD)	Orangutan (SD)	Chimpanzee (SD)
Shoulder protractors						
DC	3.2 (0.33)	2.6 (0.27)	2.3 (0.34)	1.7 (0.21)	0.32 (0.052)	0.37 (0.048)
Co	1.5 (0.13)	1.7 (0.34)	2.3 (0.14)	2.1 (0.38)	0.15 (0.011)	0.20 (0.029)
Subtotal	4.7 (0.22)	4.3 (0.17)	4.6 (0.41)	3.9 (0.32)	0.23 (0.029)	0.27 (0.036)
Shoulder retractors						
TMa	3.5 (0.13)	5.7 (1.09)	2.5 (0.59)	2.9 (0.48)	0.32 (0.069)	0.47 (0.038)
TMi	1.0 (0.15)	1.0 (0.17)	1.4 (0.27)	1.3 (0.32)	0.16 (0.008)	0.20 (0.034)
DS	1.9 (0.15)	2.0 (0.12)	1.6 (0.42)	1.2 (0.07)	0.27 (0.058)	0.43 (0.053)
Subtotal	6.3 (0.37)	8.7 (1.27)	5.5 (1.16)	5.3 (0.70)	0.27 (0.043)	0.40 (0.048)
Shoulder abductor						
DA	6.5 (0.64)	6.5 (0.91)	6.5 (1.34)	7.0 (1.24)	0.23 (0.024)	0.23 (0.031)
Rotator cuffs						
Sp	2.6 (0.86)	2.9 (0.52)	4.0 (1.39)	4.8 (0.73)	0.15 (0.037)	0.15 (0.008)
If	4.7 (0.33)	5.8 (0.24)	4.6 (0.37)	5.9 (1.13)	0.23 (0.006)	0.25 (0.046)
Sb	7.3 (0.60)	7.2 (0.73)	9.0 (0.24)	7.4 (0.84)	0.18 (0.023)	0.24 (0.018)
Subtotal	14.6 (1.42)	16.0 (1.09)	17.6 (0.99)	18.1 (1.55)	0.19 (0.016)	0.22 (0.021)
Biarticular elbow extensors						
TLo	3.0 (0.08)	5.1 (0.98)	2.6 (0.64)	3.7 (0.68)	0.27 (0.059)	0.34 (0.072)
DE	1.0 (0.28)	1.2 (0.26)	0.8 (0.37)	0.7 (0.17)	0.28 (0.062)	0.43 (0.074)
Subtotal	4.0 (0.22)	6.2 (0.87)	3.3 (1.13)	4.4 (0.56)	0.27 (0.059)	0.35 (0.073)
Biarticular elbow flexors						
BL	2.8 (0.33)	3.2 (0.47)	1.6 (0.02)	1.7 (0.30)	0.40 (0.056)	0.47 (0.078)
BS	2.4 (0.44)	4.0 (0.78)	1.1 (0.26)	1.9 (0.56)	0.49 (0.058)	0.55(0.103)
Subtotal	5.2 (0.45)	7.2 (0.70)	2.7 (0.27)	3.5 (0.62)	0.44 (0.052)	0.50 (0.082)
Monoarticular elbow extensors						
TLa	3.7 (0.40)	5.2 (1.65)	3.1 (0.64)	4.1 (1.18)	0.27 (0.020)	0.31 (0.062)
TMe	4.7 (0.93)	6.2 (1.68)	4.4 (1.00)	5.8 (1.09)	0.24 (0.006)	0.26 (0.052)
AL	0.2 (0.09)	0.3 (0.03)	0.7 (0.41)	0.6 (0.11)	0.09 (0.029)	0.13 (0.004)
Subtotal	8.6 (1.37)	11.7 (1.57)	8.4 (1.63)	10.4 (0.68)	0.24 (0.011)	0.27 (0.049)
Monoarticular elbow flexors						
B	8.0 (0.97)	5.3 (0.69)	5.7 (1.00)	3.9 (0.79)	0.32 (0.065)	0.33 (0.049)
Br	7.9 (1.12)	3.3 (0.66)	3.1 (0.76)	1.2 (0.32)	0.60 (0.115)	0.71 (0.117)
Subtotal	15.9 (2.00)	8.6 (1.29)	8.8 (1.75)	5.1 (1.10)	0.42 (0.079)	0.42 (0.057)
Wrist extensors						
ECRL	1.2 (0.29)	1.2 (0.34)	0.9 (0.32)	0.8 (0.13)	0.31 (0.093)	0.35 (0.090)
ECRB	1.5 (0.02)	1.2 (0.25)	1.6 (0.17)	1.4 (0.28)	0.22 (0.026)	0.21 (0.032)
ECU	1.4 (0.05)	0.9 (0.16)	1.7 (0.21)	1.2 (0.32)	0.19 (0.018)	0.18 (0.030)
Subtotal	4.1 (0.34)	3.3 (0.68)	4.2 (0.48)	3.5 (0.72)	0.22 (0.016)	0.24 (0.042)
Wrist flexors						
FCR	2.2 (0.14)	2.4 (0.55)	2.5 (0.35)	2.6 (0.46)	0.20 (0.034)	0.23 (0.035)
PL	0.6 (0.11)	0.2 (0.06)	0.7 (0.20)	0.3 (0.06)	0.21 (0.039)	0.17 (0.023)
FCU	1.9 (0.20)	2.1 (0.28)	2.2 (0.40)	3.1 (0.39)	0.20 (0.046)	0.17 (0.020)
Subtotal	4.7 (0.29)	4.8 (0.61)	5.4 (0.82)	6.0 (0.69)	0.20 (0.038)	0.19 (0.025)
Digital II–V extensors						
EDC	2.2 (0.51)	2.0 (0.11)	2.0 (0.51)	1.6 (0.08)	0.25 (0.022)	0.30 (0.031)
EI	0.5 (0.30)	0.2 (0.14)	0.6 (0.27)	0.2 (0.12)	0.22 (0.015)	0.24 (0.043)
EDM	0.4 (0.16)	0.3 (0.07)	0.4 (0.11)	0.3 (0.04)	0.23 (0.031)	0.23 (0.023)
Subtotal	3.2 (0.94)	2.4 (0.22)	3.0 (0.85)	2.1 (0.18)	0.24 (0.017)	0.29 (0.029)
Digital II–V flexors						
FDS	3.9 (0.39)	4.9 (0.46)	4.4 (1.68)	5.7 (0.97)	0.22 (0.070)	0.21 (0.042)
FDP	8.6 (1.55)	6.6 (0.83)	5.8 (0.99)	5.7 (0.95)	0.34 (0.065)	0.28 (0.037)
Subtotal	12.4 (1.20)	11.5 (1.10)	10.2 (1.66)	11.5 (1.90)	0.28 (0.062)	0.25 (0.039)
Pollicis extensors						
APL	1.3 (0.22)	1.3 (0.23)	2.1 (0.75)	2.3 (0.49)	0.15 (0.042)	0.14 (0.006)
EPL	0.3 (0.01)	0.2 (0.06)	0.3 (0.04)	0.3 (0.05)	0.22 (0.024)	0.19 (0.024)

Table 3 *Continued*

	Mass ratio (%)		PCSA ratio (%)		FL/upper arm length	
	Orangutan (SD)	Chimpanzee (SD)	Orangutan (SD)	Chimpanzee (SD)	Orangutan (SD)	Chimpanzee (SD)
Subtotal	1.6 (0.23)	1.5 (0.27)	2.4 (0.79)	2.6 (0.53)	0.16 (0.040)	0.14 (0.005)
Pronators						
PT	1.8 (0.17)	1.6 (0.16)	2.7 (0.45)	2.3 (0.32)	0.15 (0.013)	0.17 (0.017)
PQ	0.3 (0.09)	0.4 (0.07)	1.0 (0.20)	1.3 (0.04)	0.07 (0.010)	0.08 (0.021)
Subtotal	2.1 (0.26)	2.0 (0.15)	3.7 (0.63)	3.6 (0.32)	0.13 (0.009)	0.13 (0.010)
Supinator						
Spn	1.7 (0.20)	1.9 (0.15)	3.7 (0.14)	4.1 (0.31)	0.10 (0.017)	0.11 (0.014)
Thenar muscles						
APB	0.3 (0.04)	0.2 (0.06)	0.5 (0.06)	0.4 (0.13)	0.12 (0.003)	0.11 (0.016)
FPB	0.2 (0.06)	0.1 (0.04)	0.6 (0.03)	0.3 (0.12)	0.07 (0.022)	0.09 (0.013)
OP	0.1 (0.03)	0.1 (0.05)	0.3 (0.07)	0.4 (0.12)	0.08 (0.011)	0.07 (0.020)
AP	0.5 (0.26)	0.3 (0.03)	0.9 (0.40)	0.7 (0.05)	0.11 (0.023)	0.12 (0.005)
Subtotal	1.1 (0.31)	0.8 (0.08)	2.4 (0.38)	1.8 (0.17)	0.10 (0.016)	0.10 (0.011)
Hypothenar muscles						
ADM	0.3 (0.06)	0.3 (0.06)	0.6 (0.20)	0.8 (0.19)	0.11 (0.014)	0.10 (0.011)
FDMB	0.2 (0.03)	0.1 (0.03)	0.3 (0.03)	0.2 (0.05)	0.11 (0.012)	0.10 (0.016)
ODM	0.1 (0.02)	0.1 (0.01)	0.6 (0.04)	0.6 (0.18)	0.04 (0.007)	0.05 (0.015)
Subtotal	0.6 (0.05)	0.5 (0.08)	1.5 (0.21)	1.6 (0.32)	0.08 (0.005)	0.08 (0.009)
Interossei						
DI1	0.8 (0.10)	0.5 (0.06)	1.7 (0.43)	1.5 (0.21)	0.11 (0.016)	0.08 (0.005)
DI2	0.5 (0.13)	0.3 (0.05)	1.3 (0.30)	1.1 (0.17)	0.08 (0.004)	0.07 (0.007)
DI3	0.3 (0.02)	0.2 (0.03)	0.7 (0.10)	0.8 (0.20)	0.08 (0.005)	0.07 (0.006)
DI4	0.3 (0.01)	0.2 (0.04)	0.9 (0.06)	0.8 (0.21)	0.08 (0.006)	0.07 (0.012)
PI1	0.2 (0.06)	0.2 (0.10)	0.5 (0.08)	0.5 (0.26)	0.10 (0.020)	0.09 (0.014)
PI2	0.2 (0.09)	0.2 (0.04)	0.4 (0.13)	0.4 (0.12)	0.09 (0.016)	0.09 (0.025)
PI3	0.2 (0.06)	0.1 (0.02)	0.4 (0.06)	0.4 (0.13)	0.09 (0.018)	0.07 (0.007)
Subtotal	2.4 (0.39)	1.7 (0.23)	5.9 (0.83)	5.5 (1.14)	0.09 (0.003)	0.08 (0.006)
Lumbricales						
L1	0.1 (0.02)	0.1 (0.01)	0.1 (0.02)	0.1 (0.01)	0.28 (0.031)	0.29 (0.037)
L2	0.1 (0.03)	0.1 (0.01)	0.1 (0.03)	0.1 (0.01)	0.29 (0.041)	0.34 (0.046)
L3	0.1 (0.02)	0.1 (0.03)	0.07 (0.03)	0.04 (0.02)	0.30 (0.038)	0.34 (0.028)
L4	0.05 (0.02)	0.04 (0.01)	0.04 (0.01)	0.02 (0.01)	0.26 (0.043)	0.35 (0.053)
Subtotal	0.3 (0.09)	0.2 (0.04)	0.3 (0.09)	0.2 (0.03)	0.29 (0.020)	0.32 (0.036)

Mass ratios and PCSA ratios were calculated as a subtotal of the constituent muscles of muscle groups and normalized fascicle as weighted harmonic mean (Alexander et al. 1981). Standard deviations (SD) are shown in parentheses. Underline indicates statistically significant larger value ($P < 0.05$). FL, fascicle length. Muscle name abbreviations are as detailed in Table 2A.

brachii seems to enhance terrestrial locomotion in the chimpanzee, which actually travels more frequently on the ground.

However, what is enigmatic is that *M. biceps brachii*, the antagonistic muscle of *M. triceps brachii*, was also relatively larger in the chimpanzees, despite the fact that its synergistic muscles, *M. brachialis* and *M. brachioradialis* (Tuttle et al. 1983; Tuttle & Cortright, 1988), were larger in the orangutans (Table 3). The explanation for this is obscure but it might be linked to a difference in the speed of movements. For example, when apes climb vertically, they lift the body load by simultaneous shoulder retraction and elbow flexion (Tuttle et al. 1983; Larson & Stern, 1986). In such circumstances, the shortening velocity of *M. biceps brachii* is lower than that of the elbow flexors because of the concurrent joint movements. The force-generating capacity of a muscle is known to be affected by its shortening velocity; the faster the shortening velocity, the lower the force that it can exert (Nigg & Herzog, 1999). Therefore, the biarticular muscle is more capable of generating force in such movements due to the force–velocity relationship, especially when the movements are fast (van Ingen-Schenau et al. 1990). A monoarticular muscle could be less effective in this regard but joints can be actuated independently. Locomotion of the chimpanzees seems to be quite fast both on the ground and in arboreal settings, whereas that of the orangutans is known to be very slow and cautious (Isler, 2005). This difference in the speed of locomotion might be functionally linked to the difference in the ratio between the mono- and biarticular elbow flexor muscles between the orangutans and chimpanzees. However, it has recently been pointed out that orangutans are actually capable of fast and acrobatic locomotion, despite the fact that they are generally considered cautious, slow climbers (Thorpe & Crompton, 2006). Furthermore, biarticular muscles are also considered to be functionally important for generating favorable energy transfer among the segments by producing moments around the two joints simultaneously, especially in explosive movements such as jumping (e.g. Gregoire et al. 1984; van Soest et al, 1993), and favorable endpoint force that is different from corresponding uniarticular muscles (e.g. Hof, 2001; Ogihara et al. 2009). The actions of biarticular muscles are complex and perplexing. Further biomechanical studies are needed to better clarify the functional meaning of this difference in muscle dimensions.

Another interesting finding of the present study is that the force-generating capacity of *M. subscapularis* was significantly larger in orangutans, whereas the opposite rotator cuff muscle, *M. infraspinatus*, was larger in chimpanzees (Table 3). As a consequence, the PCSA ratio of the *M. subscapularis* is more balanced with the PCSA ratios of *M. infraspinatus* and *M. supraspinatus* in orangutans but the latter are much greater in chimpanzees. Electromyographic data by Larson & Stern (1986, 1987) showed that the three rotator cuff muscles are all active during vertical climbing in the chimpanzee (*M. subscapularis* is highly active in the support phase, and *M. infraspinatus* and *M. supraspinatus* are active in the swing phase) but, during knuckle-walking, *M. subscapularis* is not significantly active, although the other two muscles are. Therefore, the morphology of the rotator cuff muscles also seems to be functionally specialized for terrestrial adaptation in the chimpanzee.

In our previous work, we suggested that the fascicles of the wrist and the digital II–V flexor muscles were longer in the orangutans, resulting in relatively small PCSA ratios (Oishi et al. 2008). Although the same tendency was observed in the present study, the differences in the fascicle lengths normalized by the upper arm length of these muscle groups between the two species were not significant (Table 3). These findings indicate that our previous suggestion was not supported by a larger number of cases due to considerable individual variability. The present study demonstrated that multiple individuals must be studied to compare patterns of muscle dimensions among different species, despite the fact that such opportunities are usually very limited.

In this study, the mass and PCSA ratios were compared to clarify interspecies variations in the forelimb muscle morphology between orangutans and chimpanzees; however, the mass and PCSA of each muscle were not normalized by body mass and (body mass)$^{0.667}$, respectively, assuming a geometric similarity as in other similar studies (e.g. Thorpe et al. 1999; Payne, 2001; Carlson, 2006; Payne et al. 2006). The main reason for this was that body mass was not available for every specimen used but another reason was that the body mass of the same skeletal dimension could be highly variable due to such factors as obesity, aging and nutritional status and may not be always suitable as a baseline. However, our interspecies comparisons based on the ratios certainly do not allow one to determine which muscles are absolutely larger in orangutans and vice versa when corrected for body size. For example, our data do not suggest that the brachial biarticular muscles are absolutely smaller in the orangutan than in the chimpanzee of the same body weight. Comparing muscle parameters of two different animals is difficult. Care must be taken in the interpretation of the present results and comparisons with other data.

Conclusions

The present study presented a complete dataset on the forelimb musculature of the orangutan and chimpanzee based on careful dissection of eight forelimbs of three orangutans and four chimpanzees. We found that the mass and PCSA ratios of the elbow flexors were significantly larger in the orangutans. In contrast, the mass ratios of the biarticular muscles in the upper arm were significantly larger in the chimpanzees. For the rotator cuff muscles, the force-generating capacity of *M. subscapularis* was significantly larger in the orangutans, whereas the opposite rotator cuff muscle, *M. infraspinatus*, was larger in the chimpanzees. These results provide important insights for understanding the function of the forelimb musculature and its relationship to locomotion in orangutans and chimpanzees.

Acknowledgements

The authors would like to thank Dr S. Kawada of the Department of Zoology, National Science Museum, and all the staff of Tama Zoological Park, Nogeyama Zoo, Higashiyama Zoo and Botanical Gardens, Chausuyama Zoo, Yagiyama Zoological Garden, Yamajiboku and the Primate Research Institute of Kyoto University for kindly allowing us to dissect the specimens. The authors also thank Dr N. Kuze for providing us with useful information on positional behavior in orangutans. This study was partly supported by the Cooperation Research Program of the Primate Research Institute, Kyoto University, the JSPS core-to-core program HOPE and a Grant-in-Aid for Scientific Research on Priority Areas 'Emergence of Adaptive Motor Function through Interaction between Body, Brain and Environment' from the Japanese Ministry of Education, Culture, Sports, Science and Technology.

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