Original investigation

Distribution of Muscle Fibers in Skeletal Muscles of the Cheetah (*Acinonyx jubatus*)

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Abstract

We examine the muscle fiber population of skeletal muscles from whole body in the cheetah (*Acinonyx jubatus*). In the present experiments, we showed the characteristics of fiber composition in the cheetah by comparative studies among the cheetah, domestic cat, and the beagle dog. Fiber population was determined on muscle fibers stained with monoclonal antibody to each myosin heavy chain isoform. Histochemical analysis demonstrated that many muscles in the cheetah and domestic cat had a low percentage of Type I fibers and a high percentage of Type IIx fibers, while those in the beagle dog showed a high percentage of Type IIa. The hindlimb muscles in the cheetah had a higher percentage of Type II (Type IIa + IIx) fiber than the forelimb muscles. This fact suggests that the propulsive role of the hindlimb is greater than the forelimb in the cheetah. The longissimus in the cheetah had a high percentage of Type IIx fibers over a wide range from the thoracic to lumbar parts, while the population of muscle fibers in this muscle was different depending on the parts in the domestic cat and beagle dog. This indicates that the cheetah can produce a strong and quick extension of the spinal column and increase its stiffness during locomotion. Furthermore, we found the notable difference of muscle fiber type population between flexors and extensors of digits in the cheetah. The present experiments show the characteristics of muscle fibers in the cheetah, corresponded to its ability to perform high-speed running.

Keywords

cheetah, muscle fiber type, domestic cat, beagle dog

Introduction

The cheetah (*Acinonyx jubatus*) is the best sprinter on earth (Alexander 2003). It has been reported that its running speed reaches at around 29 m/s (Sharp 1997) and mainly depends on prolongation of the stride length (Alexander 2003). The cheetah uses large angular movements of the limb joints and bending of the spine to prolong the stride length (Gambaryan 1974; Hildebrand 1959, 1961). The movements are produced by activation of the muscles. To understand the movements during running in the cheetah, the studies of muscles in the cheetah is indispensable. Hudson et al. extensively studied the skeletal muscles in the cheetah. They calculated the physiological cross-sectional area (PCSA) and moment arm, and showed that the cheetah exhibits several unique skeletal adaptations that mostly act to increase muscle moment arm (Hudson et al. 2011a; 2011b). PCSA was calculated as the muscle volume /fascicle length. Maximum isometric contraction force (F_{max}) was estimated by PCSA (Wells 1965; Medler 2002), and PCSA is useful to understand the balance of F_{max} among many kinds of skeletal muscle.

It is well known that the skeletal muscles contain different types of muscle fiber (Burke, 1981). The muscle fibers can be classified into Type I, Type IIa, Type IIb and Type IIx by staining with monoclonal antibody for each myosin heavy chain (MHC) isoform and metabolic enzyme activities (Pette and Staron 1993; 1997). Type I is a muscle fiber with a high metabolic cost of maintenance and a small force output, Type IIa is a muscle fiber with high metabolic cost of maintenance and larger force output, and Type IIb is a muscle fiber with a low metabolic cost for maintenance and a largest force output. Type IIx has intermediate characteristics between Type IIa and IIb. A single motor neuron and the muscle fibers that it innervates comprise a motor unit. The motoneuron properties are exquisitely matched to the properties of the motor units supplying the muscles and the properties of the muscles themselves (Burke 1991). There are systematic differences in the size, excitability, and corresponding variation of speed, power, and endurance in different types of motor unit. Motor units are classified into S, FR, FI, and FF types (Burke 1991). The muscle fibers in S, FR, FI, and FF types correspond to Type I, Type IIa, Type IIx, and Type IIb, respectively. Henneman (1981) showed the existence of a recruitment order among different types of motor unit on the activation of muscle. The recruitment of motor units is very important for motor performance. On the progression from standing to walking, trotting, and galloping, it was reported that the motor units were recruited from S type to FR type and then FF

type (Burke 1990). It could be considered that the FF or FR type was required to perform high-speed running. Studies of the distribution of different types of muscle fiber are indispensable to understand locomotion in animals. However, studies on muscle fiber compositions are limited to humans and experimental or domestic animals (rat: Ariano et al. 1973; Hintz et al. 1980; cat: Reichmann and Pette 1982; Ariano et al. 1973; dog: Tonilo et al. 2007; horse: Kawai et al. 2009; van den Hoven et al. 1985; human: Essen et al. 1975; Johnson et al. 1973) and studies on the muscle fiber composition of skeletal muscles of the cheetah have not been done. To study the muscle fiber composition, sampling fresh muscles is required. We had a chance to sample muscles from the cheetah within 24 hours after death. In the present experiments, we showed the characteristics of the fiber composition of skeletal muscles of two cheetahs by comparative studies among the cheetah, domestic cat, and beagle dog.

Materials and methods

All experimental procedures were reviewed and approved by the Animal Welfare and Ethics Committee of Yamaguchi University.

Animals

Samples were taken from two adult cheetahs (male: 37kg, female: 35kg) that were obtained from Akiyoshidai Wild Animal Park (Japan). The cheetahs that we studied did not have any disorder of movements. The animals were stored in a freezer at 4℃ just after death. Within 24 hours after death, samples of 50 muscles (43 muscles from the male and 7 muscles from the female, Fig. 1, Tables 1-3) were taken from whole parts of the body. We studied the distribution of different muscle fiber types in a beagle dog (*Canis lupus familiaris*, female: 7.5kg) and domestic cat (*Felis silvestris catus*, male: 3.8kg) to indicate the characteristics of muscles in the cheetah. The domestic cat and beagle dog were obtained from a laboratory animal supplier. They were healthy and without disorder of movements. After death by an overdose of pentobarbital sodium (60~75mg/kg), 32 and 31 muscles were taken from the domestic cat and beagle dog, respectively (Figs. 2-4). Each whole muscle was isolated, and then a 0.25 ~0.70 cm^3 block was taken from the center of the superficial part of each muscle. The samples of m. longissimus were taken from the 8-9th thoracic (T8~9) and the 4~5th lumbar vertebrate (L4-5) levels. The blocks were frozen in liquid nitrogen and stored at -80℃

until analysis. The most important point when making a muscle preparation is the condition of muscles. We confirmed that the muscles sampled within 48 hours after death from the animal body maintained at around 4℃ were useful for staining by monoclonal antibody using rats.

Histochemical Analysis

Four to eight cross-sections of 10μm thickness were obtained from each block of frozen muscles using a cryostat (Leica, Nusslock, Germany) at -20℃. The sections were allowed to warm to room temperature and then preincubated in goat normal serum in 0.2 M phosphate buffer (pH 7.6) at 25℃ for 10 min. Primary monoclonal antibody was then applied: (1) fast myosin, which specifically reacts with MHC-IIa and –IIx (Schiaffino and Reggiani 1994); (2) BA-D58, which specifically reacts with MHC-I; and (3) SC-71, which specifically reacts with MHC-IIa. An antibody that specifically reacts with MHC-IIx was not used to identify Type IIx fibers. The sections were incubated at 25℃ for 180 min, then washed with phosphate buffer and reacts with a secondary antibody conjugated with horseradish peroxidase at 25℃ for 180 min, and then washed with phosphate buffer again. Diaminobenzidine tetrahydrochloride was used as a chromogen to localize peroxidase in secondary antibodies (Kawai et al. 2009). Images of the stained muscle fibers were obtained by microscopy (Nikon E600, Tokyo Japan) and an image-processing system (Nikon DS-U1, Tokyo, Japan). On the basis of immunohistochemical staining images, the fibers were classified as Type I, IIa, and IIx fibers (Fig. 2), and then the population (as a percentage) of each muscle fiber type were calculated in 500 muscle fibers. After sampling the block from each muscle, the muscle weight (MW), fascicle length (FL) and resting pennation angle(ά) were measured to calculate PCSA, (PCSA=MW×cosά/1.059×FL following Medler 2002; Mendez and Keys 1960; Wells 1965).

Statistical Analysis

To determine the level of significance among muscle fiber population of three types of muscle fiber, one-way ANOVA and post-hoc analysis (t-test with Bonferroni adjustment) were used. Significance was set at $P<0.05$.

Results

Population of muscle fiber types in the cheetah

Hind limb muscles (23 hind limb muscles: Table 1)

The mean percentages of Type I, IIa and IIx fibers were 20.7, 29.3 and 50.1%, respectively. Eighteen muscles out of studied 23 muscles showed the highest percentage of Type IIx fibers. The vastus intermedius, soleus, and flexor digitorum profundus had the highest percentage of Type I fibers (63.0, 53.1, and 56.2%, respectively) and had no or very few Type IIx fibers. The extensor digitorum lateralis and flexor digitorum superficialis had the highest percentage of Type IIa fibers (53.3 and 68.1%, respectively).

Neck/trunk muscles (13 neck and trunk muscles: Table 2)

The mean percentages of Type I, IIa and IIx were 28.0, 31.6 and 40.0%, respectively. The splenius, brachiocephalicus, latissimus dorsi, pectoralis profundus, longissimus thoracis (T9), longissimus lumborum (L4), and obliquus extensor abdominis had the highest percentage of Type IIx fibers (37.2, 37.2, 70.3, 84.1, 66.1, 84.1, and 51.1% respectively), while the trapezius cervicis, rhomboideus, and rectus abdominis had the highest percentage of Type I fibers (48.3, 58.6, 39.1%, respectively). Eleven muscles out of 13 muscles included three types of muscle fiber. The rhomboideus and pectoralis superficialis only consisted of Type I and Type IIa fibers.

Forelimb muscles (14 forelimb muscles: Table 3)

The mean percentages of Type I, IIa and IIx were 34.1, 29.9 and 36.0%, respectively. The triceps brachii caput mediale, deltoideus scapular part, supraspinatus, infraspinatus, and teres major had the highest percentage of Type I (68.7, 51.0, 48.9, 65.1, and 37.3%, respectively). The triceps brachii caput longum, biceps brachii, deltoideus acromial part, extensor digitorum communis, extensor digitorum lateralis, and flexor digitorum profundus had a relatively high percentage of Type IIx fibers (49.3, 58.8, 58.0, 41.9, 51.8, and 57.4%, respectively). The triceps brachii caput mediale did not include Type IIx fiber.

PCSAs (Tables 1 and 3) of forelimb and hind limb muscles shown in the present experiment were similar to those reported by Hudson et al. (2011a, 2011b). This fact indicates that our studied cheetahs exhibited similar skeletal muscles to the cheetah studied by Hudson et al. (2011a, 2011b).

Comparison of the muscle fiber type population among the cheetah, domestic cat, and beagle dog.

Figs. 2, 3, and 4 show the population of three types of fiber in the 14 hind limb muscles, 10 neck and trunk muscles, and 8 forelimb muscles of the cheetah (CH), domestic cat (DC), and beagle dog (BD). Type I, IIa, and IIx are shown in black, white, and grey bars, respectively.

The population of muscle fibers of hind limb muscles in the cheetah was similar to the domestic cat, and the muscles mainly consisted of Type IIa and Type IIx fibers. Many hind limb muscles in the beagle dog had a low percentage of Type IIx fibers. A marked difference between the cheetah and domestic cat is observed in the adductor and flexor digitorum superficialis. The adductor in the cheetah mainly consisted of Type IIx, while that in the domestic cat mainly consisted of Type I. The flexor digitorum superficialis in the cheetah did not include Type IIx, while that in the domestic cat did not include Type IIa. Our results for the domestic cat are partly similar to those reported by Ariano et al. (1973).

The splenius consisted of three types of muscle fibers (Type I, Type IIa, and Type IIx) in the cheetah, domestic cat, and beagle dog. The brachiocephalicus, trapezius cervicis, rhomboideus, and pectoralis superficialis in the cheetah have the highest values of Type I fibers among the three kinds of animal. The abdominal muscles (obliquus extensor abdominis and rectus abdominis) in the beagle dog have no Type IIx fibers. The longissimus thoracis and lumborum in the cheetah had the highest percentage of Type IIx. The population of muscle fiber types in longissimus in domestic cat and beagle dog was different between the thoracic and lumbar parts.

The eight studied forelimb muscles consisted of three types of fiber in cheetah and domestic cat, while the deltoideus scapula part, supraspinatus and biceps brachii in the beagle dog were consisted from Type I and Type IIa fibers. In the studies forelimb

muscles except the biceps brachii, the largest population of Type I fibers was observed in the cheetah. Values of Type IIx fibers in the studied forelimb muscles except the infraspinatus were lowest in the beagle dog.

Discussion

This is the first report to show the muscle fiber population of skeletal muscles obtained from the whole body excluding the head in the cheetah. In the present experiments, we classified muscle fibers into three kinds: Type I, IIa, and IIx. As shown in Materials and methods, an antibody that specifically reacts with MHC-IIx was not used to identify Type IIx fibers. Therefore, we have to mention the methodological limitation of our study concerning the lack of consideration of hybrid fibers (Type IIa/x). In the present experiments, the samples were cut off from the surface of each muscle. A previous study (van den Hoven et al. 1985) reported differences in the muscle fiber population between the middle part and surface of large and thick muscles. However, we determined that the functional properties could be represented by the three types of muscle fiber population of superficial portions in most muscles in this study.

The characteristic of cheetah skeletal muscles was that many muscles had a low percentage of Type I fibers and a high percentage of Type IIx fibers. This characteristic is also observed in the domestic cat. Many muscles in the beagle dog showed a low percentage of Type IIx and high percentage of Type IIa. It could be considered that Type I, Type IIa, and Type IIx corresponded to muscle fibers of S, FR, and FI motor units, respectively (Burke 1981; 1990). Type I is a muscle fiber with a high metabolic cost of maintenance and a small force output, used for posture and slow locomotion, Type IIx is a muscle fiber with a low metabolic cost for maintenance and a large force output, used run and gallop. Type IIa has intermediate characteristics between Type I and IIx. Both the cheetah and domestic cat are Felidae. Felidae excel in instantaneous force but have no stamina, while Canidae are excel in endurance and can run for a long distance. The population of muscle fibers shows that the cheetah has muscles for sprinting.

In terms of the muscle characteristics in three parts (hind limb, neck & trunk, and forelimb) of the cheetah body, we noticed marked difference between the forelimb and hind limb. The forelimb muscles have a higher percentage of Type I fibers than hind limb muscles ($p=0.037$), while hind limb muscles have a higher percentage of Type II (Type IIa + Type IIx) than forelimb muscles ($p=0.042$). This fact suggests that the propulsive role of the hind limbs is greater than the forelimbs in the cheetah. Some

investigators showed that forelimb of the horse play a less propulsive role that the hind limbs (Merkens et al. 1993; Niki et al. 1984; Payne et al. 2004). Kawai et al. (2009) showed that the forelimb muscle in the horse had a higher percentage of Type IIa and a lower percentage of Type IIx than the hind limb muscles. Kawai et al. (2009) suggest the relationship between muscle fiber population and functional role in the horse.

The characteristics of the muscle fiber population in cheetah are marked in the trunk muscles. The trapezius and rhomboideus are dorsal and hold the scapula. These muscles had a high percentage of Type I fibers in the cheetah (trapezius cervicis: 48.3%; trapezius thoracis: 38.9%; rhomboideus: 58.6%), while these muscles in the domestic cat and beagle dog had a high percentage of group IIa and/or IIx. The latissimus dorsi and pectoralis profundus pull the limb backward (Crouch 1969). These muscles in the cheetah had a very high percentage of Type IIx fiber (latissimus dorsi: 70.3%; pectoralis profundus: 84.1%). The characteristics of these muscles might indicate that the cheetah maintains the height of scapula and produces powerful and quick backward movements of the forelimb during locomotion. The longissimus is a powerful extensor of the spine and controls stiffness of the spinal column during locomotion (Wada et al. 2006). The longissimus in the cheetah had a high percentage of Type IIx fibers at thoracic and lumbar parts, while the population of muscle fibers was different depending on the parts in the domestic cat and beagle dog. This might suggest that the longissimus in the cheetah can produce a strong and quick extension of the spinal column and increase its stiffness. The speed of the cheetah mainly depends on the stride length. The characteristics of the muscle fibers in the trunk muscles are crucial to produce a large stride length.

We should note the muscle fiber population of flexors and extensors of the digits in the cheetah. The tips of the fingers are mainly controlled by two extensors (forelimb: extensor digitorum communis, extensor digitorum lateralis; flexor digitorum superficialis, flexor digitorum profundus; hind limb: extensor digitorum longus, extensor digitorum lateralis, flexor digitorum superficialis, flexor digitorum profundus). The flexors of the hind limb did not have Type IIx fibers, and extensors had a high percentage of Type IIa and IIx fibers. Both the flexors and extensors of the forelimb had three types of muscle fiber. PCSAs of the two flexors and two extensors in the hind limb were 52.0 and 9.6cm^2, respectively. PCSAs of the flexors and extensors in the forelimb were 43.5 and 9.5cm^2, respectively. PCSAs of the two flexors or two extensors in forelimb are similar to those in hind limb. Our results suggest a difference in neuronal control and functional differences between the digits of the forefoot and hind foot in the

cheetah. Differences in muscle fiber population between the flexor digitorum superficialis of forelimb and hind limb were observed in the domestic cat and beagle dog (Figs. 3 and 5).

The results in the present experiments show the cheetah has muscle fiber populations corresponding its high-speed running.

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Table 1 The muscle fiber type population (%) and PCSA (cm^2) of 23 skeletal muscles from hind limb in the cheetah

muscle name	abbreviation	Type I	Type IIa	Type IIx	PCSA
psoas major	PMJ	1.7	33.5	64.8	24.0
gluteus superficialis	GS	21.8	24.1	54.0	6.4
gluteus medius	GM	26.2	12.3	61.5	22.7
tensor fasciae latae	TFL	10.7	19.6	69.6	17.9
sartorius	Sar	19.5	30.2	50.3	7.4
gluteofemoralis	GF	3.6	13.1	83.3	7.4
biceps femoris	BF	25.8	20.0	54.2	18.0
vastus lateralis	VL	24.4	23.1	66.8	29.2
rectus femoris	RF	2.9	23.7	73.4	28.3
vastus medialis	VM	4.6	46.8	48.6	20.3
vastus intermedius	VI	63.0	37.0	0	7.4
gracillis	Grac	10.1	23.1	52.5	21.1
adductores	Ad	4.7	16.3	79.0	34.8
semitendinosus	SemiT	28.7	22.4	48.9	14.1
semimembranosus	SemiM	8.1	22.6	69.4	15.4
gastrocnemius-laterale	Glat	15.8	34.7	49.5	16.4
gastrocnemius-mediale	Gmed	4.2	5.6	90.3	22.3
soleus	Sol	53.1	44.9	2.0	8.7
tibialis cranialis	Tcra	17.1	23.7	59.2	7.6
extensor digitorum lateralis	EDLa	20.6	53.3	26.1	3.2
extensor digitorum longus	EDLo	20.9	30.9	48.2	6.4
flexor digitorum superficialis	FDS	31.9	68.1	0	29.8
flexor digitorum profundus	FDP	56.2	43.8	0	22.2
average		20.7	29.3	50.1	
SD		17.2	14.6	27.0	

Table 2 The muscle fiber type population (%) and PCSA (cm^2) of 13 skeletal muscles from neck and trunk in the cheetah

Muscle name	abbreviation	Type I	Type IIa	Type IIx	PCSA
splenius	Sp	26.0	32.1	37.2	
brachiocephalicus	Bc	32.7	30.1	37.2	
trapezius cervicis	Trc	48.3	30.7	21.0	2.8
trapezius thoracis	Trt	38.9	41.9	19.3	6.2
rhomboideus	R	58.6	41.4	0	11.2
latissimus dorsi	LAT	9.1	20.6	70.3	12
pectoralis superficialis	PS	38.9	61.1	0	18.7
pectoralis profundus	PP	5.0	10.8	84.1	14.1
longissimus thoracis	Lot	19.1	14.8	66.1	
longissimus lumborum	Lol	5.1	10.8	84.1	
rectus abdominis	RA	39.1	38.6	22.3	
obiliquus extensor abdominis	OEA	16.3	32.6	51.1	
transversus abdominis	TA	27.2	45.5	27.2	
average		28.0	31.6	40.0	
SD		16.7	14.7	29.0	

Table 3 The muscle fiber type population (%) and PCSA (cm^2) of 14 skeletal muscles from forelimb in the cheetah

Muscle name	abbreviation	Type I	Type IIa	Type IIx	PCSA
triceps brachii caput longum	Tlong	22.4	28.3	49.3	43.3
triceps brachii caput laterale	Tlat	31.5	39.3	29.2	10.2
triceps brachii caput mediale	Tmed	68.7	31.3	0	1.5
biceps brachii	BB	21.4	19.8	58.8	27.5
deltoideus acromial part	DA	32.3	9.7	58.0	7.1
deltoideus scapular part	DS	51.0	15.6	33.5	4.1
supraspinatus	SS	48.9	23.7	27.4	27.4
infraspinatus	IS	65.1	26.0	8.9	30.3
subscapularis	SUB	29.9	39.4	30.7	52.0
teres major	TMj	37.3	26.2	36.5	7.9
extensor digitorum communis	EDC	19.9	38.2	41.9	5.0
extensor digitorum lateralis	EDLa	9.3	38.9	51.8	4.5
flexor digitorum superficialis	FDS	30.9	48.4	20.7	23.8
flexor digitorum profundus	FDP	8.9	33.7	57.4	19.7
average		34.1	29.9	36.0	
SD		18.5	10.6	18.3	

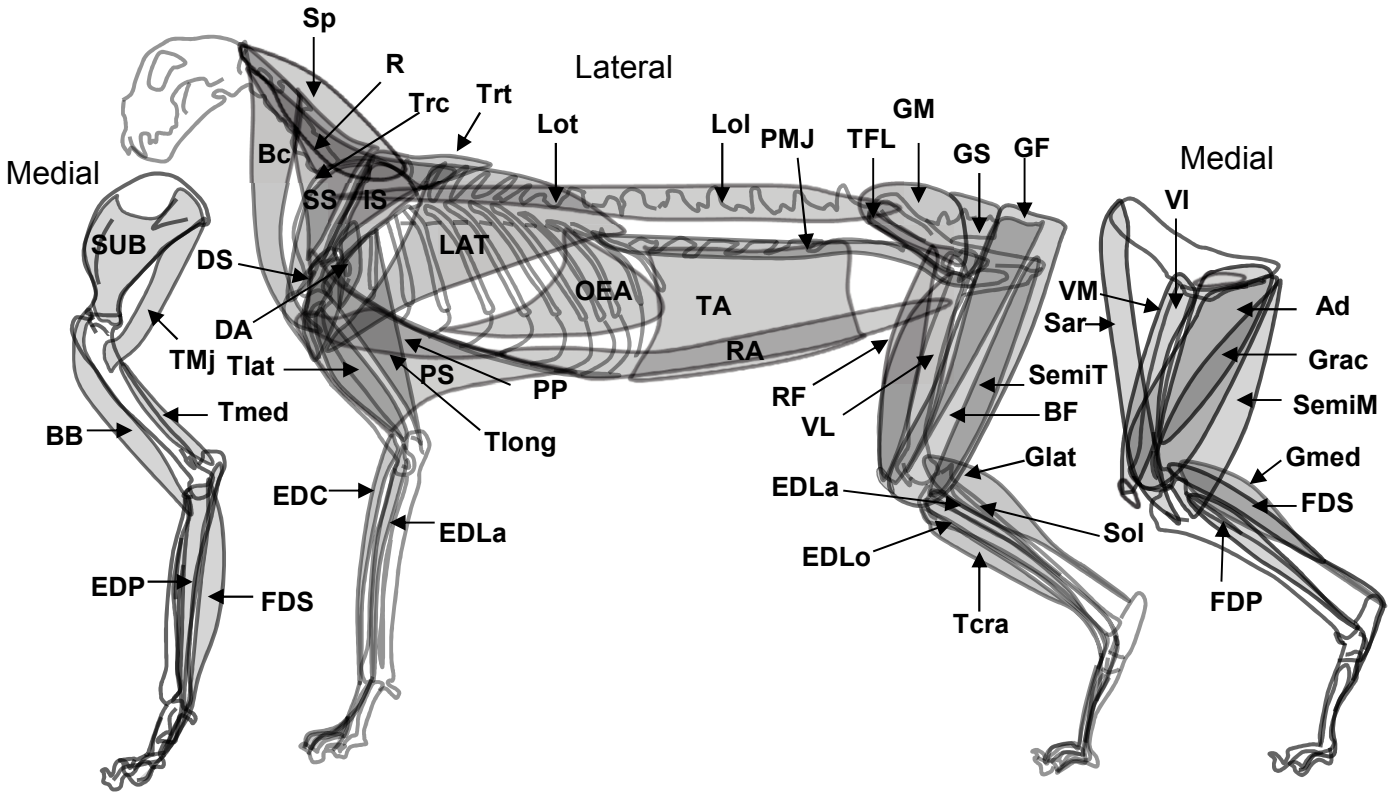

Fig. 1

The schematic illustration of the studied muscles in the cheetah. Muscle name abbreviations are given in Table 1, 2, and 3.

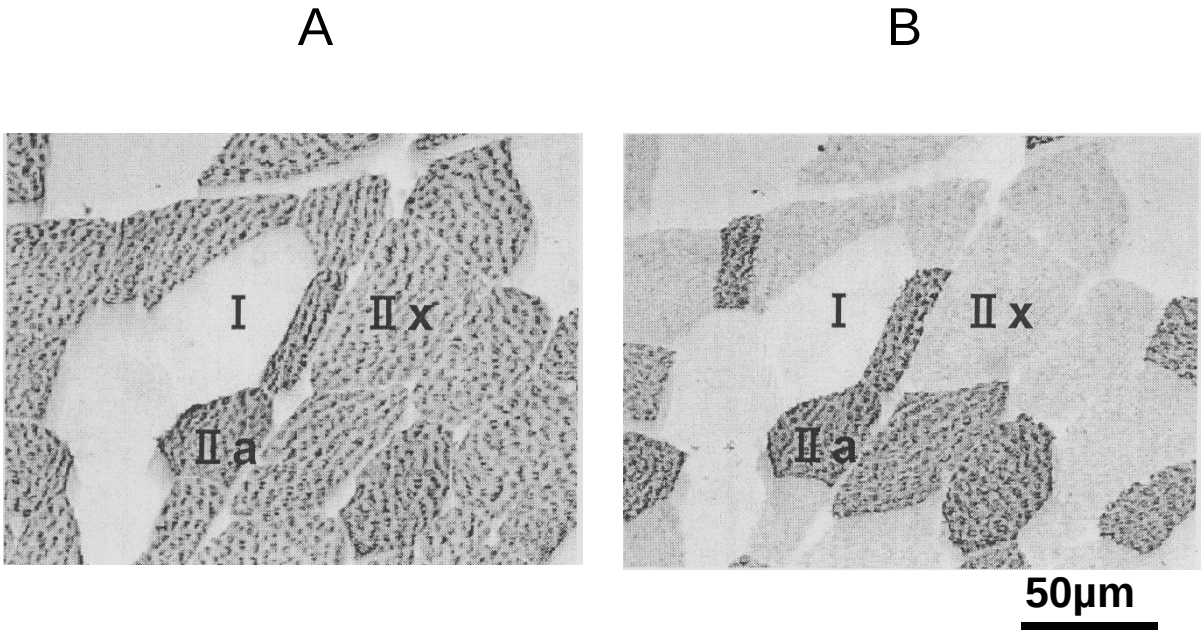

Fig. 2
Serial transverse sections of the gluteus medius muscle from a cheetah.
The sections were stained with monoclonal antibody against myosin heavy chain (MHC) isoforms. Muscle fibers were classified into Type I, Type IIa, and Type IIx. A: anti-fast myosin (anti-MHC-II) B: SC-71 (anti-MHC-IIa). Bar=50 μ m.

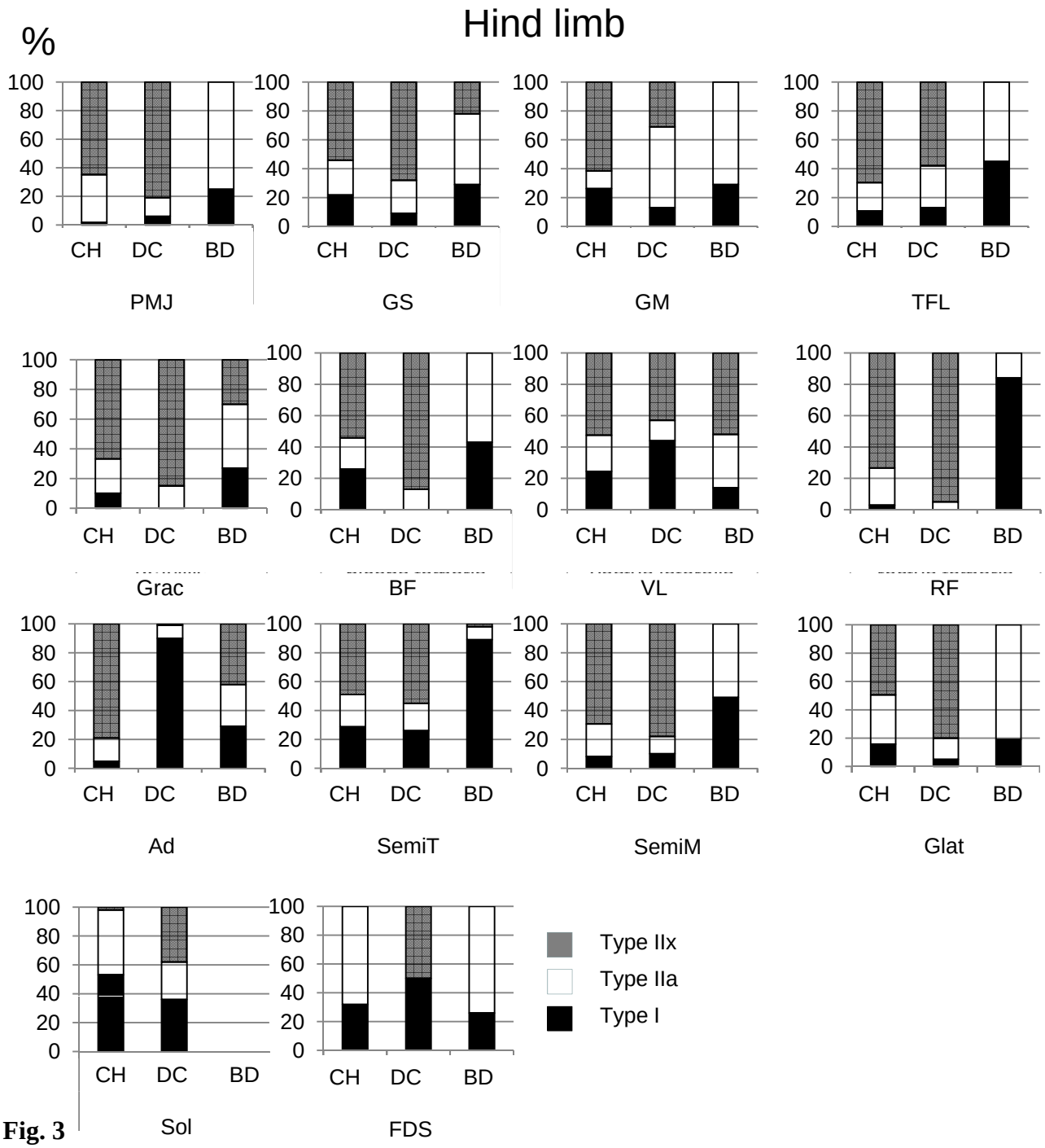

Fig. 3

Comparison of muscle fiber populations of skeletal muscles of the hind limb among the cheetah (CH), domestic cat (DC), and beagle dog (BD). The muscle fiber populations in the cheetah were similar to the domestic cat and the muscles mainly consisted of Type IIa and Type IIx fibers.
The hind limb muscles in the beagle dog mainly consisted of Type I and IIa.
Type I: black bar; Type IIa: open bar; Type IIx: grey bar

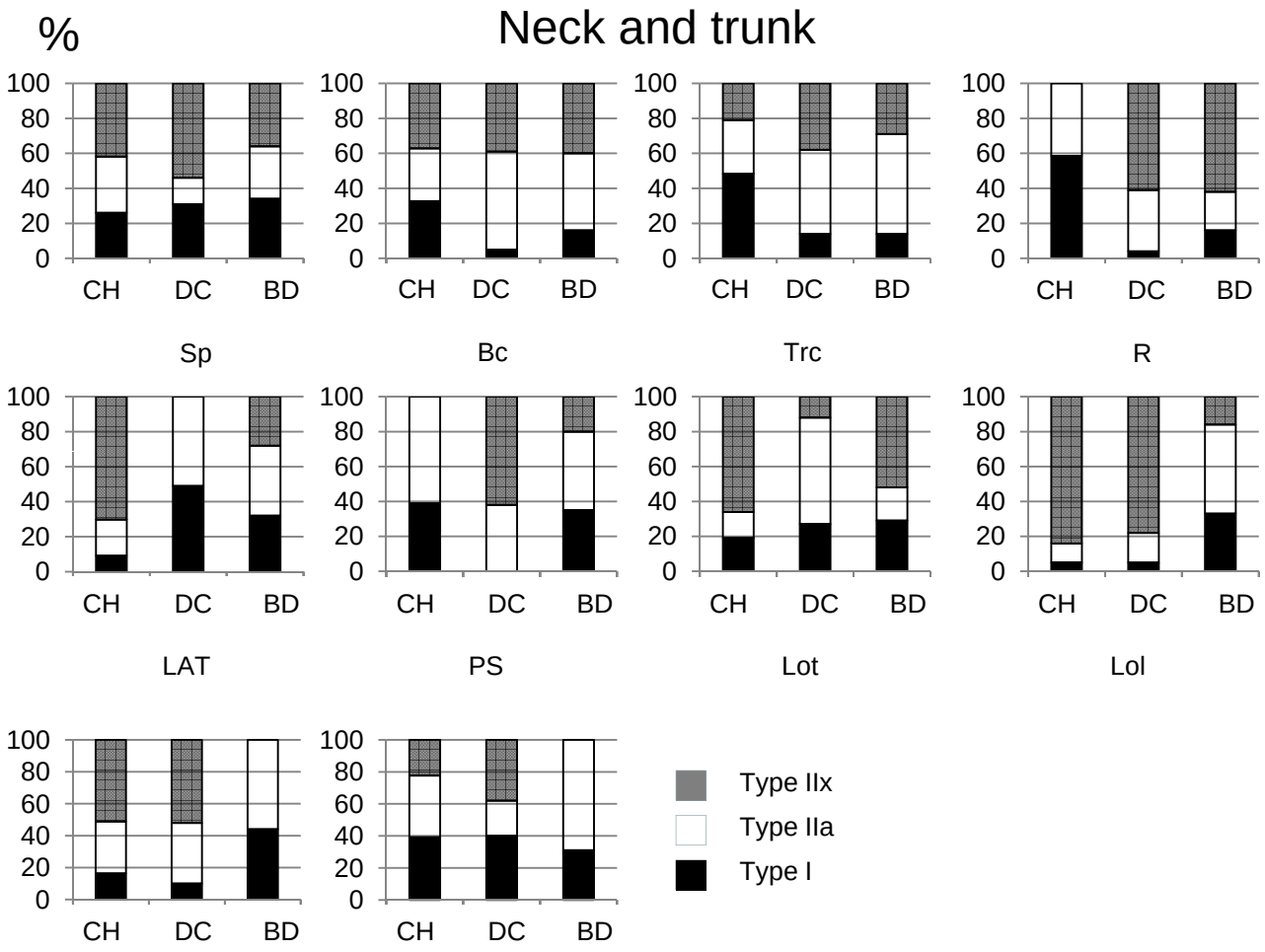

Fig. 4 Comparison of muscle fiber populations of skeletal muscles of the neck and trunk among the cheetah (CH), domestic cat (DC), and beagle dog (BD). The trapezius and rhomboideus in the cheetah had a high percentage of Type I fibers, while these muscles in the domestic cat and beagle dog had a high percentage of Type IIa and/or IIx. The latissimus dorsi, longissimus thoracis, and l ongissimus lumborum in the cheetah had a very high percentage of Type IIx fiber. Type I: black bar; Type IIa: open bar; Type IIx: grey bar

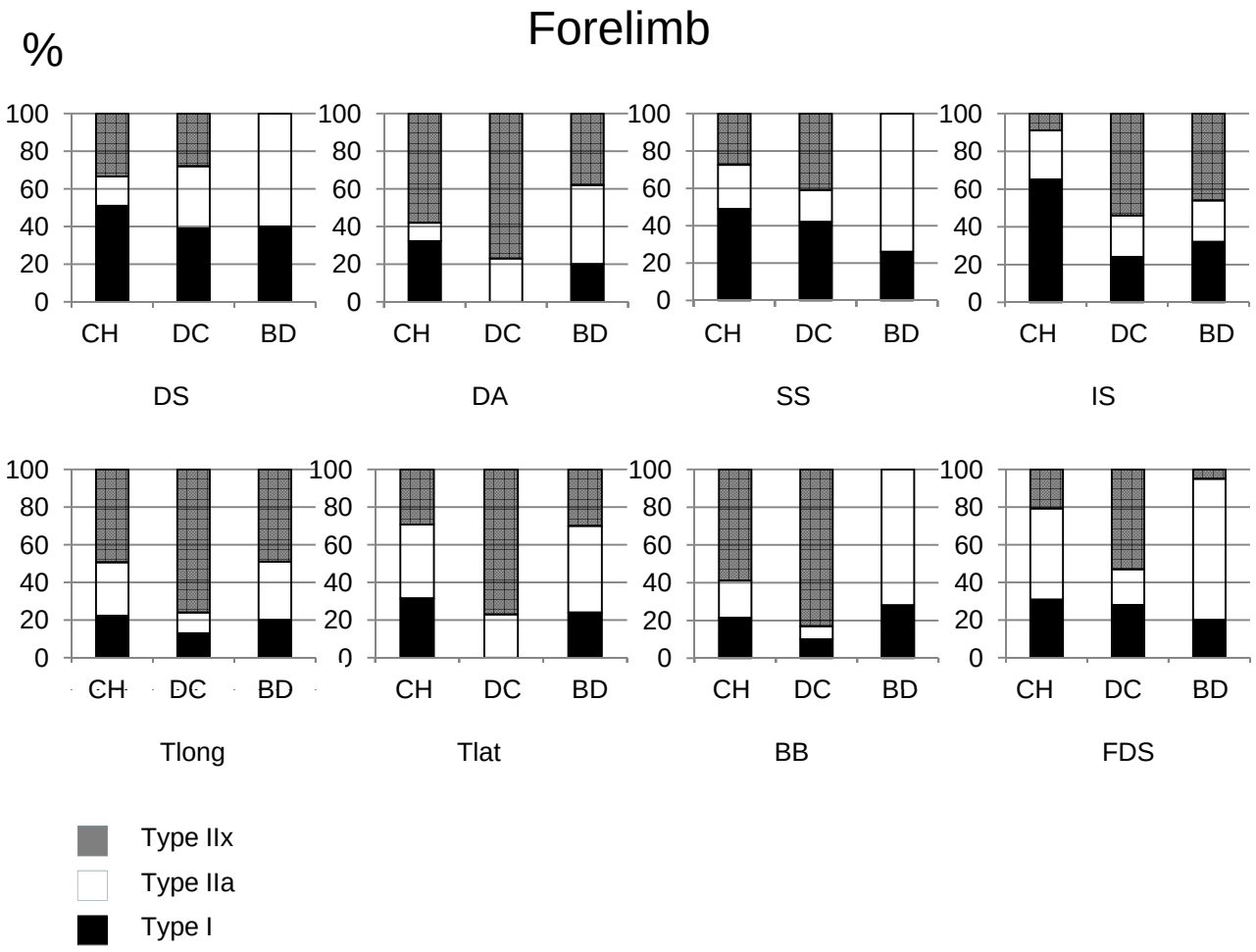

Fig 5

Comparison of muscle fiber populations of skeletal muscles of the forelimb among the cheetah (CH), domestic cat (DC), and beagle dog (BD). The forelimb muscles in the cheetah have a large percentage of Type I fibers. Type I: black bar; Type IIa: open bar; Type IIx: grey bar

Fig. 5