Doctoral Thesis

Associations of the Morphological Profiles of Individual Plantar Intrinsic Foot Muscles with Foot Structure and Toe Flexor Strength

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Associations of the Morphological Profiles of Individual Plantar Intrinsic Foot Muscles with Foot Structure and Toe Flexor Strength
（個々の足底内在筋の形態的特徴と足部構造および足趾屈曲筋力との関係）

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Chapter 1 Introduction

1-1. Preface

With the evolution of habitual bipedalism, human feet have become the only part that attaches to the ground. Human feet, especially the forefoot, also stiffen to directly transmit the propulsive force generated by the whole body to the ground during the push-off phase of walking and running (Farris et al., 2019; Holowka & Lieberman, 2018; Kelly et al., 2014; Mann & Inman, 1964). Plantar intrinsic foot muscles, which originate and insert within the foot, contribute to augmenting foot stiffness by controlling numerous joints of the foot (Farris et al., 2019; Holowka & Lieberman, 2018; Kelly et al., 2014; Mann & Inman, 1964).

The plantar intrinsic foot muscles consist of 10 muscles complexly arranged in four layers. These muscles also have distinct functions individually depending on their anatomical characteristics, such as the location and site of attachment. For example, plantar intrinsic foot muscles act in producing force at the toes because all of them control the joint movements within the toes (Neumann, 2017). In addition, the plantar intrinsic foot muscles, especially the abductor hallucis (ABH) being located immediately beneath the medial longitudinal arch (MLA) (Neumann, 2017), contribute to stabilizing this arch (Fiolkowski et al., 2003; Kelly et al., 2014). On the other hand, previous studies have estimated muscle functions by determining the contractile properties derived from the relationship between physiological cross-sectional area (PCSA) and muscle fiber length (Lieber et al., 1992; Ward et al., 2006). This idea is based on the fact that PCSA and fiber length reflect the maximum force production (Haxton, 1944) and shortening velocity (Gordon et al., 1966) of a muscle, respectively. Therefore, incorporating a morphological perspective may provide new insights into understanding the function of individual plantar intrinsic foot muscles, particularly the maintenance of MLA and force

production at the toes.

Previous studies have examined how the plantar intrinsic foot muscles associate with the force production at the toes. The previous findings showed that toe flexor strength (TFS) positively correlates with the anatomical cross-sectional area (ACSA) or muscle thickness of the plantar intrinsic foot muscles (Abe et al., 2016; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016), of which the medial region is the major contributor to TFS (Kurihara et al., 2014). Compared to ACSA and muscle thickness, however, muscle volume (MV) and maximal ACSA ($ACSA_{max}$) have been shown to be more strongly associated with muscle strength (Balshaw et al., 2021; Fukunaga et al., 2001). These findings indicate that if one intends to examine the relationship between the size of plantar intrinsic foot muscles and TFS, he/she should adopt MV or $ACSA_{max}$ rather than ACSA and muscle thickness determined at the limited and uncertain place.

In addition, the above-mentioned studies have determined different types of TFS depending on toe actions and toes intended for force production. Soysa et al., (2012) pointed out that the differences in toe actions depending on the device utilized may change the contribution of the plantar intrinsic foot muscles to TFS production. In fact, among 10 plantar intrinsic foot muscles, some muscles specialized in flexion at the great toe (i.e., flexor hallucis brevis [FHB]) or lesser toes (i.e., flexor digitorum brevis [FDB]), while others act for the add/abduction and assist with flexion at the great toe (i.e., ABH and adductor hallucis [ADDH]) or lesser toes (e.g., abductor digiti minimi [ABDM]) (Neumann, 2017). These aspects indicate the necessity to consider the functional diversity in plantar intrinsic foot muscles for elucidating how these muscles associate with TFS.

The general purpose of this thesis was to elucidate how the morphological profiles of individual plantar intrinsic foot muscles associate with foot structure and TFS. Clarifying this will provide useful information to deepen our knowledge of how the individual plantar intrinsic

foot muscles contribute to force production at the toes and maintenance of foot structure.

1-2. Publications included in this thesis and during the doctoral program

The following manuscripts are included as Chapters within this thesis:

1. Kusagawa, Y., Kurihara, T., Maeo, S., Sugiyama, T., Kanehisa, H., & Isaka, T. (2022). Associations of muscle volume of individual human plantar intrinsic foot muscles with morphological profiles of the foot. *Journal of Anatomy*, 241(6), 1336–1343.
   This manuscript is incorporated as Chapter 4 in this thesis.
2. Kusagawa, Y., Kurihara, T., Maeo, S., Sugiyama, T., Kanehisa, H., & Isaka, T. (2022). Associations between the size of individual plantar intrinsic and extrinsic foot muscles and toe flexor strength. *Journal of Foot and Ankle Research*, 15(1), 22.
   This manuscript is incorporated as section 1 of Chapter 5 in this thesis.

The following manuscript is published during the doctoral program and is used as a reference for this thesis:

1. Kusagawa, Y., Kurihara, T., Imai, A., Maeo, S., Sugiyama, T., Kanehisa, H., & Isaka, T. (2020). Toe flexor strength is associated with mobility in older adults with pronated and supinated feet but not with neutral feet. *Journal of Foot and Ankle Research*, 13(1), 55.

1-3. Terminology

Extrinsic toe flexors

"Extrinsic toe flexors" refers to the flexor digitorum longus and flexor hallucis longus which are included in the extrinsic foot muscle and act on the toe flexion.

Foot structure

In this thesis, “foot structure” is expressed as the morphological profiles of the foot, such as foot length, width, circumference, height, and toe angle.

Great toe

“Great toe” refers to the anatomical part that consists of the first proximal and distal phalange. The “Great toe” is also called the big toe or hallux.

Lesser toes

“Lesser toes” refers to the anatomical part that consists of proximal, middle, and distal phalanxes in the second to fifth toes. The “Lesser toes” is also called the lateral toes.

Muscle size

“Muscle size” refers to a spatial dimension of the muscle. This thesis describes muscle size by thickness, cross-sectional area, and volume.

Toe action

In this thesis, the “toe action” is expressed as limited to the multiple joint movements required to produce TFS. The toe gripping action (flexion at the metatarsophalangeal [MTP] joint and interphalangeal [IP] joints) and toe pushing action (flexion at the MTP joint and less excessive flexion at the IP joints) appear as “toe action” in this thesis.

Toe grip strength (TGS)

“Toe grip strength” is defined as toe flexor strength produced by the toe gripping action,

consisting of the flexion at the MTP and IP joints.

Toe flexor muscles

"Toe flexor muscles" refers to the muscle group that acts on toe flexion. Toe flexor muscles consist of two muscle groups: plantar intrinsic foot muscles and extrinsic toe flexors.

Toe flexor strength (TFS)

"Toe flexor strength" refers to the force-generation capacity of the toe flexor muscles, which is classified by the plantar intrinsic foot muscles and extrinsic toe flexors, determined by toe dynamometry or plantar pressure platform.

Toe push strength (TPS)

"Toe push strength" is defined as toe flexor strength produced by the toe pushing action, consisting of the flexion at the MTP joint and less excessive flexion at the IP joints

1-4. List of abbreviations

ABDM – abductor digit minim

ABH – abductor hallucis

ACSA – anatomical cross-sectional area

$ACSA_{max}$ – maximal anatomical cross-sectional area

ADDH – adductor hallucis

ADDH-OH – adductor hallucis oblique head

ADDH-TH – adductor hallucis transverse head

DIP – distal interphalangeal

FDB – flexor digitorum brevis

FDL – flexor digitorum longus

FHB – flexor hallucis brevis

FHL – flexor hallucis longus

FL – MRI-determined foot length

FPI-6 – 6-item foot posture index

ICC – intraclass correlation coefficient

IP – interphalangeal

LL – MRI-determined lower leg length

MLA – medial longitudinal arch

MRI – magnetic resonance imaging

MTP – metatarsophalangeal

MV – muscle volume

ND – navicular drop

NTNH –normalized truncated navicular height

PIP – proximal interphalangeal

QP – quadratus plantae

SD – standard deviation

T – tesla

T1 – longitudinal relaxation time

3D – three-dimensional

TGS – toe grip strength

TFS – toe flexor strength

TPS – toe push strength

TPS-All – toe push strength produced by all toes

TPS-Great – toe push strength produced by the great toe

TPS-Lesser – toe push strength produced by lesser toes

1-5. Literature review

The general purpose of this thesis was to elucidate how the morphological profiles of individual plantar intrinsic foot muscles associate with foot structure and TFS. First, this section reviews previous publications from the following viewpoints: 1) anatomy of the foot, 2) measurements of morphological parameters of the plantar intrinsic foot muscles, 3) associations between the size of the planter intrinsic foot muscles and foot morphological profiles, 4) measurements of TFS and its significance to physical performance, and 5) strength and size relationship of the toe flexor muscles.

1-5-1. Anatomy of the foot

1-5-1-1. Bones

The human foot has 28 bones on each side (Fig. 1-1); therefore, the total number of bones located in the feet accounts for 27% of all bones in the whole body (208 bones) (Ridola & Palma, 2001). The breakdown of the 28 bones is as follows: 7 tarsal bones, 5 metatarsal bones, 14 phalanx bones, and 2 sesamoid bones at the first metatarsal. The foot is divided into rear, mid, and forefoot regions. The anterior limit of the rearfoot region is the transverse tarsal (Chopart's) joint, and this region includes the talus and calcaneus. The midfoot region starts the Chopart's joint and is anteriorly delimited by the tarsometatarsal (Lisfranc's) joint. The navicular, cuneiforms (medial, intermediate, and lateral), and cuboid make up this region. The forefoot represents the part distal to Lisfranc's joint. This region includes 5 metatarsal bones and 5 proximal, 4 middle, and 5 distal phalanges.

The structure of the human foot is represented as a half-dome shape, which is characterized by four arches: 2 longitudinal (medial and lateral) and 2 transverse (anterior and posterior) arches (Mckenzie, 1955). The MLA (Fig. 1-2 a) consists of the calcaneus, talus, navicular, 3 cuneiforms, and 3 metatarsals in the medial region (i.e., first to third metatarsals). The navicular is recognized as the keystone for MLA. The lateral longitudinal arch (Fig. 1-2 b) is formed by the calcaneus, cuboid, and 2 metatarsals in the lateral region (fourth and fifth metatarsals). The keystone of the lateral longitudinal arch is the cuboid. The MLA is higher and more strongly resilient than the lateral longitudinal arch, which is flatter and stiffer (Mckenzie, 1955). The posterior transverse arch (Fig. 1-2 c), also called the transverse tarsal arch, is at the level of the tarsometatarsal joint and consists of the cuboid, cuneiforms, and base of metatarsals. The anterior transverse arch (Fig. 1-2 c), also called the transverse metatarsal arch, is a flat dome at the metatarsophalangeal (MTP) joint level and is formed by the heads of the metatarsals and the bases of the proximal phalanges.

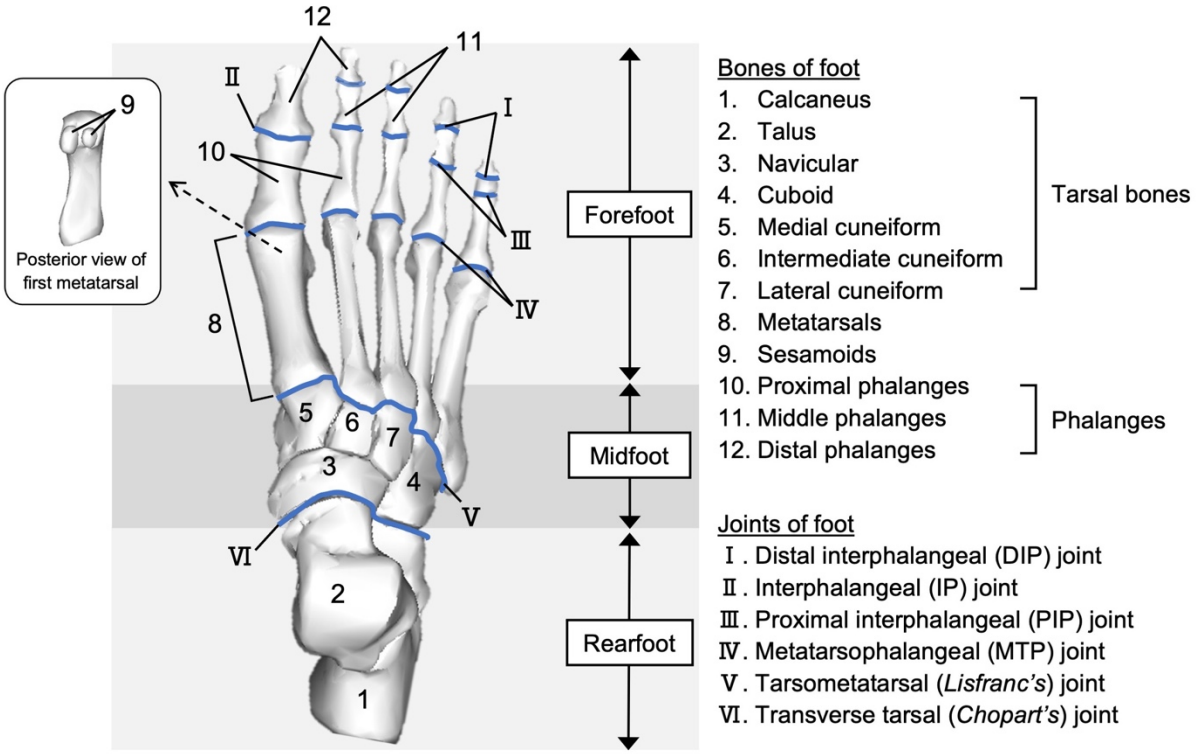

Figure 1-1. Bones and joints of the foot (right foot). All images were created by "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

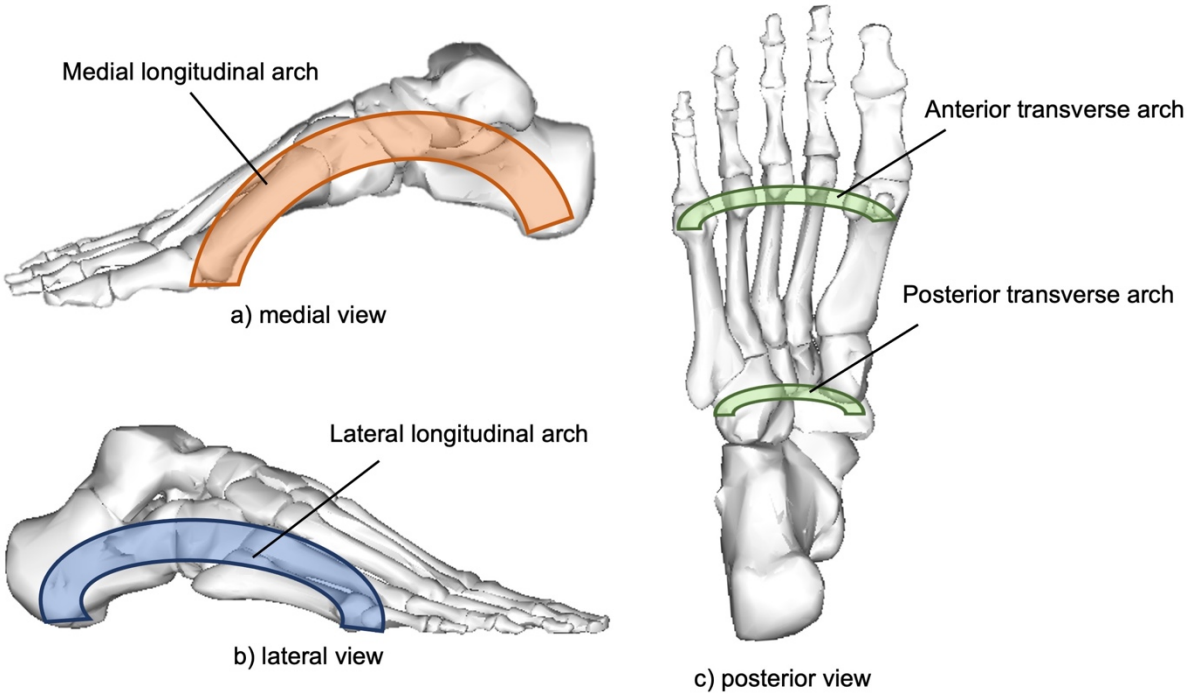

Figure 1-2. Arches of the foot (right foot). All images were created by "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

1-5-1-2. Joints in the toes and their movements

The foot has numerous joints, such as subtalar, Chopart's, Lisfranc's, MTP, and interphalangeal (IP) joints (Fig. 1-1). This section mainly describes joints in the toe region, i.e., MTP and IP joints. The MTP joint is formed between the metatarsal and proximal phalanx in every toe and has two degrees of freedom. The flexion (plantarflexion)–extension (dorsiflexion) occurs at the transverse (mediolateral) axis in the sagittal plane, while that of abduction–adduction occurs at the vertical axis in the horizontal plane. The IP joint is present in every toe, but a somewhat different feature exists in each toe. The great toe has a single IP joint, while the lesser toes (2nd to 5th toe) have two: proximal (formed between proximal and middle phalanx, PIP) and distal (formed between middle and distal phalanx, DIP) joints. The movement of the IP joint is only flexion (plantarflexion) – extension (dorsiflexion).

1-5-1-3. Muscles

The muscles that regulate joint movement in the foot are divided into intrinsic and extrinsic foot muscles. The constituents of the intrinsic foot muscles originate from and insert on the foot, while those of the extrinsic foot muscles originate from the lower leg and insert into the foot while crossing the ankle joint (McKeon et al., 2015).

Plantar intrinsic foot muscles

The intrinsic foot muscles consist of 10 plantar and 2 dorsal intrinsic foot muscles (Kura et al., 1997). Of these muscle groups, it is reported the plantar intrinsic foot muscles have functional roles in producing TFS (Abe et al., 2016; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016) and maintaining foot arch structure (Fiolkowski et al., 2003; Kelly et al., 2014). Thus, the anatomical characteristics of the 10 plantar intrinsic foot muscles are mainly described below and summarised in their origin, insertion, and movement in Table 1-1.

Plantar intrinsic foot muscles are organized into four layers (Kura et al., 1997; Neumann, 2017) (Fig. 1-3). The first layer, which is located immediately above the plantar aponeurosis (Fig. 1-3 A) consists of ABH, FDB, and ABDM. ABH is located in the most medial region of the foot. The anatomical function of ABH is abduction and assistance with flexion at the first MTP joint (Neumann, 2017). ABH has the most extended muscle length (11.6 ± 0.5 cm), the smallest muscle fiber to muscle length ratio (0.20 ± 0.002), and the largest PCSA (6.68 cm^2) and MV (15.2 ± 5.3 cc) among the intrinsic foot muscles (Kura et al., 1997). In addition, ABH is composed of three segments with no morphological differences (Tosovic et al., 2012). However, it has been reported that each segment has different functions depending on its attachment site; most posterior multipennate segment produces the abduction force of the great toe, whereas the other two segments produce stabilizing force against MLA (Tosovic et al., 2012). FDB lies immediately above the plantar aponeurosis and flexes lesser toes at the MTP and PIP joints (Neumann, 2017). The muscle fiber of FDB forms four tendons. As these tendons approach the distal foot, each of them enters one of the lesser toes, but some specimens are absent in the muscle fiber and tendon that inserts into the 5th toe (Kura et al., 1997). FDB also has three segments and the fastest contraction time among several intrinsic foot muscles (ABDM, ABH, extensor digitorum brevis, and FDB) (Tosovic et al., 2012). ABDM, which lies on the lateral side of the foot, adducts, and assists in the flexion of the 5th toe at the MTP joint (Neumann. 2017). ABDM has four segments with different morphological features (Tosovic et al., 2012). The anterior segment of ABDM produces the abduction force for the 5th digit, while others provide force to stabilize the anterior segment (Tosovic et al., 2012).

The quadratus plantae (QP) and lumbrical are in the second layer (Fig. 1-3 B). QP originates from the two heads and inserts into the lateral side of the flexor digitorum longus (FDL) tendon. From this unique insertion, QP acts to counter the oblique pull of the FDL and as lesser toes flexor (Edama et al., 2016). Moreover, a cadaveric study with 116 legs of 62

specimens revealed that the origin of QP can be classified into three types (Edama et al., 2016). The occupancy of the three types was that in 87%, 10%, and 3% of lateral and medial, absenting medial, and absenting lateral heads, respectively (Edama et al., 2016). The lumbrical consists of four worm-like muscles inserted into the FDL tendon (Neumann, 2017). The anatomical function of the lumbrical is flexion of the lesser toes at the MTP joint and extension of them at the DIP and PIP joints.

The third layer (Fig. 1-3 C) includes FHB, ADDH, flexor digiti minimi brevis, and opponens digiti minimi. FHB has two tendinous heads of origin and unites to form a muscle belly. The muscle belly separates into medial and lateral parts in the plantar surface of the first metatarsal and each part inserts into either the medial or lateral side of the base of the proximal phalanx of the great toe. The anatomical function of FHB is flexion of the great toe at the MTP joint. The ADDH is composed of two muscular heads: the oblique head (ADDH-OH) originating from the plantar surface of the second to the fifth metatarsal base and the transverse head (ADDH-TH) originating from the plantar ligaments of the third to fifth MTP joint and the deep transverse metatarsal ligaments. To the distal end, both muscular heads insert into the lateral side of the base of the proximal phalanx of the great toe. The ADDH-OH (9.1 ± 3.1 cc) has a larger MV than ADDH-TH (1.1± 0.6 cc), and the latter has the shortest muscle length (2.5 ± 0.4 cm) and the largest fibre/muscle length rate (0.82 ± 0.07) among the intrinsic foot muscles (Kura et al., 1997).

The plantar interossei muscles are in the fourth (deepest) layer of the plantar intrinsic foot muscles (Fig. 1-3 D). They include three muscles located on each of the third, fourth, and fifth digits. Each plantar interossei muscle inserts on the medial side of the corresponding toe and adducts its respective MTP joint.

Table 1-1. Origin, insertion, and movement of plantar intrinsic foot muscles

Muscle	Origin	Insertion	Function
First layer			
Abductor hallucis	Medial process of calcaneal tuberosity	The medial side of the base of proximal phalanx of the great toe	Adducts and flexes great toe at MTP joint
Flexor digitorum brevis	Medial process of calcaneal tuberosity and plantar aponeurosis	Sides of plantar surface of middle phalanges of lesser toes	Flexes lesser toes at PIP joint
Abductor digiti minimi	Lateral and medial process of calcaneal tuberosity, and band of connective tissue connecting calcaneus with base of 5th metatarsal	Sides of plantar surface of middle phalanges of lesser toes	Adducts 5th toe at MTP joint
Second layer			
Quadratus plantae	Medial surface of calcaneus and lateral process of calcaneal tuberosity	The lateral side of the tendon of flexor digitorum longus in the proximal sole of the foot	Assists flexor digitorum longus tendon in flexing lesser toes
Lumbricals	Flexor digitorum longus tendon	Medial free margins of extensor hoods of 2nd to 5th toes	Flexion of the MTP joint and extension of the DIP and PIP joint.
Third layer			
Adductor hallucis oblique head	Base of 2nd to 5th metatarsals and from sheath covering fibularis longus	Lateral side of tendon of base of proximal phalanx of great toe	Adduct great toe at MTP joint
Adductor hallucis transverse head	Ligaments associated with MTP joint of 2nd to 4th toes		
Flexor hallucis brevis	Plantar surface of cuboid and lateral coniform: tendon of tibialis posterior	Lateral and medial sides of base of proximal phalanx of the great toe	Flaxes MTP joint of great toe
Flexor digit minimi brevis	Base of 5th metatarsal and related sheath of fibularis longus tendon	Lateral side of base of proximal phalanx of lesser toes	Flexes lesser toes at MTP joint
Opponens digit minimi	Long plantar ligament, base of 5th metatarsal, fibularis longus tendon	Lateral border of 5th metatarsal	Abducts and flexes of MTP joint
Fourth layer			
Plantar interossei	Medial sides of metatarsals of 3rd to 5th toes	Extensor hoods and bases of proximal phalanges of 3rd to 5th toes	Adduction of 3rd to 5th toes at MTP joint; resist extension of MTP joint and flexion of the PIP and DIP joint

Created with reference to Neumann, (2017). MTP: metatarsophalangeal; IP: interphalangeal; PIP: proximal interphalangeal; DIP: distal interphalangeal

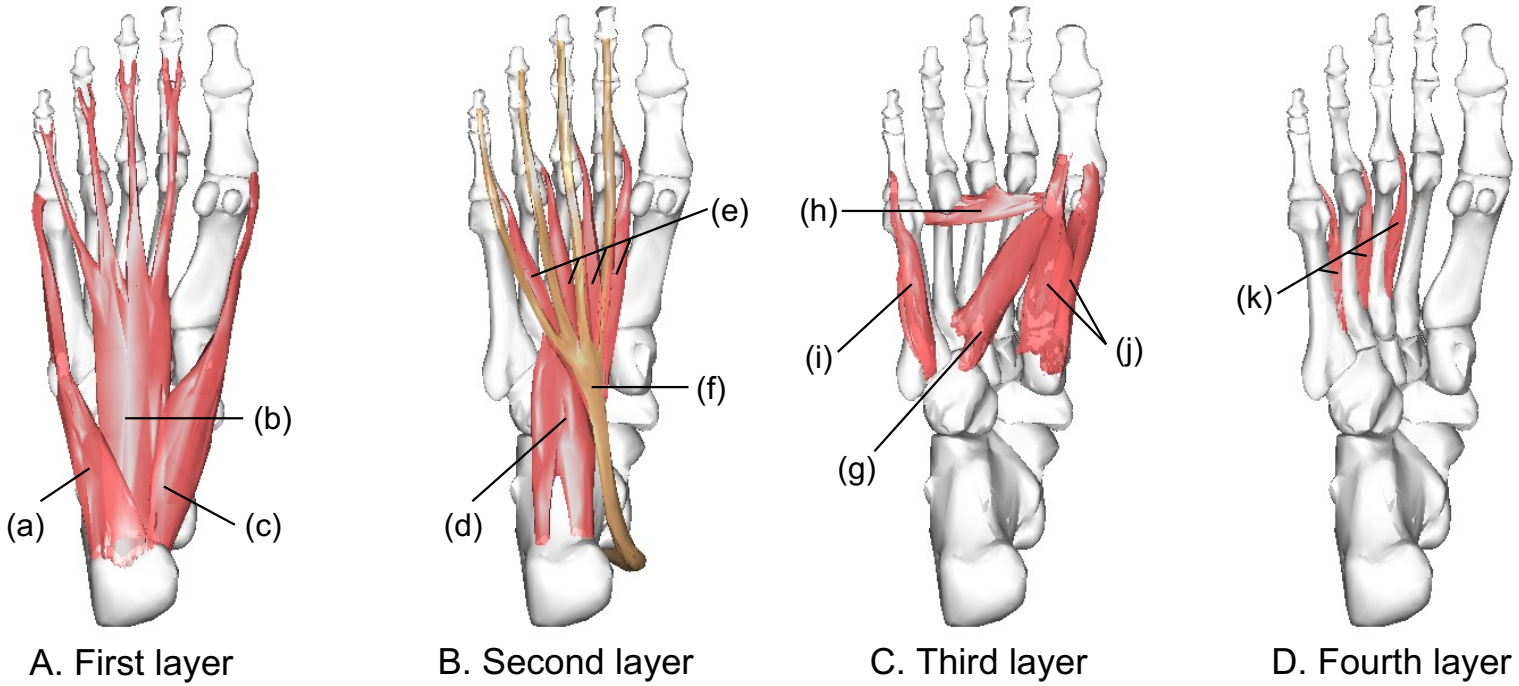

Figure 1-3. Plantar intrinsic foot muscles (right foot). A, B, C, and D show the first, second, third, and fourth layers. (a): abductor digiti minimi (ABDM); (b): flexor digitorum brevis (FDB); (c): abductor hallucis (ABH); (d) quadratus plantae (QP); (e): lumbricals; (f): flexor digitorum longus tendon (consisting of extrinsic toe flexors); (g): adductor hallucis oblique head (ADDH-OH); (h): adductor hallucis transverse head (ADDH-TH); (i): flexor digiti minimi; (j): flexor hallucis brevis (FHB); (k): plantar interossei. All images were created by "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

Extrinsic foot muscles

Extrinsic foot muscles consist of 12 muscles, and each muscle is included in one of three compartments. The anterior compartment functions as the dorsiflexion in the ankle joint and consists of the tibialis anterior, extensor hallucis longus, extensor digitorum longus, and fibularis tertius. The fibularis longus and brevis are in the lateral compartment and evert at the ankle joint. The posterior compartment is divided into superficial and deep groups by separating a layer of deep fascia. The superficial group acts as plantarflexors of the ankle joint and includes gastrocnemius, soleus, and plantaris. The deep group consists of the tibialis posterior, flexor hallucis longus (FHL), and FDL, and these muscles invert at the ankle joint.

Among the extrinsic foot muscles, FHL and FDL (Fig. 1-4), including in the deep group of the posterior compartment, act to flex toes. In this thesis, these muscles were defined as extrinsic toe flexors. FHL and FDL originate from the lateral and medial sides of the posterior compartment and pass through the posterior and medial sides of the ankle joint, respectively. The FHL tendon runs between the medial and lateral sesamoid bone of the first metatarsal to the distal end of the foot and attaches to the base of the distal phalanx of the great toe. The distal part of the FDL branches to four tendons. Each of the four tendons insets into a corresponding toe among the lesser toes and attaches to the base of the distal phalanx. Thus, FHL and FDL act on plantarflexion at both IP and MTP joints of the great and lesser toes, respectively.

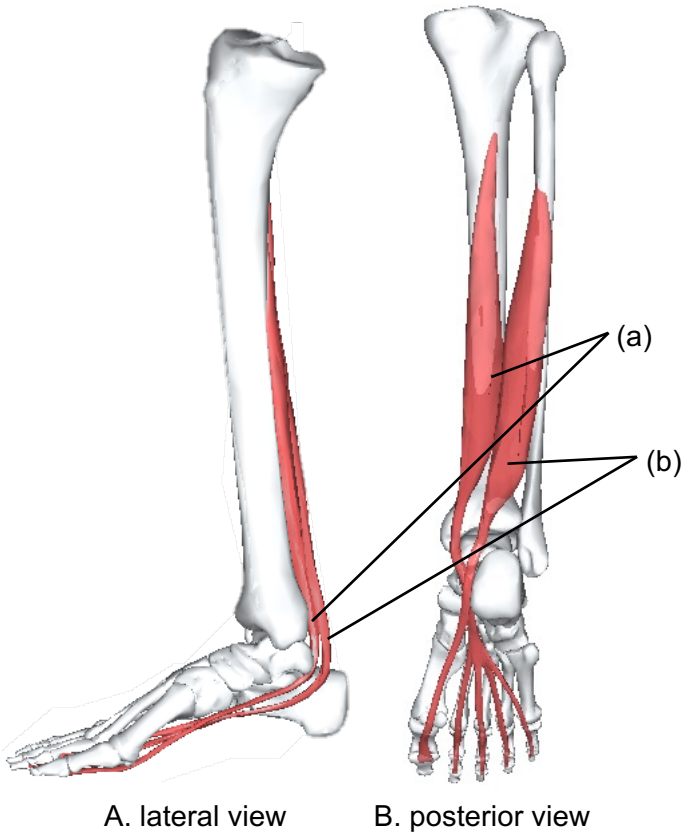

Figure 1-4. Extrinsic toe flexors (right lower limb). A and B show the lateral and posterior view of the right lower limb, respectively. (a): flexor digitorum longus (FDL); (b): flexor hallucis brevis (FHL). Images were created by "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

1-5-2. Measurements of morphological parameters of the plantar intrinsic foot muscle in humans

The morphological parameters of a muscle relate to its contractile properties. For example, muscle fiber length is proportional to the maximum shortening velocity of a muscle since it refers to the number of sarcomeres in a series (Gordon et al., 1966). Moreover, PCSA is proportional to the maximum force production of a muscle because this conceptually reflects the cross-sectional area perpendicular to the long axis of all fibers (Haxton, 1944). Given these, previous studies have attempted to determine the relationship between PCSA and fiber length for understanding the contraction properties of individual muscles in the upper (Lieber et al., 1992) and lower (Ward et al., 2009) limbs. Thus, it is likely that quantification in the morphological profiles of individual plantar intrinsic foot muscles is important for understanding their function. This section describes how morphological profiles, in particular, muscle size parameters of the plantar intrinsic foot muscles have been quantified in previous studies.

The cadaveric studies have been reported detailed information on muscle size and architectural parameters of plantar intrinsic foot muscles (Kura et al., 1997; Lachowitzer et al., 2007; Ledoux et al., 2001; Tosovic et al., 2012). On the other hand, among these studies, Kura et al. (1997) has only provided information on muscle size (i.e., PCSA and MV) as well as architectural parameters (e.g., fiber length) of all individual plantar intrinsic foot muscles, except for pennation angle. However, the subject targeted in this previous study was limited to a small number of middle-aged and older adults (age: 70.7 ± 10.8, n = 11) (Kura et al., 1997).

Ultrasonography and magnetic resonance imaging (MRI) have been commonly used in vivo to measure the size of plantar intrinsic foot muscles but have not provided any architectural parameters. While the resolution of an ultrasonographic image is low (Soysa et al., 2012), ultrasonography has the advantage of the cost requirements and high utility for clinical

and field surveys compared to MRI. In fact, many studies have adopted ultrasonography to determine the size of plantar intrinsic foot muscles in young to middle-aged (Abe et al., 2016; Angin et al., 2014; Angin et al., 2018; Latey et al., 2018) and older adults (Mickle et al., 2016), athletes (Ichikawa et al., 2021; Koyama et al., 2019), and pathological populations (Fraser et al., 2018, 2020, 2021; Taş & Çetin, 2019). In these studies, the ACSA and muscle thickness were measured in the limited muscles (ABH, ABDM, FDB, FHB, and QP) among the ten plantar intrinsic foot muscles. Of these muscles, ABH, ABDM, and FDB were located in the first layer (superficial region) of the plantar intrinsic foot muscles and run close to the body surface in the medial, lateral, and plantar regions, respectively. Moreover, QP exists immediately above the FDB in the second layer and FHB in the third layer appears close to the plantar surface in the forefoot region. Thus, the quantification of the plantar intrinsic foot muscle size using ultrasonography has been only performed on the muscle located relatively close to the body surface, where its shape can be easily visualized. In addition, most of the previous reports cited above have measured ACSA or muscle thickness from the position where the thickest region of the muscle belly can be visually identified in accordance with the procedures used in previous studies (Latey et al., 2018; Mickle et al., 2016). However, the magnitude of these variables depends on the site where these are determined (Blazevich et al., 2006; Fukunaga et al., 1992), and ultrasonographic measurements are potentially dependent on the operator's scanning technique (Soysa et al., 2012).

MRI is recognized as the gold standard technique to assess the plantar intrinsic foot muscle size because it can visualize the whole plantar intrinsic foot muscle with a high spatial resolution of images (Soysa et al., 2012). However, muscle size variables adopted and methods for segmenting muscles used varied among previous MRI studies. Most studies determined MV for plantar intrinsic foot muscles in healthy adults (Feger et al., 2016; Franettovich Smith et al., 2021, 2022), recreational runners (Chen et al., 2016), or pathological populations with chronic

ankle instability (Feger et al., 2016) and plantar fasciitis/plantar heel pains (Chang et al., 2012; Cheung et al., 2016; Franettovich Smith et al., 2022). Some of these studies quantified MV of all plantar intrinsic foot muscles individually (Feger et al., 2016; Franettovich Smith et al., 2021; Franettovich Smith et al., 2022), while others obtained MV by dividing whole plantar intrinsic foot muscles into the entire, rear, and forefoot regions (Chang et al., 2012; Chen et al., 2016; Cheung et al., 2016). On the other hand, Kurihara et al. (2014) determined the ACSA of plantar intrinsic foot muscle at 80% of the MRI-determined foot length where the ACSA of the entire intrinsic foot muscle was largest at the corresponding position (Chang et al., 2012). They analyzed the plantar intrinsic foot muscles except for ADDH (presumed to be ADDH-OH based on the analysis position and typical images, by segmenting them into medial and lateral compartments including several muscles (Kurihara et al., 2014).

1-5-3. Associations between the size of the planter intrinsic foot muscles and morphological profiles of the foot

In the evolution process, humans have undergone realignments of their foot skeleton, such as the enlarged calcaneus, adducted and non-opposable great toe, and shortened lesser toe to adopt habitual bipedalism (Bramble & Lieberman, 2004). In general, the human foot structure is characterized by multi-dimensional morphological parameters, such as foot length, width, circumference, and height (Kouchi, 1998; Waseda et al., 2014). Of these parameters, it is well known that the maintenance of MLA height is associated with the function of plantar intrinsic foot muscles (Fiolkowski et al., 2003; Kelly et al., 2012). For example, electromyographic studies have shown that impaired activation of plantar intrinsic foot muscles caused by the tibial nerve block decreases the MLA height (Fiolkowski et al., 2003). Moreover, increased activation of these muscles by electrical stimulation counters the collapse of the MLA (Kelly et al., 2014). These findings imply that the morphological development of plantar

intrinsic foot muscles is related to that of the foot structure, particularly the magnitude of MLA height. In fact, positive correlations were found between the ACSA of the ABH and dorsal arch height in sitting/standing conditions and between ACSA of FHB and the 6-item foot posture index (FPI-6) score (Latey et al., 2018). Moreover, individuals with a flat foot (pes planus or pronated foot), characterized by lowered MLA, have small ACSAs and muscle thickness of ABH and FHB compared to those with a normal foot (Angin et al., 2014). In contrast to these findings, another study reported that individuals with a flat foot have larger muscle thickness of the ABH compared to those with a normal foot (Taş et al., 2018). In addition, the size of ABH and FHB relates to foot length parameters (Latey et al., 2018). However, the previous studies cited here have only examined the interrelationship between the limited morphological profiles of the foot and the size for three (ABH, FDB, and FHB) of the ten plantar intrinsic foot muscles in humans (Kura et al., 1997).

1-5-4. Measurement of TFS and its significance to physical performance

TFS measurements have been conducted to evaluate the force-generation capacity of the toe flexor muscles, consisting of the plantar intrinsic foot muscles and extrinsic toe flexors (Goldmann & Brüggemann, 2012). A previous review has also suggested that no approach has been developed for determining the force-generation capacity of the plantar intrinsic foot muscles only (Soysa et al., 2012). Thus, it should be notated that for the TFS measurement, the force-generation capacity of the plantar intrinsic foot muscles and extrinsic toe flexors cannot have separately assessed each other. This section first refers to the significance of TFS for physical performance (section 1-5-4-1). Then, the type of TFS measurements (section 1-5-4-2) and the differences in the toe actions and toes intended for force production on the magnitude of TFS (section 1-5-4-3) are described.

1-5-4-1. Significance of TFS for physical performance

It is well known that TFS is associated with physical performance in various populations. For example, TFS positively associate with athletic performance scores in adolescents to young adults (Kurihara et al., 2021; Otsuka et al., 2015; Yamauchi & Koyama, 2020) and athletes (Yuasa et al., 2018; Yuasa et al., 2019). On the other hand, decreased TFS relates to impairments of mobility (Menz et al., 2006; Misu et al., 2014) and dynamic postural control (Menz et al., 2006; Misu et al., 2014; Uritani et al., 2016) in older adults. One previous study of our research group tried to develop these findings in community-dwelling healthy women (Kusagawa et al., 2020). The results showed that an association between reduced TFS and impairment of mobility was observed in individuals with pronated and supinated feet, but not in those with neutral feet (Kusagawa et al., 2020). Furthermore, older adults with reduced TFS also have a high risk of falls (Mickle et al., 2009). In addition, an intervention program aiming to enhance TFS increases the scores of athletic performances in young adults (Goldmann et al., 2013) and those of a dynamic balance test and quality of life in older adults (Nagai et al., 2011). Thus, identifying influential factors for TFS will provide useful information for designing a training program aiming to enhance physical performance in various populations or improve the quality of life in older adults.

1-5-4-2. Type of quantitative measurements of TFS

In previous studies, TFS has been measured using quantitative (Abe et al., 2016; Goldmann & Brüggemann, 2012; Goldmann et al., 2013; Kurihara et al., 2021; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016; Misu et al., 2014; Morita et al., 2018; Otsuka et al., 2015; Suwa et al., 2016; Yamauchi & Koyama, 2020; Yuasa et al., 2018) and qualitative (Menz et al., 2006; Mickle et al., 2009) methods. The quantitative measurements were conducted using a variety of toe dynamometers, such as toe grip, toe push, and hand-held

dynamometers (Abe et al., 2016; Goldmann & Brüggemann, 2012; Goldmann et al., 2013; Kurihara et al., 2021; Kurihara et al., 2014; Latey et al., 2018; Misu et al., 2014; Otsuka et al., 2015; Suwa et al., 2016; Yamauchi & Koyama, 2020; Yuasa et al., 2018), and sometimes using a plantar pressure platform (Latey et al., 2018; Mickle et al., 2016). On the other hand, qualitative measurements have been adopted in limited studies which performed a paper grip test (Menz et al., 2006; Mickle et al., 2009). As described above, most previous studies have adopted quantitative methods for measuring TFS. However, the devices used have not been consistent and are varied in previous studies. This section refers to detailed information on devices utilized for TFS measurements.

Toe grip dynamometry

Toe grip dynamometry has been conducted using a commercially available toe grip dynamometer developed based on a handgrip dynamometer (Uritani et al., 2012). The device has been used to investigate the association between TFS and physical performance in adolescents (Kurihara et al., 2021; Morita et al., 2018; Otsuka et al., 2015), young (Abe et al., 2016; Abe et al., 2015; Yamauchi & Koyama, 2019b, 2020) and older adults (Abe et al., 2015; Misu et al., 2014; Suwa et al., 2016; Uritani et al., 2016), and athletes (Yuasa et al., 2018; Yuasa et al., 2019).

In the TFS measurement with the toe grip dynamometer, the participants first place their proximal phalangeal of the great toe along the grip bar, and the others are positioned to grip the bar in reference to the great toe (Uritani et al., 2012). Then, the participants are required to grip the bar using all toes as much as possible. TFS determined with the device requires the combination of the flexion at the MTP and IP joints, called a toe gripping (curling) action (Soysa et al., 2012), and the determined score is referred to as a toe grip strength (TGS). It is also pointed out that TGS is produced at the MTP joint plantarflexed position (Kurihara et al., 2021;

Yuasa et al., 2018). The TGS has been measured in seated (Kurihara et al., 2021; Kurihara et al., 2014; Misu et al., 2014; Morita et al., 2018; Suwa et al., 2016; Uritani et al., 2012; Uritani et al., 2014, 2015, 2017) or bilateral standing (Abe et al., 2016; Abe et al., 2015; Otsuka et al., 2015; Yamauchi & Koyama, 2019b, 2020) conditions. In most previous studies, TGS has been determined in a seated position with 90º of the ankle joint (Kurihara et al., 2021; Kurihara et al., 2014; Misu et al., 2014; Morita et al., 2018; Suwa et al., 2016; Uritani et al., 2012; Uritani et al., 2014, 2015, 2017). The TGS measured in a seated position has consistently demonstrated good to excellent inter-session intra-rater reliability, with interclass correlation coefficients (ICC) values of 0.71 to 0.96 (Uritani et al., 2012). However, the magnitude of the TGS is affected by the ankle joint angle (Yamauchi & Koyama, 2019a). The ankle joint at 0º – 20º dorsiflexed is identified as the optimal position for TGS production, while the magnitude of TGS is gradually decreased toward the plantarflexed position (Yamauchi & Koyama, 2019a).

Toe push dynamometry

TFS determination by toe push dynamometry has been conducted using a custom-made toe push dynamometer. TFS production with the device requires flexion at the MTP joints and minimum excessive flexion at the IP joints, called a toe pushing action (Soysa et al., 2012), and the measured value is designated as a toe push strength (TPS). Goldmann and Brüggemann (2012) first introduced the device and adopted it to investigate the influence of the MTP and ankle joint angles on the TPS (Goldmann & Brüggemann, 2012). Thereafter, similar devices mimicking the toe push dynamometer used in Goldmann and Brüggemann's study have been developed by Rowley et al. (2015) and Saeki et al. (2015). The imitative toe push dynamometer, developed by Rowley et al. (2015), has been used to examine the association between TFS and physical performances in adolescents (Kurihara et al., 2021) and athletes (Rowley et al., 2015; Yuasa et al., 2018, 2019). In addition, the imitative toe push dynamometer, developed by Saeki

et al. (2015), have used to examine the effects of the MTP and ankle joint angles on TPS produced by the great toe and lesser toes.

In all cases, TPS measurements using the toe push dynameter have been performed in a seated position. The TPS produced by all toes (TPS-All) has excellent inter-session test-retest reliability (r = 0.91) (Goldmann & Brüggemann, 2012). Moreover, Yuasa et al., (2018) confirmed that TFS-All measured using the toe push dynamometers had as good intra-session intra-rater reliability (ICC value of 0.73–0.81) as those measured using the toe grip dynamometer. Furthermore, TPS produced by the great toe (TPS-Great) and that produced by lesser toes (TPS-Lesser) have excellent test-retest repeatability on the different days, with ICCs (1.1) values of 0.81 and 0.87, respectively (Saeki et al., 2015). In addition, it is reported that the magnitude of the TPS is affected by the MTP and ankle joint angles (Goldmann & Brüggemann, 2012; Saeki et al., 2021). The highest TPS-All values have been observed at 0º–10º of dorsiflexion at the ankle joint and 25º–45º degrees of dorsiflexion at the MTP joint. In contrast, the lowest values were observed at 35º of plantarflexion at the ankle joint and 0º of dorsal flexion at the MTP joint (Goldmann & Brüggemann, 2012). Moreover, the values of TPS-Great and TPS-Lesser increased with the increment in dorsiflexion angle at the MTP joint, and the highest value appeared at 45º at the MTP joint and 0º at the ankle joint (Saeki et al., 2021). Based on the findings by Goldmann and Brüggemann. (2012), most studies that measured TPS-All with a toe push dynamometer have adopted the measurement condition that the ankle joint at 0º of dorsiflexion (neutral position) and the MTP joint at 45º of dorsiflexion (Kurihara et al., 2021; Yuasa et al., 2018, 2019).

Hand-held dynamometry

TFS determined by hand-held dynamometry has been conducted using a commercially available hand-held dynamometer and has been used to examine the association between TFS

and physical performances in older adults (Spink et al., 2011). TFS determination with the device requires multiple joint movements consisting of flexion at the MTP joint and less excessive flexion at the IP joints called a toe pushing action. The determined score using the device is designated as TPS. Previous studies have measured TPS-Great (Latey et al., 2018; Spink et al., 2011) and/or TPS-Lesser (Spink et al., 2011) in the bilateral stance. However, TPS-All has not been determined by hand-held dynamometry. Only one study has examined the intra-rater reliability of TFS measurement with a hand-held dynamometer. From the limited finding, TFS determined by hand-held dynamometry has good intra-rater reliability, with an ICC value of 0.75 (Latey et al., 2018).

Plantar pressure platform

TFS measurement using a plantar pressure platform has been developed to mimic the procedure of the paper grip test (Soysa et al., 2012), which is a quantitative assessment developed to assess the intrinsic foot muscles paralysis for patients with leprosy (Hansen's disease) in the clinical field (Win et al., 2002). TFS determination by plantar pressure platform requires participants to stand bilaterally and exert TFS using the lesser toes (Mickle et al., 2016) (Mickle et al., 2009) or using the great toe (Latey et al., 2018; Mickle et al., 2016). The plantar pressure platform has been shown to have a good to excellent between-day intra-rater reliability, with the ICC values of 0.83 for only the great toe (Latey et al., 2018) and 0.92 for the great toe only combined with lesser toes (Mickle et al., 2009). The plantar pressure platform has been mainly employed to measure TFS in older people (Mickle et al., 2009, 2016) as well as hand-held dynamometry.

The above-mentioned studies showed that toe dynamometry has been widely accepted to measure TFS in various generations. Two types of TFS have been determined using the toe

dynamometry depending on the actions required by the device utilized: the TGS determined by the toe gripping action for the toe grip dynamometer and the TPS determined by the toe pushing action for the hand-held or toe push dynamometer. It is also noted that TGS production required force output at the MTP joint plantarflexed position, while TPS with toe push dynamometry was produced by the force at the MTP joint dorsiflexed position. Soysa et al. (2012) reviewed the methods for measuring intrinsic foot muscle strength and noted that different toe actions would change the contribution of plantar intrinsic foot muscles and extrinsic toe flexors to TFS production (Soysa et al., 2012). Therefore, the type of device utilized, and the toe action required should be remarked on when evaluating the force-generation capacity of the toe flexor muscles by determining TFS.

1-5-5. The influence of the difference in the toe actions and toes intended for force production on the TFS

As mentioned above sections, TFS has been assessed by the two types of toe actions for force production i.e., TGS and TPS, depending on the device utilized. A previous study has examined the difference/relationship between TGS and TPS (Kurihara et al., 2021). Their limited findings showed that while TPS-All (measured using the toe push dynamometer) and TGS were significantly correlated with each other, the former was significantly greater than the latter.

In addition, there are differences in the toes intended for force production among previous studies: TFS production by all toes (TGS and TPS-All), great toe (TPS-Great), or lesser toes (TPS-Lesser). In previous studies, it is reported that the magnitude of TFS depends on the toes intended for force production. The TFS production by all toes is approximately three times greater than that by lesser toes (Abe et al., 2016). Moreover, the TFS produced by the great toe was larger than that produced by the lesser toes (Mickle et al., 2016; Saeki et al., 2021),

with the former being about 1.5 times greater than the latter (Mickle et al., 2016). Considering these aspects, when measuring TFS, caution should be taken not only for the difference in toe actions depending on the device utilized but also for those in toes intended for force production.

1-5-6. Strength and size relationship of the toe flexor muscles

It is reorganized that TFS production reflects the force-generation capacity of the toe flexor muscles, comprising the plantar intrinsic foot muscles as well as extrinsic toe flexors (Goldmann & Brüggemann, 2012). This has been substantiated by the studies showing that the size of plantar intrinsic foot muscles and/or extrinsic toe flexors significantly relates to TFS (Abe et al., 2016; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016). Furthermore, Kurihara et al., (2014) found that the ACSA of medial and lateral parts of the plantar intrinsic foot muscles was selected as determinant factors for TGS production as a result of stepwise multiple linear regression analysis.

In the previous studies cited here, the methods of measuring TFS were inconsistent. Abe et al., (2016) and Kurihara et al., (2014) determined TFS using a toe grip dynamometer (i.e., TGS), while others measured TFS using a hand-held dynamometer, i.e., TPS (Latey et al., 2018) or plantar pressure platform (Latey et al., 2018; Mickle et al., 2016). Moreover, the toes intended for force production during TFS measurement in these studies varied: two studies measured TFS produced by all toes (Abe et al., 2016; Kurihara et al., 2014), while others measured TFS produced by the great toe only (Latey et al., 2018; Mickle et al., 2016) or that produced by lesser toes (Mickle et al., 2016).

The muscle size variable and number of muscles adopted as independent variables for TFS also varied. Most studies determined ACSA and/or muscle thickness of limited toe flexor muscles using ultrasonography. On the other hand, Kurihara et al., (2014) used MRI and determined ACSA of individual extrinsic toe flexors and that of a compartment containing

several plantar intrinsic foot muscles.

1-6. Research questions and hypothesis

The major functions of plantar intrinsic foot muscles are to maintain the foot structure, particularly MLA, and to produce force at the toes based on an anatomical perspective, such as location or attachment site (section 1-5-1-3). On the other hand, the functions of individual muscles have also been estimated from their morphological parameters, which reflect the contractile properties of a muscle. Therefore, characterizing each of the plantar intrinsic foot muscles using its morphological parameters may provide a new perspective to understand the function of these muscles beyond that derived from the anatomical profiles.

In previous studies, the ACSA and muscle thickness have been adopted as independent variables for examining how muscle size relates to TFS and foot structure (sections 1-5-3 and 1-5-6). However, compared to ACSA and muscle thickness, MV and $ACSA_{max}$ are more strongly associated with muscle strength (Balshaw et al., 2021; Fukunaga et al., 2001). Moreover, the magnitude of ACSA and muscle thickness depends on the determination site (Blazevich et al., 2006; Fukunaga et al., 1992), and so it only provides regional/limited information about the entire muscle size. In addition, plantar intrinsic foot muscles have distinct anatomical functions individually (section 1-5-1-3). Considering these aspects, to elucidate the association of the size of the plantar intrinsic foot muscle with TFS and multi-dimensional foot structures, it should be desirable to adopt the MV or $ACSA_{max}$ of each muscle as independent variables.

The TFS measurement has been conducted by two types of toe actions (i.e., toe gripping and pushing actions) and three types of toes intended for force production (i.e., TFS produced by all toes, great toe only, and lesser toes). In previous studies, the ACSA and muscle

thickness of limited muscles or ACSA of including several muscles as one mass has been adopted as independent variables for examining the relationship with TFS production with different toe actions or toes intended for force production. On the other hand, the magnitude of TFS depends on the toe action and toes intended for force production (section 1-5-5). Moreover, the anatomical functions of the plantar intrinsic foot muscles vary depending on their attachment site. For example, some of the plantar intrinsic foot muscles are specialized in toe flexion (i.e., FDB and FHB), while others mainly act on the add/abduction and assist in the flexion of toes (e.g., ADDH and ABH) (section 1-5-1-3). Therefore, it remains unclear which muscle(s) primarily contributes to each TFS production with different toe actions and/or toes intended for force production.

1-7. Purpose

The general purpose of this thesis was to elucidate how the morphological profiles of individual plantar intrinsic foot muscles associate with foot structure and TFS. To this end, this thesis adopted two approaches: one based on the muscle size and its relation to foot structure and TFS that addresses the issues of the previous literature, and the other based on morphological parameters reflecting the contractile properties. Firstly, Chapter 2 examined the morphological profiles of individual plantar intrinsic foot muscles by obtaining the basic data concerning muscle size ($ACSA_{max}$ and MV), ACSA distribution, and the position where $ACSA_{max}$ was observed. Chapter 3 examined how the morphological parameters of individual plantar intrinsic foot muscles could be categorized in relation to contractile properties, derived from the PCSA and muscle fiber length. Chapters 4 and 5 determined associations of muscle size with the foot morphological profile and TFS, respectively as an approach based on the muscle size and its relation to foot structure and TFS. On the basis of the findings obtained in

previous chapters, Chapter 6 discussed associations of individual plantar intrinsic foot muscles with foot structure and TFS. The outline of this thesis is shown in Fig. 1-5.

The experiments undertaken in each chapter are briefly described below.

Chapter 2: Morphological Profiles of Individual Plantar Intrinsic Foot Muscles

Morphological profiles of individual plantar intrinsic foot muscles, particularly the size of individual plantar intrinsic foot muscles was determined as the basic data for the subsequent Chapters. First, serial longitudinal relaxation time (T1)-weighted MR images of the whole foot were acquired. From the series of MR images obtained, ACSA along the foot length (i.e., ACSA distribution) was analyzed for each of the individual plantar intrinsic foot muscles. $ACSA_{max}$ and MV were determined as representing muscle size variables, and ACSA distribution the position where the $ACSA_{max}$ was observed also were identified. Second, the MV magnitude of each muscle was compared with those reported in previous literature.

Chapter 3: Clustering Analysis in the Contractile Properties of Individual Plantar Intrinsic Foot Muscle Based on the Relationship between Physiological Cross-Sectional Area and Muscle Fiber Length

Whether individual plantar intrinsic foot muscles can be classified based on their morphological profiles reflecting the contractile properties was examined. The PCSA and muscle fiber length of plantar intrinsic foot muscles, which reflect maximal force production and shortening velocity of a muscle, respectively, were estimated by combining data from living subjects obtained in Chapter 2 and cadavers in Kura et al., (1997) and Ledoux et al., (2001). Next, K-means clustering analysis was conducted using PCSA and muscle fiber length as attributes, and individual muscles were classified into some clusters with similar contractile properties. Then, the function of each cluster, especially the maintenance of the foot arch

structure and the force production at the toes was deduced from their contractile properties.

Chapter 4: Associations between the Size of Individual Plantar Intrinsic Foot Muscles and Multi-dimensional Morphological Profiles of the Foot

How the size of plantar intrinsic foot muscles relates to multidimensional foot morphological parameters was examined by adopting MV, determined in Chapter 2, as a representing muscle size variable. The multi-dimensional foot morphological parameters (i.e., foot length, width, circumference, toe angles, and MLA height) were measured using a three-dimensional (3D) laser foot scanner. Then, associations between the MV of each plantar intrinsic foot muscle and multi-dimensional foot morphological profiles were examined.

Chapter 5: Strength and Size Relationships of Toe Flexor Muscles

The relationship between TFS and the size of the toe flexor muscles was examined for determining the muscles that primarily contribute to TFS production. In section 1, MV and $ACSA_{max}$ for each toe flexor muscle were determined using MRI, and their relations to TFS measured using the toe grip dynamometer (i.e., TGS), which is the most common device for measuring TFS, were examined. Then, the muscle(s) that primarily contribute to TGS production was determined by stepwise multiple regression analysis. In section 2, three types of TPS, depending on the toes intended for force production were measured using the custom-made toe push dynamometer as follows: TPS produced by all toes (TPS-All), great toe (TPS-Great), and lesser toes (TPS-Lesser). Then, whether the strength and size relationships of the toe flexor muscles vary depending on the toes intended for force production was determined by examining the association between muscles size and three types of TPS production (i.e., TPS-All, TPS-Great, and TPS-Lesser).

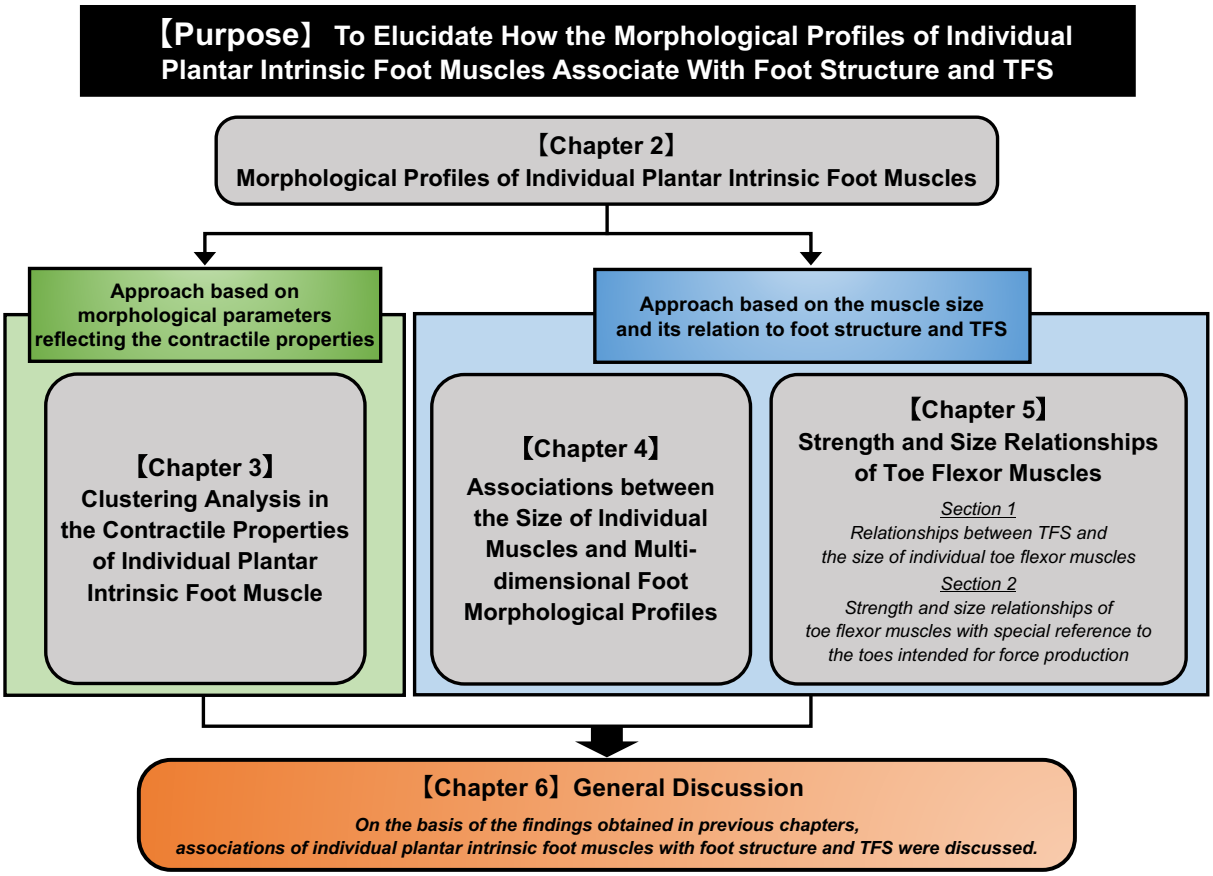

Figure 1-5. Outline of this thesis.

Chapter 2 Morphological Profiles of Individual Plantar Intrinsic Foot Muscles

2-1. Introduction

Previous studies have measured the ACSA and muscle thickness of a limited number of individual muscles as independent variables for examining how the size of plantar intrinsic foot muscles relates to TFS (Abe et al., 2016; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016) and foot structure (Angin et al., 2014; Latey et al., 2018; Taş et al., 2018). Compared to ACSA and muscle thickness, however, MV and $ACSA_{max}$ have been shown to be more strongly associated with muscle strength compared to ACSA and muscle thickness (Balshaw et al., 2021; Fukunaga et al., 2001). Moreover, since the magnitude of ACSA and muscle thickness are dependent on the site of determination (Blazevich et al., 2006; Fukunaga et al., 1992), these only provide regional/limited information about the entire muscle size. Thus, it should be desirable to adopt the MV or $ACSA_{max}$ of a muscle as independent variables for examining the association with muscle strength or foot morphological profiles. Therefore, this Chapter aimed to quantify morphological parameters, especially muscle size (the MV and $ACSA_{max}$) for each individual plantar intrinsic foot muscle by MRI, and then ACSA distribution and the position where $ACSA_{max}$ was observed were also determined as the morphological profiles of these muscles. This will provide the basic data for examining the association of size for plantar intrinsic foot muscles with muscle strength or foot morphological profiles in subsequent chapters.

2-2. Methods

Participants

Twenty-six healthy young men (age, 21.8 ± 2.4 yrs; height, 171.5 ± 5.2 cm; body mass, 63.8 ± 5.4 kg; mean ± standard deviation [SD]), with no history of a diagnosed neuromuscular disorder or lower limb injury, voluntarily participated in this Chapter. All participants provided prior written informed consent based on the guidelines of the Declaration of Helsinki.

MRI measurement

The participants were placed in a prone position on the examination table of 1.5 (Signa HDxt, GE Healthcare UK Ltd., Buckinghamshire, England) or 3.0 tesla (T) (Magnetom Skyra, Siemens Healthcare, Erlangen, Germany) MR systems. Then, their right foot and ankle were encased in the ankle coils (1.5 T MR system: HD Knee/Foot coil, GE Healthcare UK Ltd.; 3.0 T MR system: Foot/Ankle coil, Siemens Healthcare) and their ankle joint was positioned at 90° of plantarflexion (neutral position) to reduce the motion artifact using Velcro straps. With maintaining this body position, serial T1-weighted MR images of the whole foot were scanned from the sesamoids and calcaneal tuberosity perpendicular to the plantar aspect of the foot, using a fast spin-echo sequence in a 1.5 T MR system according to Chang et al., (2012) (repetition time = 500 ms, echo time = 16 ms, average = 3, slice thickness = 4 mm, gap between slices = 0 mm, field of view = 120 ×120 mm, flip angle = 90°, matrix = 512 × 512) and 3.0 T MR system (repetition time = 700 ms, echo time = 12 ms, average = 3, slice thickness= 3.5 mm, gap between slices= 0 mm, field of view=125×125 mm, flip angle=120°, and matrix = 512 × 512). The data acquisition time of each scan was approximately 4 min.

Determination of $ACSA_{max}$, MV, and position where $ACSA_{max}$ is observed

The obtained MR images were analyzed by using image analysis software

(SliceOmatic version 5.0Rev-3b, Tomovision, Montreal, Canada). One examinator manually traced and segmented the ACSA of each of the seven plantar intrinsic foot muscles (detailed below) in every MR image from the most proximal to distal MR images in which the muscles were visible (Fig. 2-1 B) by using a graphics tablet (Intuos pro, Wacom Co., Ltd., Saitama, Japan). In this segmentation process, non-contractile tissues such as bone, tendon, fat, connective tissue, nerve tissue, and blood vessels were carefully excluded. The measured muscles were ABDM, ABH, ADDH-OH, ADDH-TH, FDB, FHB, and QP. The other three muscles (i.e., lumbricals, flexor digiti minimi, and plantar interossei) were excluded from the analysis due to their small size and resulting difficulties in visually separating these muscles.

Furthermore, MRI-determined foot length (FL) was calculated from the number of slices between the medial calcaneal tuberosity and the sesamoid bones of the first metatarsal (Fig. 2-1 A), multiplied by the slice thickness. The position of each image was expressed as the value relative to FL [0% FL: the medial calcaneal tuberosity, 100% FL: the sesamoid bones of the first metatarsal (Fig. 2-1 A)]. The ACSA of each individual muscle and functional muscle group (detailed below) was calculated at 5% intervals of FL by linear interpolation using Excel (Microsoft Corp., Redmond, WA). The maximal ACSA value along the 5% intervals of FL was defined as $ACSA_{max}$ and the position where $ACSA_{max}$ appears along 5% intervals of FL was measured. The position of the navicular tuberosity and 1st tarsometatarsal joint was also determined at 5% intervals of FL. Moreover, MV was calculated by summing all the measured ACSAs (not calculated as 5% intervals of FL) for each muscle multiplied by the slice thickness. The $ACSA_{max}$ and MV were also analyzed as following functional muscle groups: whole plantar intrinsic foot muscles (all analyzed plantar intrinsic foot muscles), intrinsic great toe (including FHB, ABH, ADDH-OH, and ADDH-TH), and intrinsic lesser toes flexors (including QP, FDB, and ABDM). Intra-rater repeatability for measuring $ACSA_{max}$ and MV of four participants in this study was assessed by ICC. The ICC (1, 3) values of $ACSA_{max}$ and MV of individual

muscles were 0.869 – 0.999 and 0.842 – 0.996, respectively, and good to excellent repeatability was confirmed (Koo & Li, 2016). Furthermore, the FL was divided into the rear, mid, and forefoot regions using the position of the navicular tuberosity (45 ± 2% FL) and 1st tarsometatarsal joint (72 ± 2% FL) as reference points. The rear, mid, and forefoot regions were defined as those up to the navicular tuberosity (0–45% FL), between the navicular tuberosity and 1st tarsometatarsal joint (46–72% FL), and far from the 1st tarsometatarsal joint (73–100% FL), respectively.

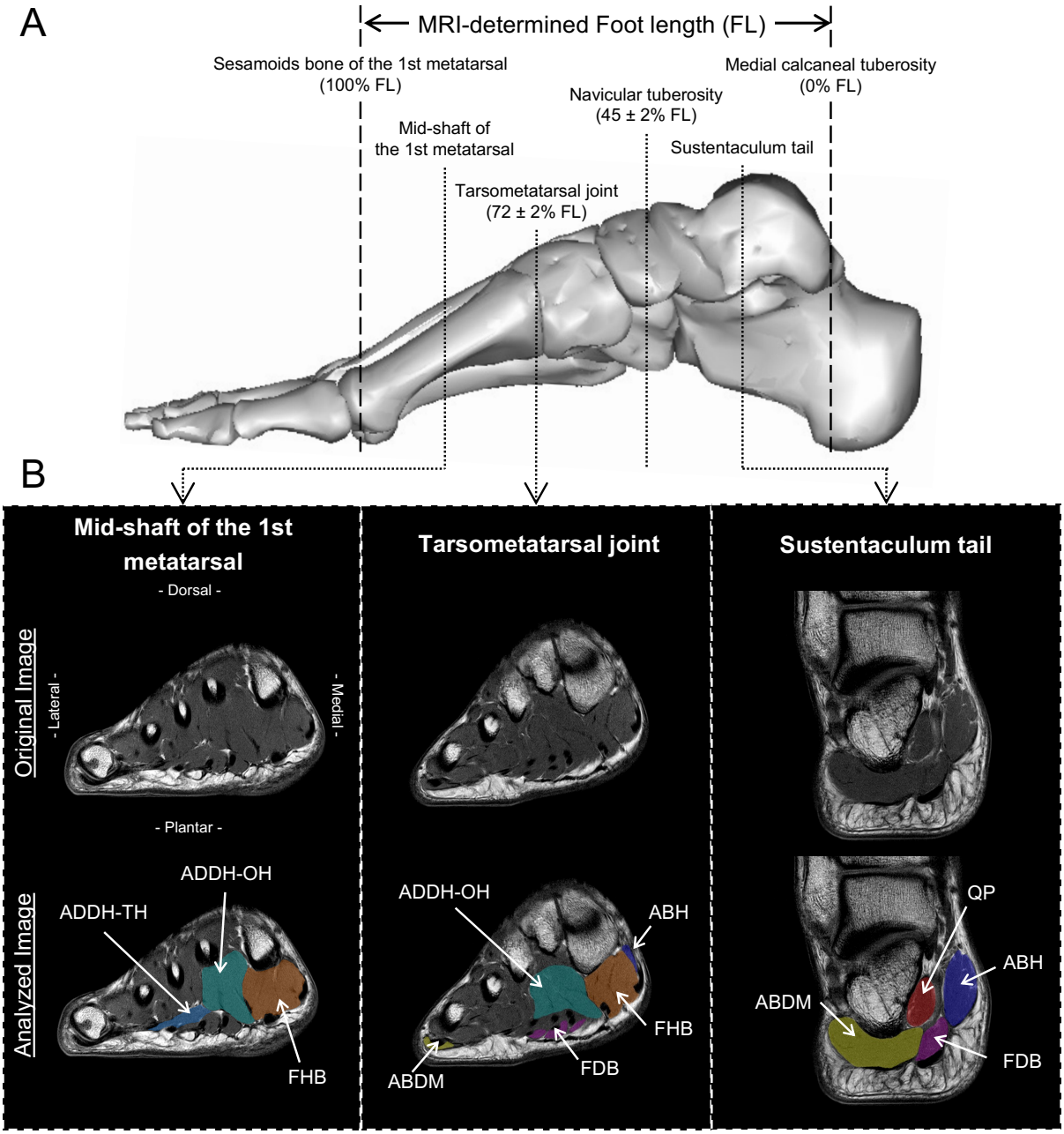

Figure 2-1. Definition of MRI-determined foot length (A) and MR images (B) of the right foot. ABDM (abductor digiti minimi), ABH (abductor hallucis), ADDH-OH (adductor hallucis oblique head), ADDH-TH (adductor hallucis transverse head), FDB (flexor digitorum brevis), FHB (flexor hallucis brevis), and QP (quadratus plantae) were manually segmented. The foot image of the A was created using "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

Statistical analysis

Descriptive data are presented as means ± SDs.

Comparison of MV values between this present study and previous literature

In the present study, the MV value of individual muscles was compared to those obtained from previous literature targeted in cadavers (Kura et al., 1997) and healthy populations (Feger et al., 2016; Franettovich Smith et al., 2022). Of these, Feger et al., (2016) reported only data normalized by body size (body mass and height), so the estimated values, which removed normalization using their body size data were calculated.

2-3. Results

Distribution of ACSAs along FL and $ACSA_{max}$ position

Fig. 2-2 and 2-3 show the distributions of ACSAs along the % FL in each functional muscle group and individual muscle, respectively. The ACSA of whole plantar intrinsic foot muscles (Fig. 2-2 a) was distributed over the whole FL (0 to 100% FL) and showed bimodal distribution in the rearfoot and forefoot regions. Moreover, intrinsic great toe (Fig. 2-2 b) and lesser toes flexors (Fig. 2-2 c) were widely distributed along the FL (intrinsic great toe flexors: 5 to 100 % FL, intrinsic lesser toes flexors: 0 to 100 %FL). For individual plantar intrinsic foot muscle (Fig. 2-3), the ACSAs of QP (Fig. 2-3 a), ABDM (Fig. 2-3 b), ABH (Fig. 2-3 c), and FDB (Fig. 2-3 d) were widely distributed along the FL: 0 – 70 % FL for QP, 0 – 90 % FL for ABDM, 5 – 95 % FL for ABH, and 5 – 90 % FL for FDB. The ACSA of FHB (Fig. 2-3 e) and ADDH-OH (Fig. 2-3 f) were distributed in the midfoot and forefoot regions (35 – 100 % FL and 50 – 100 % FL, respectively), while those of ADDH-TH (Fig. 2-3 g) in only forefoot region (85 –100 % FL).

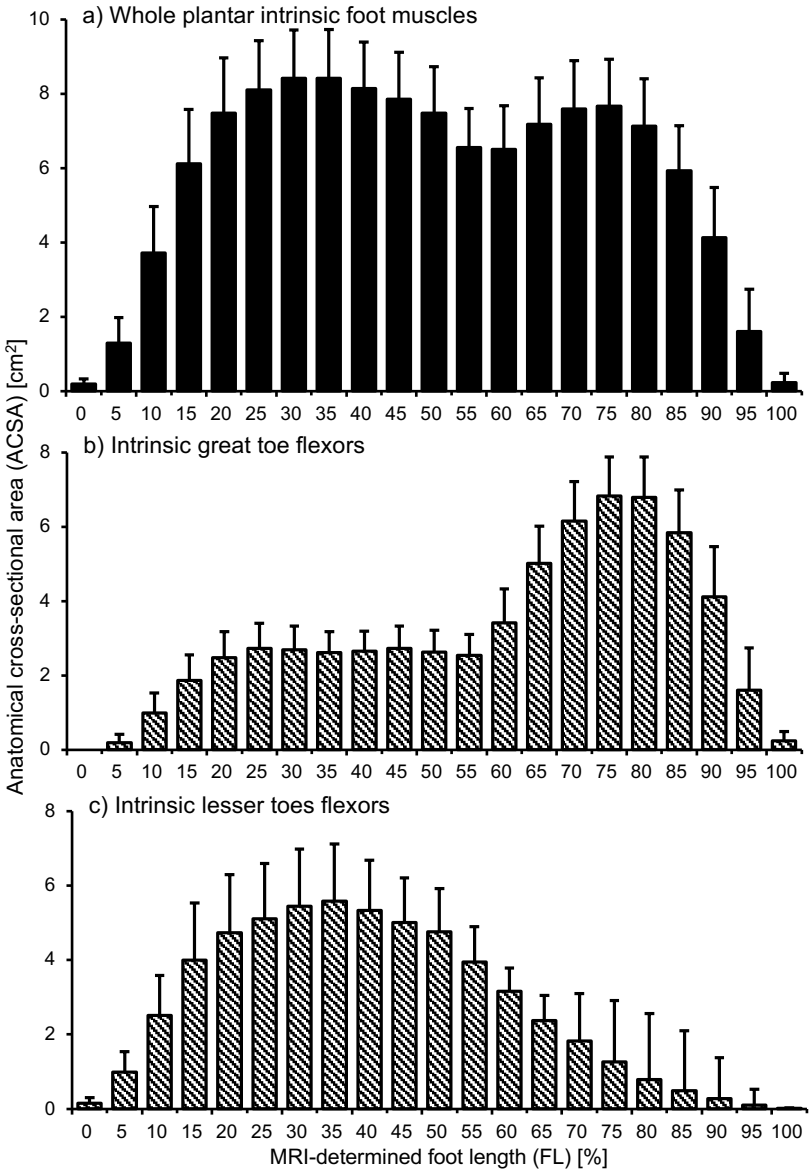

Figure 2-2. Distribution of anatomical cross-sectional area of each functional muscle group along the % foot length (0%: calcaneal medial tuberosity, 100%: sesamoid bones of the first metatarsal). The bar of each graph represents the mean (+SD) of the anatomical cross-sectional area for all participants (n = 26). (a): Whole plantar intrinsic foot muscles indicate all analyzed plantar intrinsic foot muscles; (b): intrinsic great toe flexors include abductor hallucis (ABH), adductor hallucis oblique head (ADDH-OH), adductor hallucis transverse head (ADDH-TH), and flexor hallucis brevis (FHB); (c): intrinsic lesser toes flexors include abductor digiti minimi (ABDM), flexor digitorum brevis (FDB), and quadratus plantae (QP).

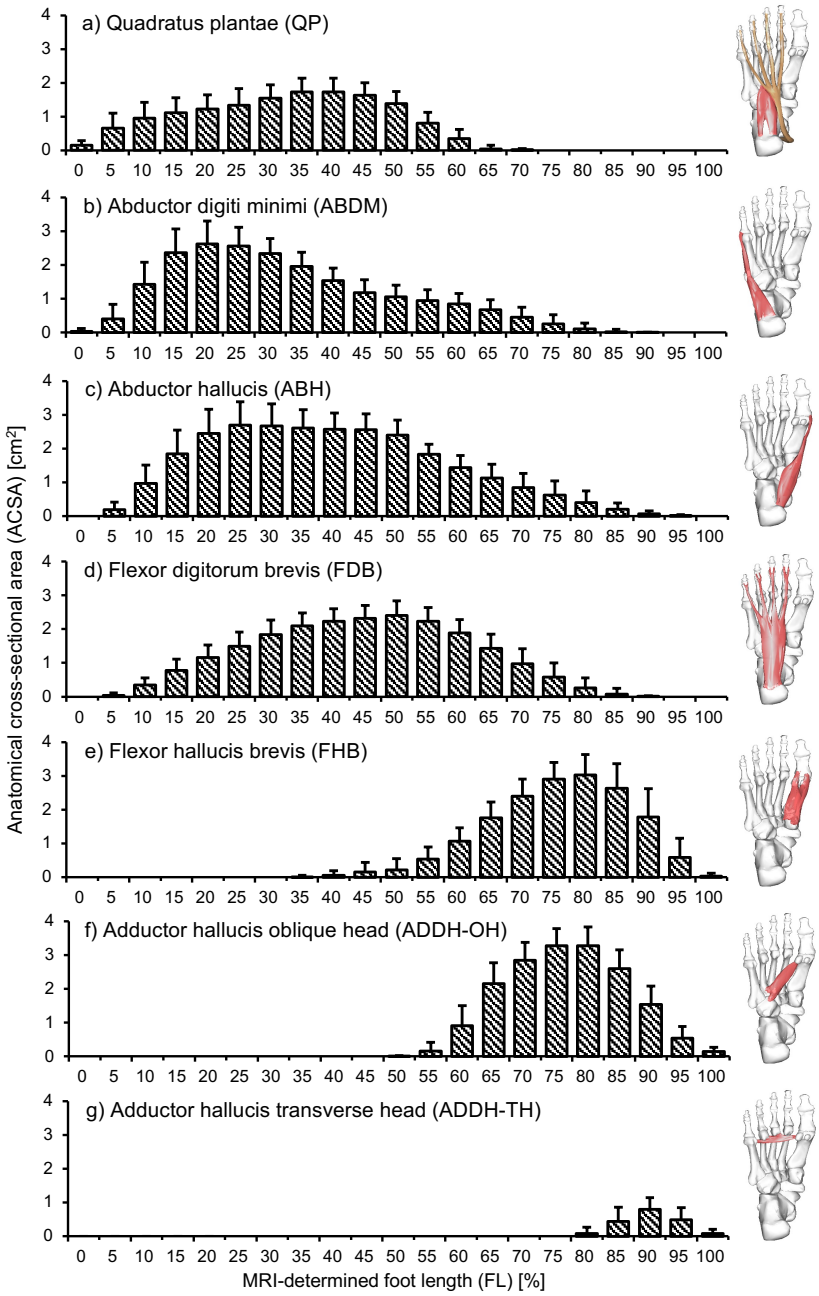

Figure 2-3. Distribution of anatomical cross-sectional area of each individual muscle along the % foot length (0%: calcaneal medial tuberosity, 100%: sesamoid bones of first metatarsal). The bar of each graph represents the mean (+SD) of the anatomical cross-sectional area for all participants (n = 26). The muscle images on the right side of each graph were created using "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan"

Fig. 2-4 shows the position where $ACSA_{max}$ was observed for each plantar intrinsic foot muscle. The position where $ACSA_{max}$ was observed for whole plantar intrinsic foot muscles was observed in the rearfoot region (42 ± 18 % FL). The $ACSA_{max}$ value of the intrinsic great toe and lesser toes flexors were observed in the rearfoot (37 ± 13 % FL) and forefoot region (78 ± 3 % FL), respectively. The ABDM, ABH, and QP had their $ACSA_{max}$ position at 22 ± 4 % FL, 32 ± 10 % FL, and 35 ± 10 % FL in the rearfoot region, respectively. The position where $ACSA_{max}$ was observed of FDB was located in the midfoot region (48 ± 5 % FL). The position where $ACSA_{max}$ was observed of FHB, ADDH-OH, and ADDH-TH were located in the forefoot region (79 ± 3 % FL for FHB, 78 ± 3 % FL for ADDH-OH, and 91 ± 3 % for ADDH-TH).

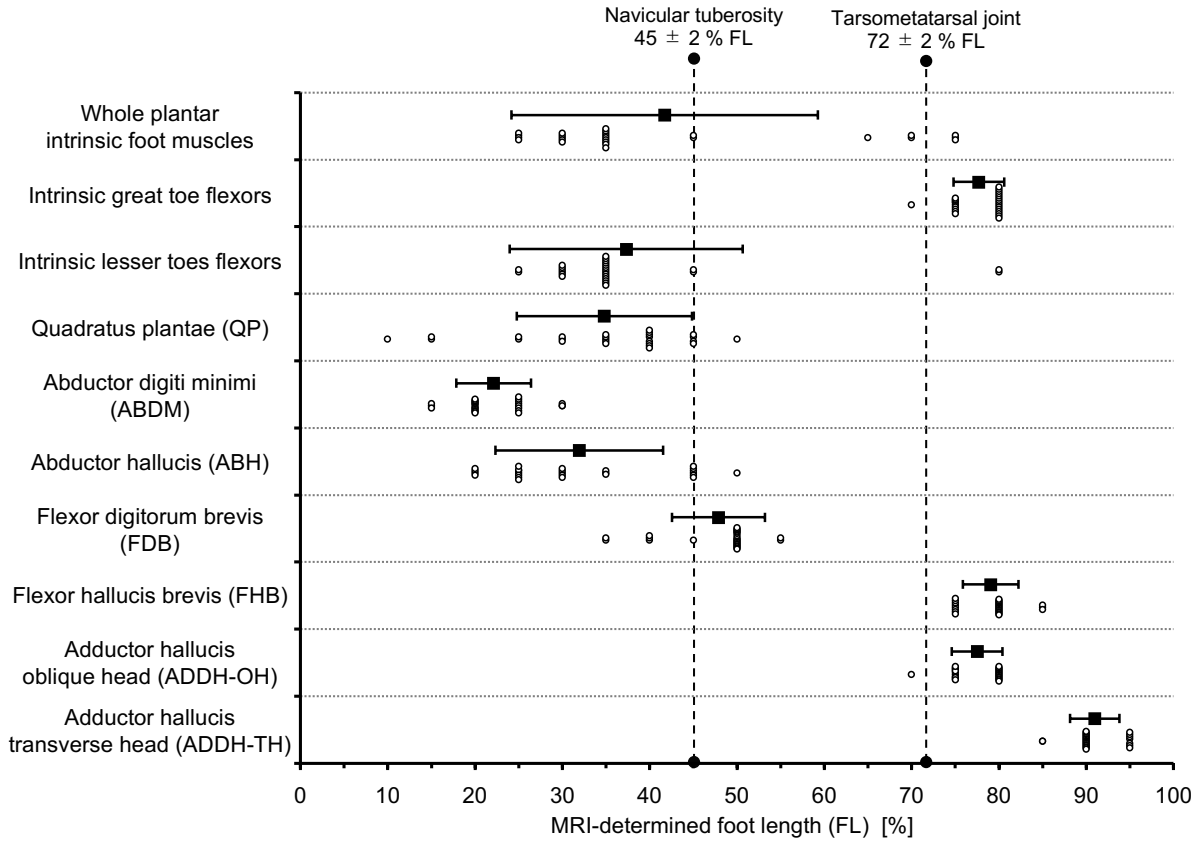

Figure 2-4. The $ACSA_{max}$ position of each functional muscle group and individual muscle (0%: calcaneal medial tuberosity, 100%: sesamoid bones of the first metatarsal). Square plots (with error bars) show the mean (± SD) for all participants (n = 26). Circle plots show the measured data for each participant. Whole plantar intrinsic foot muscles include all analyzed plantar intrinsic foot muscles; intrinsic great toe flexors include abductor hallucis (ABH), adductor hallucis oblique head (ADDH-OH), adductor hallucis transverse head (ADDH-TH), and flexor hallucis brevis (FHB); intrinsic lesser toes flexors include abductor digiti minimi (ABDM), flexor digitorum brevis (FDB), and quadratus plantae (QP).

The values of MV and $ACSA_{max}$

Fig. 2-5 shows the mean value of MV and $ACSA_{max}$ of each muscle group and individual muscle. The MV and $ACSA_{max}$ of the intrinsic great toe flexors tended to be slightly greater than those in intrinsic lesser toes flexors (Fig. 2-5 A). The MV value in the intrinsic great toe and lesser toes flexors accounted for 53% and 47% of that in whole plantar intrinsic foot muscles, respectively. In individual muscles, the largest MV value was observed in ABH, followed by FDB, ABDM, ADDH-OH, FHB, QP, and ADDH-TH (Fig. 2-5 B, a). Twenty-four participants (92.3%) showed the largest MV value for the ABH, while the others (7.6%) showed the largest MV value for the FDB. Unlike the order of MV magnitude, the largest $ACSA_{max}$ value was found in ADDH-OH, followed by FHB, ABH, ABDM, FDB, QP, and ADDH-TH (Fig. 2-5 B, b).

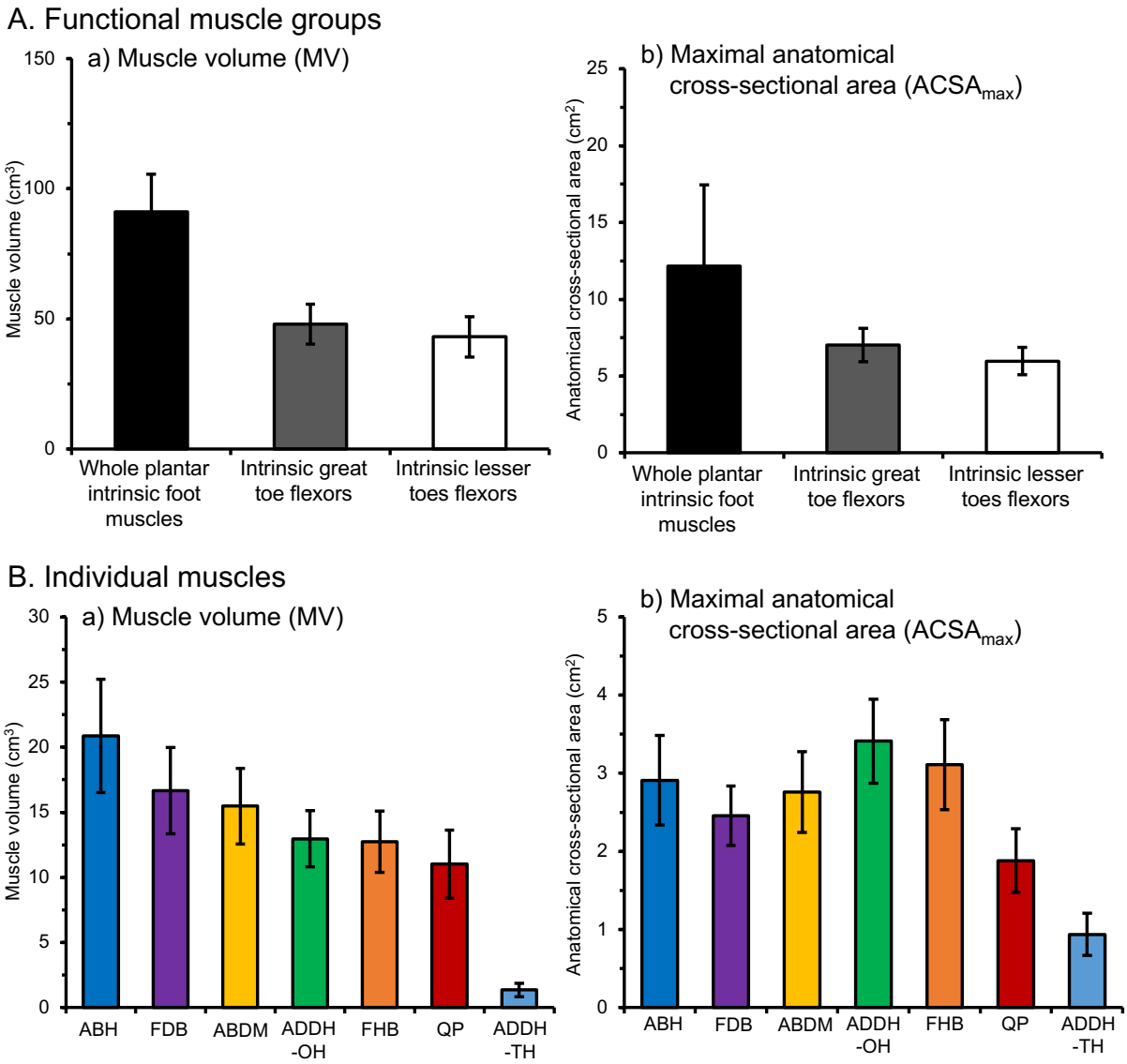

Figure 2-5. Muscle volume and maximal anatomical cross-sectional area for each functional muscle group (A) and individual muscle (B). Whole plantar intrinsic foot muscle consists of all analyzed plantar intrinsic foot muscles. Intrinsic great toe flexors includes abductor hallucis (ABH), adductor hallucis oblique head (ADDH-OH), adductor hallucis transverse head (ADDH-TH), and flexor hallucis brevis (FHB). Intrinsic lesser toes flexors include abductor digiti minimi (ABDM), flexor digitorum brevis (FDB), and quadratus plantae (QP).

Comparison of the MV values between the present study and previous literature

Fig. 2-6 shows the mean values of MV of each individual muscle in the present study and previous studies. In the middle-aged to older cadavers reported by Kura et al., (1997), the largest MV value was observed for ABH, followed by FDB, ADDH-OH, ABDM, QP, FHB, and ADDH-TH. From the data reported by Franettovich Smith et al., (2022), the largest MV value was observed for the ABH, followed by ABDM, FDB, ADDH-OH, FHB, QP, and ADDH-TH in a healthy population. Feger et al., (2016) also reported data on healthy young adults. From their data, the largest MV value was observed for the FDB, followed by ABH, ABDM, QP, ADDH-OH, FHB, and ADDH-TH.

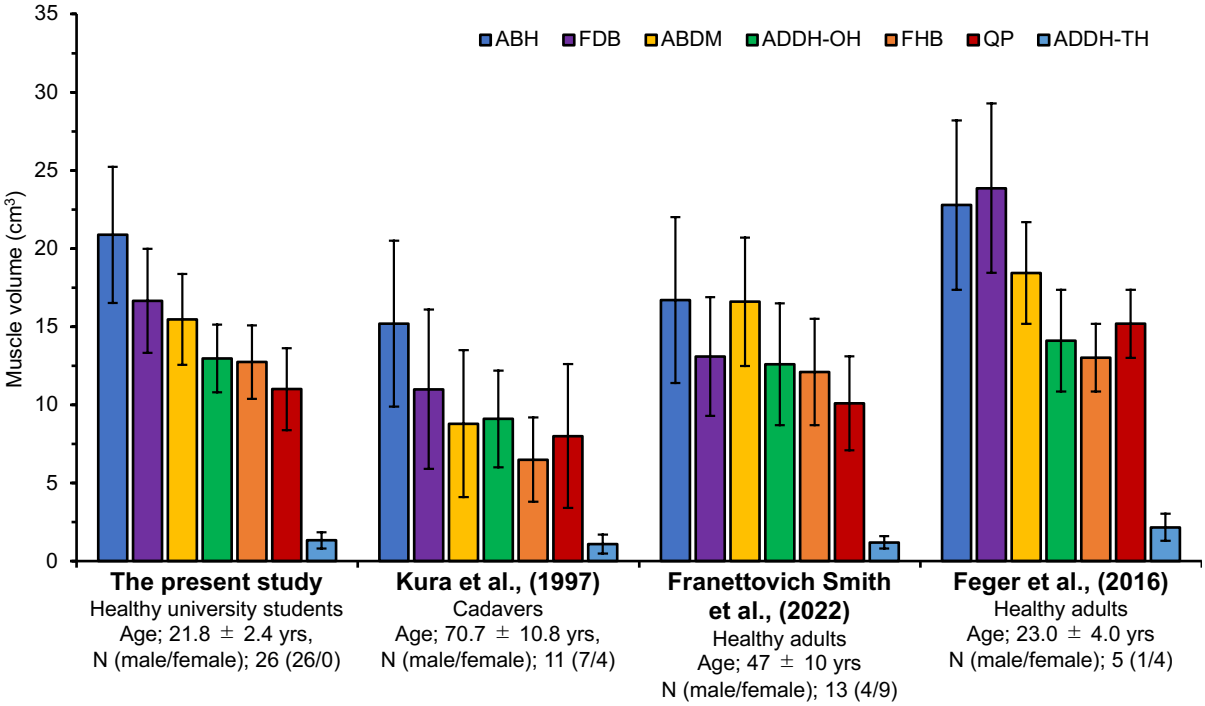

Figure 2-6. MV of individual muscles among the present and previous studies. Blue, purple, yellow, green, orange, red, and sky blue refer abductor hallucis (ABH), flexor digitorum brevis (FDB), abductor digiti minimi (ABDM), adductor hallucis oblique head (ADDH-OH), flexor hallucis brevis (FHB), quadratus plantae (QP), and adductor hallucis transverse head (ADDH-TH). The data from Feger et al., (2016) was those excluded the normalization by the body size.

2-4. Discussion

This Chapter confirmed that the morphological parameters of the seven planar intrinsic foot muscles can be quantified by MRI. The results showed that muscle size (i.e., MV and $ACSA_{max}$) varied among individual muscles, and this diversity among muscles was also observed in the ACSA distribution along the FL and the position where $ACSA_{max}$ was observed. In the previous studies, detailed information on the morphological profiles of the planar intrinsic foot muscles has been provided from the cadaveric dissection only (Kura et al., 1997). Morphological profiles of individual plantar intrinsic foot muscles in living subjects have been reported using MRI (Feger et al., 2016; Franettovich Smith et al., 2022), but the parameters measured were only MV from a limited number of subjects (N = 5–13). Therefore, the data obtained here from the 26 living young males, which was larger than other previous studies, may be utilized as the basic one for the subsequent Chapters of this thesis as well as future studies.

Three previous studies (Feger et al., 2016; Franettovich Smith et al., 2022; Kura et al., 1997) provided the MV value of individual muscles and therefore it can compare MV values in the current result to those in previous ones. In the current results obtained from the healthy male university students, ADDH-TH had the smallest values for both MV (Fig. 2-5 B, a) and $ACSA_{max}$ (Fig. 2-4 B, b) among individual plantar intrinsic foot muscles. This corresponding result was observed in all populations (Fig. 2-5), i.e., middle to older-aged cadavers (Kura et al., 1997) and mixed-sex healthy populations (Feger et al., 2016; Franettovich Smith et al., 2022). In addition, the current results showed that the largest MV value was observed in the ABH (Fig. 2-4 B, a). As a whole, all populations had the largest MV value found in ABH, except for sex-mixed healthy young adults reported by Feger et al., (2016) (Fig. 2-6). However, the MV values of FDB (23.87 cm^3) and ABH (22.78 cm^3) of healthy young adults in Feger et al. (2016) were almost the same. Considering these aspects, the current findings that MV value

was greatest in ABH and smallest in ADDH-TH among plantar intrinsic foot muscles would be consistent views regardless of the population targeted.

This Chapter is the first case attempting to determine the $ACSA_{max}$ value of individual plantar intrinsic foot muscles by quantifying continuous ACSA values along the FL. This differed from the methods for measuring ACSA adopted in previous studies; studies with ultrasonography have measured ACSA from the position where the thickest region of the muscle belly can be visually identified (Latey et al., 2018; Mickle et al., 2016), while that with MRI (Kurihara et al., 2014) has measured ACSA from a position at the largest ACSA values of whole plantar intrinsic foot muscles observed, i.e., 80% FL (Chang et al., 2012). From the current results, it was worth noting that the largest $ACSA_{max}$ value was observed in ADDH-OH. In this Chapter, serial MR images were scanned perpendicular to the plantar surface from the first metatarsal and calcaneal tuberosity (Chang et al., 2012). It seems that this scanning direction is not perpendicular to the running direction of ADDH-OH. This may be involved in the current results that the largest $ACSA_{max}$ value was observed in ADDH-OH among individual plantar intrinsic foot muscles.

The current results showed that the position where $ACSA_{max}$ was observed for each plantar intrinsic foot muscle was located at different sites along the FL (Fig. 2-4). Namely, the position where $ACSA_{max}$ was observed for each individual muscle was categorized into one of three regions: the rear (ABDM, ABH, and QP), mid (FDB), and forefoot (FHB, ADDH-OH, and ADDH-TH) regions. A previous study utilizing MRI quantified the ACSA of plantar intrinsic foot muscle at 80% FL (Kurihara et al., 2014), based on the previous finding that the ACSA of total plantar intrinsic foot muscle was largest at the corresponding position (Chang et al., 2012). In the current results, the value of $ACSA_{max}$ position was 79 ± 3 % for FHB and 78 ± 3 % for ADDH-OH. These were close to the position adopted in the previous study (Kurihara et al., 2014), 80 %, for quantifying ACSA (Fig. 2-4). However, the position where $ACSA_{max}$

was observed for the muscles located in the rear to midfoot (ABDM, ABH, FDB, and QP) and forefoot (ADDH-TH) regions in the current results was far from the position adopted to determine ACSA in the previous MRI study (Kurihara et al., 2014).

Furthermore, previous studies adopting ultrasonography have quantified ACSA or muscle thickness of a limited number of muscles (ABH, ABDM, FDB, FHB, and QP) of plantar intrinsic foot muscles, which locate relatively close to the body surface. These studies have not reported accurate information about the scanning positions of each muscle (Latey et al., 2018; Mickle et al., 2016). However, for the limited muscles quantified in previous studies, some anatomical landmarks have been described as a guide to scanning positions (Latey et al., 2018; Mickle et al., 2016). Based on these descriptions, therefore, it is possible to compare the measurement sites with the position where the $ACSA_{max}$ was observed in the present study. In these previous studies adopting ultrasonography, the shaft of the 1st metatarsal has been adopted as a position indicating the thickest part of FHB (Mickle et al., 2016). This position approximately corresponds to the tarsometatarsal joint which was located at 72 ± 2% FL in the present study (Fig. 2-4). Thus, the position adopted as the thickest part of FHB in previous studies (Mickle et al., 2016) roughly coincides with $ACSA_{max}$ position in the current study (79 ± 3% FL, Fig. 2-4). Moreover, the thickest site of ABH and ABDM have been identified at the proximal part of the navicular tuberosity and around the calcaneocuboid joint, respectively (Latey et al., 2018; Mickle et al., 2016). From the current results, the position corresponding to the navicular tuberosity was 45 ± 2% FL (Fig. 2-4). However, the position where $ACSA_{max}$ was observed for each ABH (32 ± 10% FL) and ABDM (22 ± 4% FL) was observed in a more proximal position than the navicular tuberosity (Fig. 2-4). Based on the comparisons with the current results, therefore, it is said that for FHB located in the forefoot region, the positions adopted in previous studies to quantify the muscle size approximately correspond to those where the $ACSA_{max}$ is obtainable, but not for the muscles with the position where $ACSA_{max}$

was observed in the rearfoot region (ABH and ABDM).

2-5. Conclusions

This Chapter confirmed that the seven planar intrinsic foot muscles can be quantified by MRI. The results of this Chapter indicate that in addition to the magnitude of muscle size (MV and $ACSA_{max}$), the ACSA distribution and the position where $ACSA_{max}$ appeared differs among individual muscles. Information on morphological profiles of individual plantar intrinsic foot muscles obtained here can be utilized as basic data for subsequent Chapters.

Chapter 3 Clustering Analysis in the Contractile Properties of Individual Plantar Intrinsic Foot Muscle Based on the Relationship between Physiological Cross-Sectional Area and Muscle Fiber Length

3-1. Introduction

In Chapter 2, muscle size (MV and $ACSA_{max}$), ACSA distribution, and the position where $ACSA_{max}$ differed among individual plantar intrinsic foot muscles. This implies that each plantar intrinsic foot muscle possesses distinct contractile properties. In previous studies, contractile properties of individual muscles have been investigated by determining the relationship between PCSA and fiber length for each region, such as in the lower (Ward et al., 2009) and upper (Lieber et al., 1992) limbs. This idea is based on the fact that PCSA and fiber length reflect maximal force production (Haxton, 1944) and shortening velocity (Gordon et al., 1966) of a muscle, respectively. On the basis of this idea, this Chapter aimed to elucidate the contractile properties of individual plantar intrinsic foot muscles in humans. To this end, the relationship between PCSA and fiber length of each plantar intrinsic foot muscle was firstly estimated in accordance with procedures used in a previous study (Fukunaga et al., 1992). Then, a K-means clustering analysis using PCSA and muscle fiber length as attributes was conducted to categorize individual muscles into some clusters with similar morphological characteristics. This approach may provide a new perspective to understand the function of plantar intrinsic foot muscles, especially the maintenance of the foot arch structure and the force production at the toes, by their morphological characteristics that enable to estimate of the contractile properties of a muscle, which are difficult to ascertain from the anatomical perspective of the depth of location and site of attachment that has been utilized (Kura et al., 1997; Neumann, 2017).

3-2. Methods

Data sample

In this Chapter, the PCSA and fiber length of seven plantar intrinsic foot muscles (ABDM, ABH, ADDH-OH, ADDH-TH, FDB, FHB, and QP) were estimated by combining data from twenty-six participants in Chapter 2 with those from the cadavers in Kura et al., (1997) and Ledoux et al., (2001).

Estimation of PCSA and fiber length

The PCSA and fiber length which are defined as parameters reflecting the maximum force production capacity (Haxton, 1944) and shortening velocity of a muscle (Gordon et al., 1966), respectively were estimated in accordance with the procedure described by Fukunaga et al. (1992) who used combined data obtained from living subjects and cadavers. Fiber length was calculated from the following equation (Fukunaga et al., 1992):

$$\text{Fiber length } (cm) = \text{muscle length } (cm) \times \text{fiber length to muscle length ratio}$$

where muscle length is the value measured from Chapter 2, the fiber length to muscle length ratio is the average value obtained from cadavers reported by Kura et al. (1997) as described in Table 3-1. Muscle length was measured as the distance between the most proximal and most distal MR images where the muscle was visible, except for ADDH-TH. Since the running direction of ADDH-TH is orthogonal to the scanning direction of the MR image, the muscle length of this muscle was measured as the distance from the most medial to the most lateral borders of the areas segmented as this muscle on multiple MR images. The PCSA of each muscle was calculated from the following equation (Fukunaga et al., 1992):

$$\text{PCSA } (cm^2) = \frac{\text{MV } (cm^3) \times \cos\theta}{\text{fiber length } (cm)}$$

where MV is the value obtained from Chapter 2, θ is the pennation angle reported by Ledoux et al., (2001), and fiber length is reported by Kura et al., (1997). The data of pennation angle

and fiber length was described in Table 3-1. It should be noted that the data from the cadavers of Kura et al., (1997) and Ledoux et al., (2001) for the fiber length to muscle length ratio and pennation angle required to calculate PCSA and fiber length for some muscles (FHB, FDB, and QP) were used as the average values for all muscular heads.

Table 3-1. Descriptive data on the muscle fiber length, fiber length to muscle length ratio, and pennation angle of each plantar intrinsic foot muscle reported by Kura et al., (1997) and Ledoux et al., (2001).

	Fiber length (cm)	Fiber length to muscle length ratio	Pennation angle (°)
ABDM	2.39 ± 0.74	0.25 ± 0.03	19.1 ± 11.9
ABH	2.30 ± 0.55	0.20 ± 0.02	16.5 ± 7.5
ADDH-OH	1.86 ± 0.53	0.29 ± 0.04	9.0 ± 7.3
ADDH-TH	1.87 ± 0.52	0.82 ± 0.07	13.3 ± 7.8
FDB	2.18 ± 0.38	0.25 ± 0.05	11.4 ± 8.0
attached 2nd toe	2.54 ± 0.45	0.28 ± 0.04	15.4 ± 7.2
attached 3rd toe	2.28 ± 0.40	0.24 ± 0.06	11.7 ± 9.2
attached 4th toe	2.08 ± 0.45	0.22 ± 0.05	7.0 ± 7.4
attached 5th toe	1.82 ± 0.22	–	–
FHB	1.70 ± 0.41	0.28 ± 0.08	7.8 ± 7.7
medial head	1.75 ± 0.48	0.29 ± 0.11	–
lateral head	1.65 ± 0.34	0.26 ± 0.05	–
QP	2.55 ± 0.71	0.47 ± 0.09	8.1 ± 4.8
medial head	2.75 ± 0.70	0.50 ± 0.09	–
lateral head	2.34 ± 0.71	0.44 ± 0.09	–

The value of fiber length and fiber length to muscle length ratio were reported by Kura et al., (1997) and that of pennation angle was reported by Ledoux et al., (2001). The values fiber length and fiber length to muscle length ratio of FHB, FDB, and QP were averaged for all muscular heads. Data not reported are shown with a hyphen. ABDM: abductor digit minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; QP: quadratus plantae.

Statistical analysis

Descriptive data are presented as means ± SDs. The normality of each data was tested by the Kolmogorov-Smirnov test using statistical software (SPSS version 27.0, IBM Co., USA) and confirmed as a normal distribution.

K-means clustering analysis

This Chapter firstly determined the relationship between PCSA and fiber length of each muscle. Then, after normalizing each data set by z-scored transformation, a K-means clustering analysis was performed on 182 data sets (7 muscles × 26 participants) with fiber length and PCSA as attributes. In addition, this Chapter utilized the average silhouette and elbow methods to determine the optimal number of clusters for K-means clustering analysis. The highest average silhouette value obtained was at four clusters (Fig. 3-1 A) and the elbow method also supported that four clusters were optimal (Fig. 3-1 B). The procedure involved in the clustering analysis described above was conducted using MATLAB software (version 2021b, MathWorks, Massachusetts, USA). Finally, the number of constituents assigned to individual clusters was counted for each muscle and their percentage of the number of individual samples (i.e., 26 participants) was calculated for each muscle.

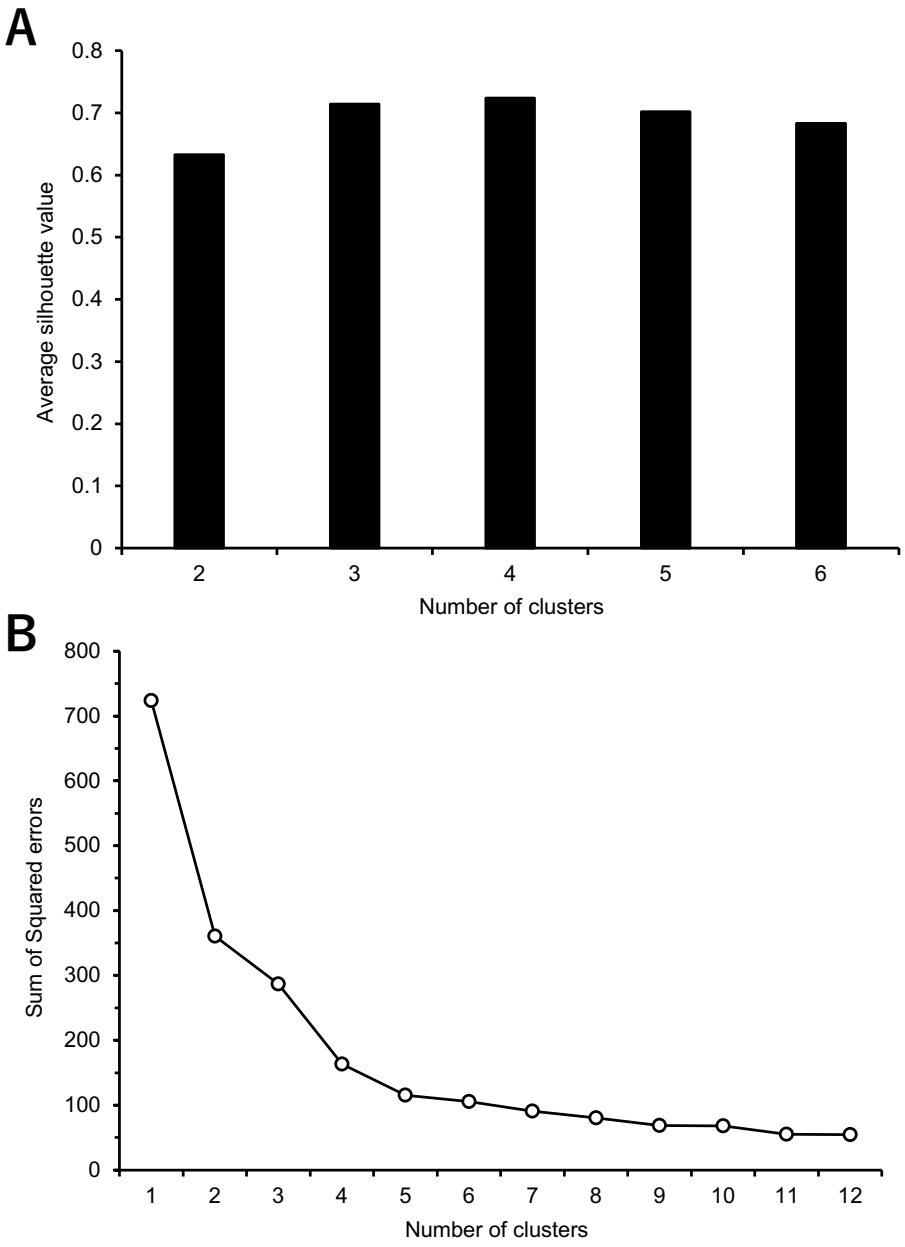

Figure 3-1. Average silhouette (A) and elbow (B) methods for K-means clustering analysis

3-3. Results

The descriptive data on morphological parameters including muscle length, fiber length, and PCSA of each plantar intrinsic foot muscle are summarized in Table 3-2. The mean value of MRI-determined muscle length was greatest in ABH, followed by ABDM, FDB, QP, FHB, ADDH-OH, and ADDH-TH. On the other hand, QP had the greatest mean value of estimated fiber length, followed by ABDM, FDB, ABH, ADDH-TH, FHB, and ADDH-OH. The mean value of estimated PCSA was greatest for ABH, followed by FDB, FHB, ADDH-OH, ABDM, QP, and ADDH-TH.

Table 3-2. Descriptive data on the muscle length, fiber length, and PCSA of each plantar intrinsic foot muscle

	MRI-determined muscle length (cm)	Estimated fiber length (cm)	Estimated PCSA (cm^2)
QP	9.20 ± 0.72	4.32 ± 0.34	4.28 ± 1.02
ABH	12.82 ± 0.97	2.56 ± 0.19	8.70 ± 1.82
FDB	10.78 ± 1.05	2.66 ± 0.26	7.49 ± 1.50
ABDM	11.31 ± 1.04	2.83 ± 0.26	6.35 ± 1.20
FHB	7.39 ± 1.25	2.03 ± 0.34	7.42 ± 1.37
ADDH-OH	6.34 ± 0.54	1.02 ± 0.16	6.89 ± 1.15
ADDH-TH	2.80 ± 0.39	2.30 ± 0.32	0.70 ± 0.27

Values are means ± SD. Estimated fiber length = MRI-determined muscle length × fiber length to muscle length ratio reported by Kura et al., (1997); PCSA: physiological cross-sectional area = muscle volume (data from Chapter 2) × cos θ × fiber length, where θ is the pennation angle reported from Ledoux et al. (2001), and fiber length is obtained from Kura et al. (1997).

The relationship between PCSA and fiber length of each plantar intrinsic foot muscle is shown in Fig. 3-2 A. ABDM, FDB, ABH, and FHB had overall moderate to large PCSA and moderate fiber length. Among them, the distribution of plots for FHB, ABH, and ABDM tended to have shorter muscle fiber lengths, larger PCSA, and smaller PCSA, respectively. The ADDH-OH had moderate to large PCSA and short fiber length. The ADDH-TH possessed extremely small PCSA and moderate fiber length. QP had extremely long fiber length and moderate PCSA.

The result of the K-means clustering analysis is shown in Fig. 3-2 B. Table 3-3 shows the breakdown of each muscle into four clusters as the results of a K-means clustering analysis. Cluster 1 (red symbols of Fig. 3-2 B) is composed of 100 % of ADDH-OH and approximately 60 % of FHB, being moderate to large PCSA and short FL. Cluster 2 (purple symbols of Fig. 3-2 B) included 100% of ABH and FDB, about 90% of ABDM, and about 40% of FHB. The morphological profiles of this cluster were moderate to large PCSA and moderate fiber length. Cluster 3 (blue symbols of Fig. 3-2 B) included all of ADDH-TH and about 10% of ABDM with extremely small PCSA and moderate fiber length. Cluster 4 consisted of 100% of QP with small to moderate PCSA and long fiber length (yellow symbols of Fig. 3-2 B).

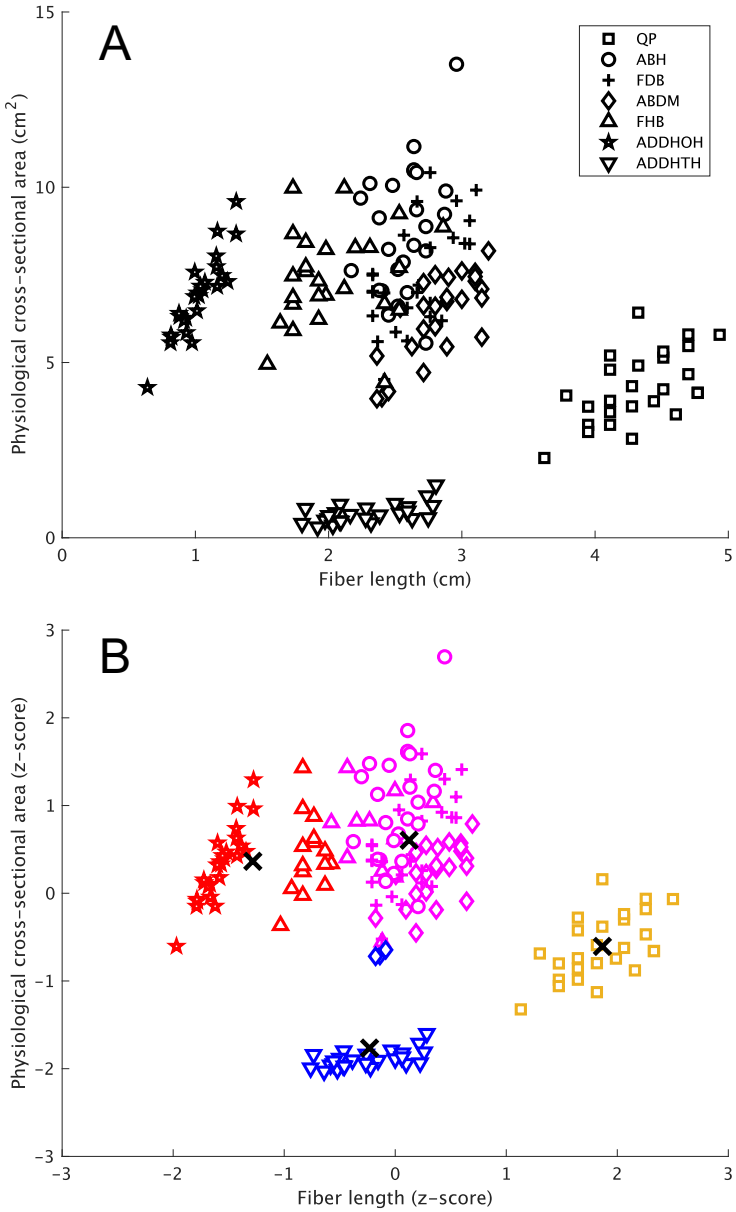

Figure 3-2. Relationship between PCSA and fiber length for individual plantar intrinsic foot muscles (A) and the corresponding relationship by K-means clustering analysis with each data normalized by z-score (B). The red, purple, blue, and yellow plots of Panel B indicate clusters 1, 2, 3, and 4, respectively. Black cross plots in Panel B indicate the center of each cluster. ABDM: abductor digit minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; QP: quadratus plantae.

Table 3-3. Number of components assigned to each cluster per individual plantar intrinsic foot muscles by a K-means clustering analysis

	ABDM	ABH	ADDH-OH	ADDH-TH	FDB	FHB	QP
	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)	N (%)
Cluster 1	–	–	26/26 (100 %)	–	–	15/26 (57.7 %)	–
Cluster 2	23/26 (88.5 %)	26/26 (100 %)	–	–	26/26 (100 %)	11/26 (42.3 %)	–
Cluster 3	3/26 (11.5 %)	–	–	26/26 (100 %)	–	–	–
Cluster 4	–	–	–	–	–	–	26/26 (100 %)

ABDM: abductor digit minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; QP: quadratus plantae.

3-4. Discussion

The main findings obtained in this Chapter were that individual plantar intrinsic foot muscles were clearly assigned to each of the four clusters by a K-means clustering analysis, except for FHB and ABDM which were classified into two clusters (Fig. 3-3). This approach is the first case attempting to classify contractile properties of individual plantar intrinsic foot muscles from their morphological information that enables estimating functions of individual muscles, especially the maintenance of the foot arch structure and force production at the toes. The findings obtained here will provide a new perspective beyond that derived from the anatomical profiles such as depth of location and site of attachment.

Cluster 1 consisted of all ADDH-OH, which acts on the adduction and assists with the flexion of the great toe, and about 60% of the FHB, which specializes in great toe flexion (Table 3-2). The constituents of this cluster (ADDH-OH and FHB) occupy the medial region of the foot in the third layer of plantar intrinsic foot muscles (see Fig. 1-3 C) and locate below the medial (first to third) metatarsals forming the MLA, being the most prominent and resilient arch structure of the foot (Mckenzie, 1955). Among the plantar intrinsic foot muscles, all muscles involved in cluster 1 had morphological characteristics of a short fiber length and moderate to large PCSA, suggesting that this cluster is specific to force production at a high level with a slow shortening velocity. These characteristics seem to be similar to those of the soleus muscle, which has a large PCSA and extremely short fiber length among the individual muscles in the lower limb (Ward et al., 2009). It is speculated that these characteristics are designed for tension production at the expense of velocity and furthermore, these may reflect the function as an anti-gravity muscle (Ward et al., 2009). Thus, cluster 1 which had similar morphological characteristics to the soleus may also act as an anti-gravity muscle in the foot. This notion is supported by the evidence that the activation level of plantar intrinsic foot muscles prominently increases with a load on the foot reaching more than 50% of body mass

(e.g., single leg standing) (Kelly et al., 2012). Taken together, it can be said that cluster 1 is specific to force production under the slower contraction velocity and may act as anti-gravity muscles to support the MLA during dynamic conditions and as a primary force generator at the great toe. Thus, strengthening the muscles involved in cluster 1 may be beneficial to enhance the ability for force production at the great toe and stabilizing force for the MLA.

Cluster 2 included ABH (100% of this muscle), FDB (100% of this muscle), ABDM (about 90% of this muscle), and FHB (about 40 % of this muscle) (Table 3-2). Most of the muscles consisting of this cluster (ABDM, ABH, and FDB) were located in the first layer, which is the closest position to the sole of the foot (see Fig. 1-3 A). ABH and ABDM run along the MLA and the lateral longitudinal arch, respectively, and the former mainly acts on the abduction of the great toe and the latter on the abduction of the little toe (Neumann, 2017). FDB, which widely lies immediately above the plantar aponeurosis (see Fig. 1-3 A) regulates the lesser toes flexion (Neumann, 2017) and has the greatest contraction velocity among intrinsic foot muscles (Tosovic et al., 2012). Another constituent, FHB is located in the third layer and is positioned directly underneath the first metatarsal bone forming the MLA as described above (see Fig. 1-3 C). Furthermore, the activation of ABH and FDB increases with the increment of postural demand, and the amplitude of the electromyogram activities of these muscles occurs co-ordinately with that of the center of pressure in the mediolateral direction during single leg standing (Kelly et al., 2012). Considering these aspects, cluster 2, which is specialized in maximum force production with a high level under a moderate shortening velocity, may function as the primary regulator of postural control by rapidly responding to external stimuli and subsequently generating force that expands the toes and stabilizes the arch and sole structure. In accordance with this notion, the strengthening of muscles involved in cluster 2 may contribute to enhancing the force production for stiffening the whole foot structure and to acquiring the ability to control posture as a stable condition in situations with high postural

demands, such as single leg standing.

Cluster 3 included all of ADDH-TH and about 10% of ABDM (Table 3-2), so the role of this cluster was discussed based on the representative muscle, ADDH-TH. The morphological characteristics of the muscle involved in this cluster were characterized by extremely small PCSA and moderate fiber length. This implies that cluster 3 has a contractile profile of producing very small forces at moderate shortening velocity. A recent study has suggested that ADDH-TH, which runs parallel to the anterior transverse arch activated during the pushing phase of walking and contributes to the stabilization of this arch in the forefoot (Robb et al., 2021). In addition, the size of this muscle differs between non-hominoid primates and humans. Comparing data obtained in healthy young males from Chapter 2 and in non-hominid primates from Oishi et al. (2018), the MV of ADDH-TH in non-hominid primates is 12–15 times larger than that in humans. The reason for this is considered to be less functional requirements of ADDH-TH with the transition from arboreal to terrestrial lifestyles, such as loss of the opposable movement at the hallux for grasping branches (Moriyama, 1981). Thus, it is likely that cluster 3, which was mainly composed of ADDH-TH, acts to stabilize the anterior transversal arch during the push-off phase, but the magnitude of stabilizing force may be extremely small, presumably due to the adaptation of habitual bipedalism in humans.

Cluster 4 consisted of QP (Table 3-2), having a very long fiber length and moderate PCSA. This suggests that cluster 4 is capable of producing moderate force at a very high shortening velocity. QP is the only muscle that does not directly attach to any toes among plantar intrinsic foot muscles, but this muscle alternatively inserts the tendon of FHL (extrinsic toe flexors) (Neumann, 2017). In addition, a cadaveric study with 116 legs of 62 specimens reported that in most cases, QP attaches to all FDL tendons where FHL branched (Edama et al., 2019). Such unique insertion of QP also suggests that this muscle acts on lesser toes flexion as well as the flexion of the great toe (Edama et al., 2019). Considering these, it is assumed that

cluster 4 may contribute to regulating the force production at the toes by the plantar intrinsic foot muscles and extrinsic toe flexors via quickly controlling the direction of the muscle tension produced by extrinsic toe flexors. If this notion can be accepted in the actual settings, activating the function of this cluster (i.e., QP) may be the key factor for controlling or synchronizing the function of plantar intrinsic foot muscles and extrinsic toe flexors.

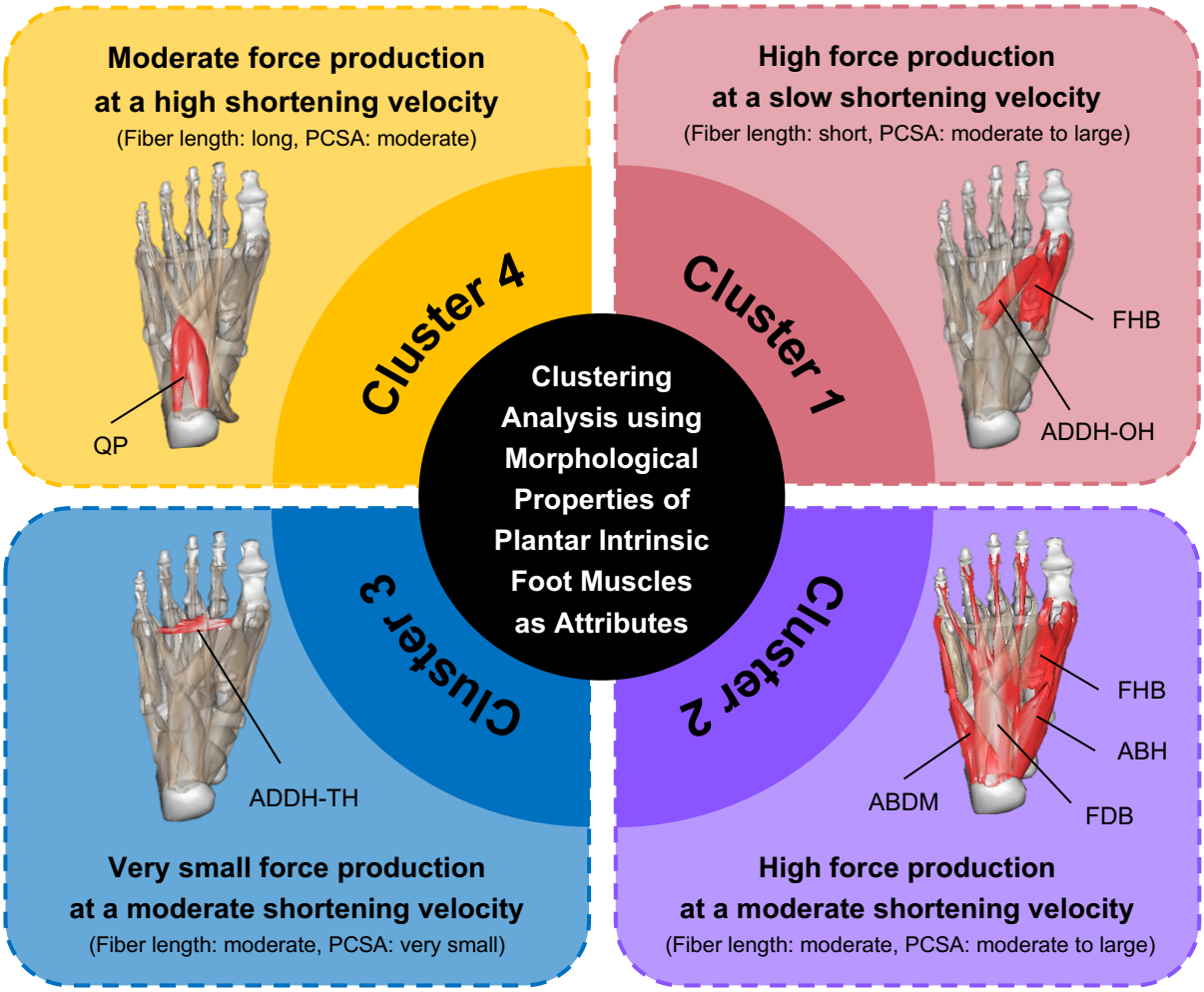

Figure 3-3. Contractile properties and involved muscles of each cluster categorized by K-means clustering analysis adopting morphological parameters of the individual plantar intrinsic foot muscles as attributes. ABDM: abductor digit minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; QP: quadratus plantae. The muscle images on the right side of each graph were created using "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan"

3-5. Conclusions

K-means clustering analysis with PCSA and fiber length as attributes shows that individual plantar intrinsic foot muscles were assigned to each of the four clusters. The involved muscles in each cluster and the contractile properties, estimated from the relationship between PCSA and fiber length, are as follows: cluster 1) high force production at slow shortening velocity, ADDH-OH and FHB; cluster 2) high force production at moderate shortening velocity, ABDM, ABH, FDB, and FHB; cluster 3) very small force production at moderate shortening velocity, ADDH-TH only; cluster 4) moderate force production at high shortening velocity, QP only. The approach adopted in this Chapter, which determines the contractile properties of a muscle by analogy with its morphological characteristics may provide a novel perspective in interpreting the function of individual plantar intrinsic muscles in humans.

Chapter 4 Associations between the Size of Individual Plantar Intrinsic Foot Muscles and Multi-dimensional Foot Morphological Profiles

4-1. Introduction

The human foot structure is generally evaluated by multi-dimensional morphological parameters, such as foot length, width, circumference, and MLA height (Kouchi, 1998; Waseda et al., 2014). Previous studies showed that ACSAs of the ABH and FHB were associated with the measures representing MLA height (Latey et al., 2018; Taş et al., 2018). Moreover, individuals with a flat foot, characterized by lowered MLA, have small ACSAs and muscle thickness of ABH and FHB compared to those with normal feet (Angin et al., 2014). On the other hand, another study reported that individuals with flat feet have larger muscle thickness of the ABH compared to those with normal feet (Taş et al., 2018). In addition, it is known that foot length measures positively associate with the ACSAs of ABH and FHB (Latey et al., 2018). These findings imply that there remains no consensus on whether the size of plantar intrinsic foot muscles relates to multi-dimensional morphological parameters of the foot, particularly the MLA height. One of the reasons for this is that previous studies have investigated the interrelationship between the size of a limited number of 10 human plantar intrinsic foot muscles (Kura et al., 1997) and the morphological profiles of the foot. Therefore, it remains unclear how each plantar intrinsic foot muscle relates to the multi-dimensional morphological parameters of the foot. This Chapter aimed to elucidate how the size of each plantar intrinsic foot muscle relates to the morphological profiles of the foot. This Chapter tested the hypothesis that MV for each muscle would be associated with not only the MLA height but also the other parameters such as foot length and width.

4-2. Methods

Participants

Thirteen male university students (age, 22.4 ± 3.0 yrs; height, 170.5 ± 5.0 cm; body mass, 63.7 ± 5.7 kg, mean ± SD) who had no history of a diagnosed neuromuscular disorder, or a lower limb injury voluntarily participated in this study by convenience sampling. They usually wore sports shoes outside but not inside the house.

Experimental procedure

All participants firstly attended measurements of the general morphological parameters (body height and body mass) and foot morphological profiles. After the completion of morphological measurements, MRI measurements were conducted to obtain the foot MR images.

Determination of MV

T1-weighted MR images of the right foot were scanned using a 3.0 T MR system (Magnetom Skyra, Siemens Healthcare, Erlangen, Germany) and determined MV of each plantar intrinsic foot muscle as representing muscle size variable. The overall procedures of scanning MR images and determining MV were conducted in accordance with Chapter 2.

Measurement of foot morphological parameters

The foot morphological parameters were measured using a laser 3D foot scanner (JMS-3110, Dream GP Inc., Osaka, Japan). The data collection of foot morphological parameters by 3D foot scanner showed relatively higher precision, accuracy, and robustness compared to other methods (digital caliper and digital/ink footprint) (Lee et al., 2014). First, the participants bilaterally stood with bare feet and a sticker was put on the most prominent

point of the navicular tuberosity by one examiner. The examiner had good repeatability for measuring navicular height in a standing condition with the procedure of palpating the most prominent point of the navicular tuberosity and measuring the distance between the point and the floor using a digital height gauge on 3 occasions, 2–5 days apart (ICC [1, 3] = 0.89). Then, their right foot was encased in the 3D foot scanner and the following parameters were measured: total and truncated foot length, forefoot width, great toe eversion and little toe inversion angle, ball and instep circumferences, and navicular height. Additionally, navicular height was measured in a sitting position using the same scanner. Furthermore, the navicular drop (ND), defined as the difference in navicular height between the sitting and standing conditions, and normalized truncated navicular height (NTNH), defined as the ratio of navicular height in the standing to truncated foot length (Menz & Munteanu, 2005; Murley et al., 2009), were obtained as the indices of MLA height. The navicular height and its normalized value (i.e., NTNH) have a moderate to high correlation with radiographic measures (calcaneal inclination and calcaneal-first metatarsal angle) (Menz & Munteanu, 2005; Murley et al., 2009), which is recognized as a gold standard technique for assessing the MLA height. The definitions of each parameter were described in Fig. 4-1 and Table 4-1.

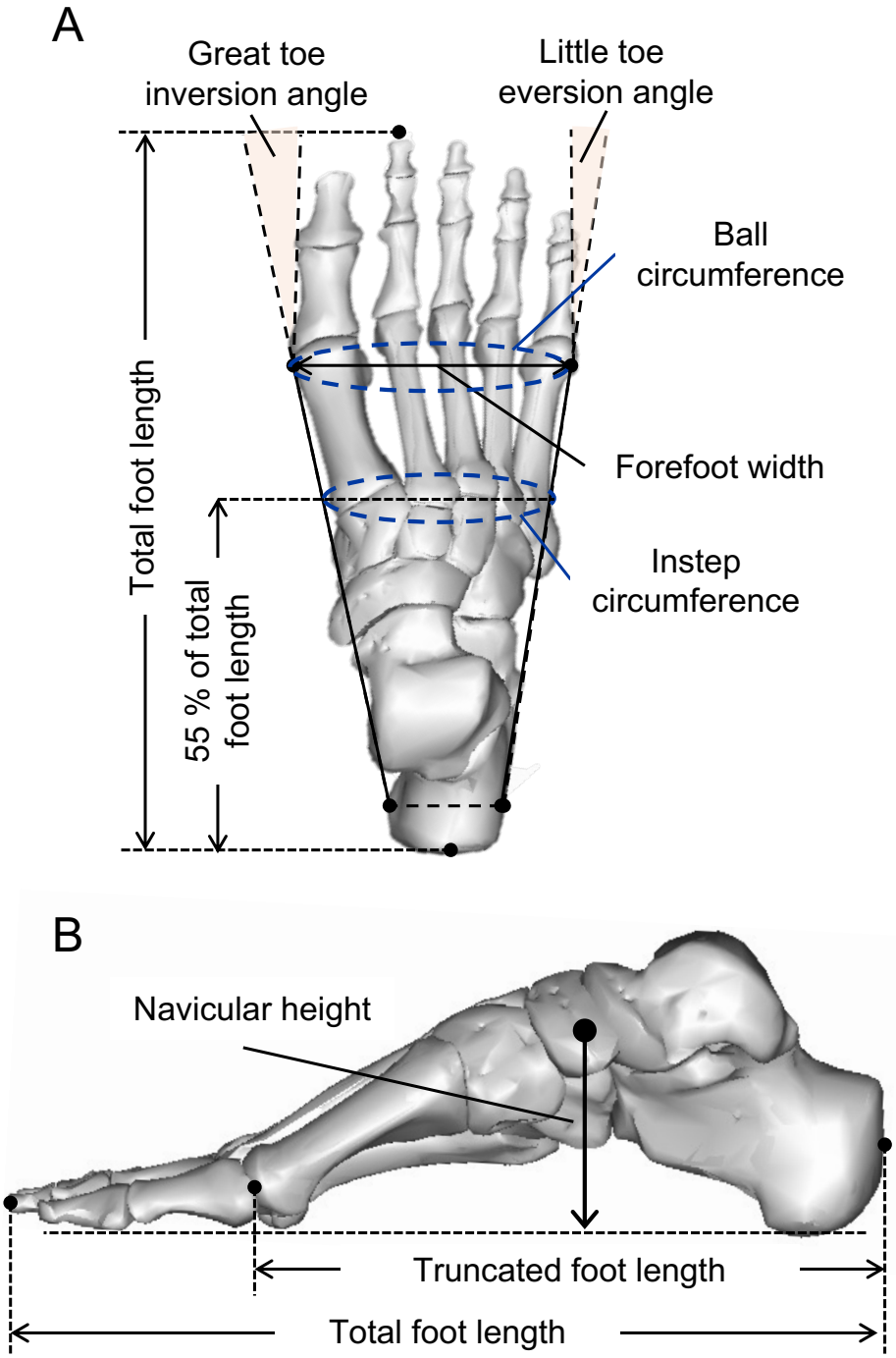

Figure 4-1. Definition of morphological parameters of the right foot in top (A) and medial side (B) views. Each foot image was created by using "BodyParts3D, © The Database Center for Life Science licensed under CC Attribution-Share Alike 2.1 Japan".

Table 4-1. Definition of anthropometric parameters of foot.

Parameters	Definitions
Total foot length (cm)	Distance between the most posterior/prominent point of the calcaneus and the most anterior/prominent point of the furthest toe.
Truncated foot length (cm)	Distance between the most posterior/prominent point of the calcaneus and that of the first MTP joint.
Forefoot width (cm)	Distance between the most medial/prominent point of the first MTP joint and that of the fifth MTP joint.
Ball circumference (cm)	Total perimeter between the most medial point the first MTP joint and the most lateral point of the fifth MTP joint.
Instep circumference (cm)	Total perimeter of the longitudinal section of 55% of total foot length.
Great toe eversion angle (degree)	Angle between the line along the medial side of the great toe and the line connecting the medial side of the heel (at the widest section of heel) and the first MTP joint. A positive value indicated eversion and a negative value indicated inversion.
Little toe inversion angle (degree)	Angle between the line along the lateral side of the little toe and the line connecting the lateral side of the heel (at the widest section of heel) and the fifth MTP joint. A positive value indicated inversion and a negative value indicated eversion.
Navicular height at standing position (cm)	Distance between the most prominent point of navicular tuberosity and the floor of a scanner in standing position.
Navicular height at sitting position (cm)	Distance between the most prominent point of navicular tuberosity and the floor of a scanner in sitting position.
ND (cm)	Difference in navicular height between the sitting and standing position.
NTNH	Ratio of navicular height in the standing to truncated foot length.

MTP: metatarsophalangeal; ND: navicular drop; NTNH: normalized truncated navicular height.

Statistical analysis

The normality of measured variables was assessed by Shapiro-Wilk test and was confirmed in all variables except for the great toe eversion angle. Thus, to examine the associations between MV of plantar intrinsic foot muscles and the morphological parameters, Spearman's rank-order correlations were calculated when concerning great toe eversion angle, and otherwise Pearson's correlation coefficients were calculated. The level of significance was set at $p < 0.05$. All data were analyzed using statistical software (SPSS version 27.0, IBM Co., USA).

4-3. Results

Descriptive data on MV values of each individual muscle and muscle group and those on morphological profiles of the foot are shown in Table 4-2 and 4-3, respectively.

Table 4-2. Descriptive data on MV values of each plantar intrinsic foot muscle.

	Mean ± SD	Range
Whole plantar intrinsic foot muscles (cm^3)	85.94 ± 10.69	71.74 – 106.64
ABDM (cm^3)	13.87 ± 2.61	9.67 – 17.73
ABH (cm^3)	18.73 ± 3.39	13.32 – 25.00
ADDH-OH (cm^3)	12.63 ± 1.91	10.48 – 16.47
ADDH-TH (cm^3)	1.16 ± 0.38	0.59 – 1.83
FDB (cm^3)	15.38 ± 2.70	12.49 – 22.06
FHB (cm^3)	12.94 ± 2.21	10.14 – 17.12
QP (cm^3)	9.75 ± 2.32	5.85 – 14.89

ABDM: abductor digit minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; MV: muscle volume; QP: quadratus plantae.

Table 4-3. Descriptive data on morphological profiles of the foot

	Mean ± SD	Range
Length parameters (cm)		
Total foot length	25.1 ± 1.0	23.7 – 27.2
Truncated foot length	18.0 ± 0.8	16.6 – 19.4
Width parameter (cm)		
Forefoot width	10.2 ± 0.2	9.8 – 10.6
Circumferential parameters (cm)		
Ball girth	24.6 ± 0.6	23.7 – 25.3
Instep circumference	22.7 ± 0.8	24.4 – 25.7
Toe Angles (degrees)		
Great toe eversion angle	8.2 ± 4.2	-3.9 – 12.8
Little toe inversion angle	13.3 ± 3.8	5.0 – 18.2
MLA height parameters		
Navicular height at standing position (cm)	4.6 ± 0.5	4.0 – 5.4
Navicular height at sitting position (cm)	5.0 ± 0.5	4.3 – 5.7
ND (cm)	0.4 ± 0.1	0.2 – 0.6
NTNH	0.26 ± 0.03	0.22 – 0.33
Ratio		
Foot width / total foot length	0.41 ± 0.01	0.38 – 0.42
Foot width / truncated foot length	0.57 ± 0.02	0.53 – 0.60
Truncated foot length / total foot length	0.72 ± 0.01	0.70 – 0.72

ND: navicular drop; NTNH: normalized truncated navicular height

Table 4-4 shows associations between MV of the plantar intrinsic foot muscles and morphological parameters of the foot. The MV of whole plantar intrinsic foot muscle was significantly associated with the forefoot width, ball circumference, and instep circumference. Positive correlations were found between the forefoot width and the MV of FDB, FHB, and QP, between ball circumference and the MV of QP, between instep circumference and the MV of FHB, and between little toe inversion angle and MV of QP. However, a negative correlation was found between truncated foot length and MV of ADDH-TH. The MV of ABDM, ABH, and ADDH-OH were not significantly correlated with any anthropometric parameters of the foot. Similarly, no correlations were found between MV of each individual muscle and functional muscle group and any of the MLA height indices.

Table 4-4. Correlation coefficients between the MV of plantar intrinsic foot muscles and anthropometric parameters of the foot.

	QP	ABH	FDB	ABDM	FHB	ADDH-OH	ADDH-TH	WHOLE
	r	r	r	r	r	r	r	r
Length								
Total foot length	0.369	0.242	0.416	0.015	0.134	0.318	-0.534	0.331
Truncated foot length	0.321	0.222	0.390	-0.027	0.144	0.288	-0.560 *	0.293
Width								
Forefoot width	0.564 *	0.390	0.653 *	0.448	0.598 *	0.482	-0.542	0.711 **
Circumference								
Ball circumference	0.559 *	0.440	0.516	0.518	0.531	0.293	-0.404	0.665 *
Instep circumference	0.348	0.405	0.483	0.540	0.609 *	0.449	-0.467	0.647 *
Toe Angles								
Great toe eversion angle	-0.385	0.115	0.104	-0.044	0.236	-0.500	-0.104	-0.093
Little toe inversion angle	0.570 *	-0.002	0.241	-0.146	-0.145	0.269	0.376	0.180
MLA height								
Navicular height at standing position	0.078	-0.015	0.343	0.354	0.166	0.226	-0.197	0.253
Navicular height at sitting position	0.131	-0.011	0.262	0.366	0.096	0.260	-0.174	0.241
ND	0.181	0.016	-0.305	0.020	-0.256	0.104	0.096	-0.059
NTNH	-0.030	-0.091	0.162	0.319	0.089	0.120	0.041	0.124
Ratio								
Foot width / total foot length	-0.056	-0.017	-0.062	0.313	0.270	-0.052	0.297	0.100
Foot width / truncated foot length	-0.010	-0.007	-0.044	0.350	0.230	-0.021	0.355	0.126
Truncated foot length / total foot length	-0.147	-0.039	-0.039	-0.215	0.069	-0.085	-0.267	-0.117

Significance of Pearson's correlations coefficients is indicated as follows: *$p < 0.05$, **$p < 0.01$.

ABDM: abductor digiti minimi; ABH: abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FHB: flexor hallucis brevis; ND: navicular drop; NTNH: normalized truncated navicular height; QP: quadratus plantae; WHOLE: all analyzed plantar intrinsic foot muscles.

4-4. Discussion

The major findings obtained here were that while MVs of individual plantar intrinsic foot muscles were not significantly correlated with the indices of MLA height, those of whole muscles, especially the muscles specialized in toe flexion (FDB, FHB, and QP) were positively correlated with width and circumferential parameters involved in the formation of anterior and posterior transverse arches. These results partially supported our hypothesis and indicate that the size of the limited plantar intrinsic muscles associates with foot morphological parameters other than the indices of MLA height.

The Indices of MLA height were not significantly correlated with MV of any individual muscles and muscle groups (Table 4-4). This denied our hypothesis derived from the previous reports indicating the association of the size of ABH and FHB with morphological profiles of the foot (Angin et al., 2014; Latey et al., 2018). This unexpected result might be due to the following possibilities. First, the indices representing the MLA height differed between the present and previous studies. The present study is the first to determine the relationship between the size of individual plantar intrinsic foot muscles and MLA height using indices directly and quantitatively assessing navicular height. On the other hand, the previous studies visually assessed and scored (5-point scale) the MLA height in the procedure of the FPI-6 scoring (Angin et al., 2014; Latey et al., 2018; Taş et al., 2018), which may not precisely reflect the magnitude of the MLA height. Second, this study measured MV as a representative variable of muscle size. The prior studies (Angin et al., 2014; Latey et al., 2018; Taş et al., 2018) quantified muscle size as ACSA and muscle thickness. However, these variables depend on the site where these are determined (Blazevich et al., 2006; Fukunaga et al., 1992) and therefore only provide regional/limited information about the entire muscle size (i.e., less robust indices than MV). Finally, the function of the plantar intrinsic foot muscles is considered posture dependent (Kurihara et al., 2020). The activation of plantar intrinsic foot muscles increases by

applying an incremental vertical load against a lower limb in the seated position (Kelly et al., 2014), while the activation level of these muscles did not reach the same level in the bilateral stance even though the identical load was applied on the foot (Kurihara et al., 2020). These three aspects would explain why the size of the plantar intrinsic foot muscles did not associate with MLA height, which was directly assessed in this study.

The observed positive correlations of the forefoot width and circumferential parameters (ball and instep circumferences) with MV of whole plantar intrinsic foot muscles and several individual muscles partly supported our hypothesis. Habitually barefoot populations have wider forefoot than those with a conventional shoe (Ashizawa et al., 1997). Moreover, wearing minimalist shoes, which is enabling to imitate barefoot running or walking (Squadrone & Gallozzi, 2009), increases plantar pressure in the forefoot region (Bergstra et al., 2015) and induces hypertrophy of plantar intrinsic foot muscles to counter the load against the foot (Ridge et al., 2019). Furthermore, lifesavers who compete with bare feet had wider forefoot width and increased the size of some plantar intrinsic and extrinsic foot muscles compared to controls with no exercise habits (Ichikawa et al., 2021). On the other hand, based on the measurement position, width and circumferential parameters may be involved in forming the anterior/posterior transverse arches. A recent study that examined foot stiffness mechanisms using a combination of simulations and actual measurements with cadaveric feet showed that the curvature of the posterior transverse arch, acting through inter-metatarsal tissues (such as muscles), contributes to stiffening the longitudinal structure of the foot (Venkadesan et al., 2020). Considering these, it seems that the plantar intrinsic foot muscles function to stabilize the anterior and posterior transverse arches and through them contribute to the structural integrity of the whole foot structure, particularly the MLA. Taken together, the observed correlations between forefoot width and circumferential parameters and the MV of plantar intrinsic foot muscles, especially those that run along the longitudinal direction of the foot and

specialized in toe flexion (FHB, FDB, and QP), may reflect the structural development of transverse arches in human feet.

Interestingly, truncated foot length (i.e., a longitudinal distance of the foot) was found to be negatively correlated with the MV of ADDH-TH which runs along the transverse direction of the foot. This somewhat contradicts with the prior finding that the total and truncated foot length were positively associated with the size of ABH and FHB (Latey et al., 2018). The reason for this contradiction is unknown but might involve the change of functional requirement in the ADDH-TH via the transmission from an arboreal to a terrestrial lifestyle. In non-hominoid primates, the great toe, similarly to the thumb, requires the opposable movement to grasp and balance on the branches (Moriyama, 1981). Consequently, non-hominoid primates' MV of ADDH-TH, which acts on the opposable movement of the great toe, is about 0.9 - 2.0 times larger than that of ADDH-OH (Oishi et al., 2018). In human feet which no longer require the opposable movement of the great toe (Moriyama, 1981), however, the MV of ADDH-TH was the smallest among the plantar intrinsic foot muscles and one-tenth as large as that of ADDH-OH (Fig. 2-5 B of Chapter 2). On the other hand, the longer foot length is known to be an anatomical factor for effective bipedal locomotion (Adamczyk & Kuo, 2013). Taking these aspects, it seems that as a result of habitual bipedalism in humans, less functional requirements of ADDH-TH might have induced the smallest MV and consequently yielded a negative association with the truncated foot length. Further investigation would be needed to interpret this interesting association.

4-5. Conclusions

The overall results of this Chapter that forefoot width and circumferential parameters relate to the MV of plantar intrinsic foot muscles, especially those specialized in toe flexion,

indicate the existence of potential relationships between transverse arches and these muscles. On the other hand, the association between medial longitudinal arch height and the MV of any plantar intrinsic foot muscle could not find in this Chapter.

Chapter 5 Strength and Size Relationships of Toe Flexor Muscles

Section 1 Relationships between TFS and the size of individual toe flexors muscles

5-1-1. Introduction

The size of toe flexor muscles, comprising plantar intrinsic foot muscles and extrinsic toe flexors relates to TFS (Abe et al., 2016; Kurihara et al., 2014; Latey et al., 2018; Mickle et al., 2016). These findings have been only obtained by adopting ACSA and/or muscle thickness of a limited number of the plantar intrinsic foot muscles (Abe et al., 2016; Latey et al., 2018; Mickle et al., 2016) or ACSA consisting of several muscles as a mass (Kurihara et al., 2014) as an independent variable for examining the association with TFS. Compared to ACSA and muscle thickness, however, MV and $ACSA_{max}$ have been shown to be more strongly associated with muscle strength (Balshaw et al., 2021; Fukunaga et al., 2001). Thus, the anatomical function of individual plantar intrinsic foot muscles has not been considered for examining the relationship between TFS and muscle size, and therefore little information is available from previous findings as to which muscle(s) primarily contributes to the magnitude of TFS. This section aimed to elucidate the muscle(s) that primarily contributes to TFS production. To this end, this section firstly determined $ACSA_{max}$ and MV of each muscle and measured TFS using the toe grip dynamometer (i.e., TGS) which is the most common device for measuring TFS. Then, the association of $ACSA_{max}$ and MV of each muscle with TGS was examined. Finally, a stepwise multiple linear regression analysis by using TGS as a dependent variable with the $ACSA_{max}$ and MV values of the muscles as independent variables was conducted. It is

hypothesized that the muscles that mainly act on great toe flexion, i.e., the FHB and FHL, would be selected as the primary contributors to TGS among the individual plantar intrinsic and extrinsic foot muscles.

5-1-2. Methods

Participants

Seventeen healthy young men (age, 21.4 ± 1.9 yrs; height, 171.0 ± 5.9 cm; body mass, 62.3 ± 5.8 kg; mean ± SD), with no history of a diagnosed neuromuscular disorder or lower limb injury, voluntarily participated in this study. All participants provided prior written informed consent based on the guidelines of the Declaration of Helsinki.

Experimental procedure

In this section, all participants first attended morphological measurements (body height and body mass). Then, MRI measurements were conducted to obtain the foot and lower leg images. After the completion of morphological and MRI measurements, TGS was determined as a representing TFS measure by using a toe grip dynamometer.

Determination of muscle size measures ($ACSA_{max}$ and MV)

T1-weighted MR images of the right foot and lower leg were scanned using 1.5 T and 3.0 T MR systems. Of all participants in this section, eleven participants were scanned by 1.5 T MRI, and the others (six participants) were scanned by 3.0 T MRI, due to the update of the MR system. The whole foot images were scanned by using a similar procedure in Chapter 2. Similarly, the $ACSA_{max}$ and MV of each individual muscle and muscle group in plantar intrinsic foot muscles were determined in accordance with Chapter 2.

To acquire the lower leg image, the participants were placed in the prone position on the examination table with their lower legs placed parallel to the main magnetic field. Serial cross-sectional right lower leg images were acquired from the knee cleft to just proximal to the malleoli, with the following parameters: repetition time = 600 ms, echo time = 7.7 ms, slice thickness = 10 mm, gap between slices = 0 mm, field of view = 360 × 360 mm, flip angle = 90 deg, matrix = 256 × 256 (1.5 T MR system); repetition time = 700 ms, echo time = 9.4 ms, slice thickness = 5 mm, gap between slices = 0 mm, field of view = 360 × 360 mm, flip angle = 120 deg, matrix = 1024 × 1024 (3.0 T MR system). The data acquisition time for each scan was approximately 3 min. MRI-determined lower leg length (LL) was determined as the distance between the most prominent point of the medial malleolus at the tibia and intercondylar eminence of tibia in MR images. The ACSAs of each extrinsic toe flexors were expressed relative to LL (0% LL: most prominent point of medial malleolus, 100% LL: intercondylar eminence of tibia). The $ACSA_{max}$ and MV were determined in FHL, FDL, and extrinsic toe flexors (FHL and FDL): $ACSA_{max}$ was defined as the maximal ACSA along the LL, and MV was calculated by summing all the ACSAs for each muscle multiplied by the slice thickness.

Measurement of TGS

In accordance with the procedure adopted in a previous study (Uritani et al., 2012), the maximum voluntary isometric TGS was measured using a commercially available toe grip dynamometer (Fig. 5-1-1). The participants were seated in a chair and positioned their hip and knee joints at 90 degrees of flexion with the ankle joint at 90 degrees of dorsiflexion (Fig. 5-1-2 A). This measurement position is identified as the optimal joint angle for TGS production (Yamauchi & Koyama, 2019a). The participant's right foot was placed on the device with the posterior heel adjusted at the heel stopper, and the first proximal phalangeal gripped the grip bar (Fig. 5-1-2 B). During the measurement, the participants were instructed to cross their arms

in front of their chest and gripped the grip bar using all toes as much as possible without any extraneous movements. Familiarization trials for 2-3 times with submaximal force outputs were conducted before the actual measurements. After participants completed the familiarization trials and a rest period of three minutes, the participants performed the task with maximal effort for at least 3 seconds. The trial with maximal force output was performed twice with at least one-minute rest intervals. In the case that any extraneous movements other than the instructed ones or visually obvious contraction of the calf muscles were observed, the trial was counted as a failed trial. If the difference between the two values was more than 10% of the higher one, the TGS measurement was measured 1 more time. The test trial was repeated up to 5 times, and the largest value was used for further analysis. The intra-rater reliability of TGS measurement was assessed as the repeatability of two trials in which the largest values were obtained among all test trials. ICC (1, 2) value was 0.97, confirming excellent repeatability according to the classification reported in a previous study (Koo & Li, 2016). Furthermore, in another experiment that targeted 11 healthy young males, the reproducibility of TGS measurement, which was performed three times at 2-5 days apart with the same procedure, was examined. The ICC (1, 3) value was 0.78, confirming good repeatability according to the classification reported in a previous study (Koo & Li, 2016).

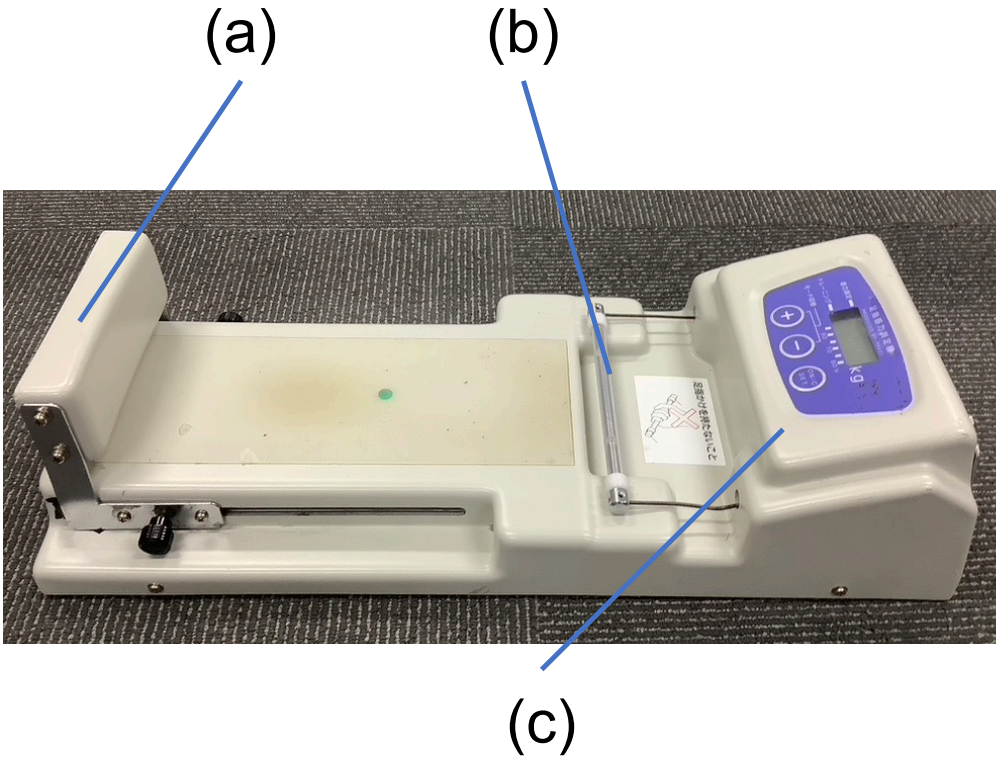

Figure 5-1-1. Toe grip dynamometer. (a): heel stopper; (b): grip-bar; (c): strain gauge load cell. The strain gauge load cell has a measurement range from 1.0 and 400.0 N and accuracy of 1.0 N. Dimensions of the device: 200 (width), 480 (depth), 110 (height) mm and 4.0 kg.

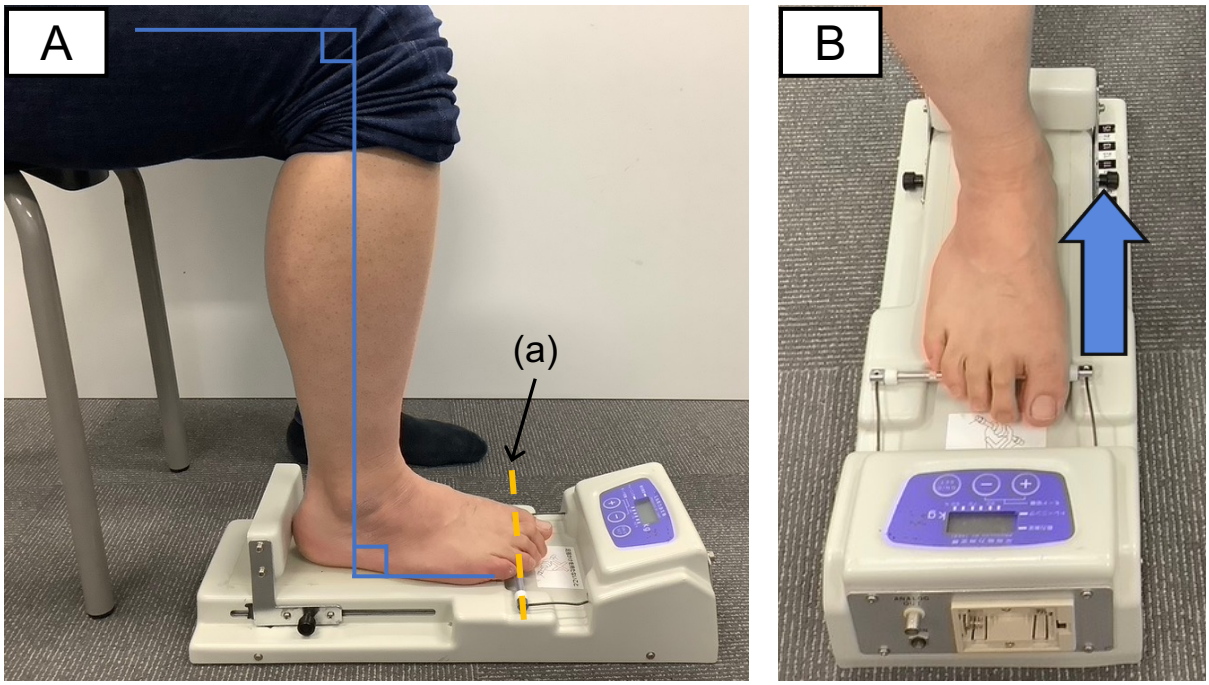

Figure 5-1-2. Measurement of toe grip strength (TGS). Panel A lateral view of the measurement of toe grip strength (TGS). (a): transverse axis of the interphalangeal (IP) joint of the great toe. Panel B: anterior view of the measurement of TGS. The blue arrow in Panel B shows the direction of force production.

Statistical analysis

Descriptive data are presented as means ± SDs. The normality of measured variables was assessed by the Shapiro-Wilk test. MV of the ABDM was the only variable that was not normally distributed, and it was log-transformed for further analysis. All subsequent analysis was conducted by using parametric statistical tests. Pearson's correlation coefficients were computed to examine the relationship between muscle size and TGS. When either or both of $ACSA_{max}$ and MV had a significant correlation with TGS, the differences between these correlation coefficients for TFS in that muscle were statistically assessed by an online resource (http://comparingcorrelations.org [Diedenhofen & Musch, 2015] was used to implement Meng et al.'s [1992] z test [two dependent groups, overlapping, and two-tailed test]). Stepwise multiple linear regression analysis was conducted by using TGS as a dependent variable, with $ACSA_{max}$ or MV of individual muscles that were significantly correlated with TGS as independent variables. The level of significance was set at $p < 0.05$. All data were analyzed using statistical software (SPSS version 27.0, IBM Co., USA) unless otherwise stated.

5-1-3. Results

$ACSA_{max}$ and MV of each individual muscle and functional muscle group

FL, LL, and TGS were 15.4 ± 0.8 cm, 35.4 ± 1.8 cm, and 148.1 ± 35.0 N, respectively. Descriptive data on $ACSA_{max}$ and MV of each toe flexor muscle are summarized in Table 5-1-1. Among the analyzed individual plantar intrinsic foot muscles, the $ACSA_{max}$ was the largest in the ADDH-OH, followed by the FHB, ABH, ABDM, FDB, QP, and ADDH-TH. The MV was the largest in the ABH followed by the FDB, ABDM, ADDH-OH, FHB, QP, and ADDH-TH. Moreover, in the extrinsic toe flexors, the $ACSA_{max}$ and MV for the FHL were larger than those of FDL.

Table 5-1-1. $ACSA_{max}$ and MV in each of toe flexor muscles.

	$ACSA_{max}$ (cm^2)		MV (cm^3)	
	Mean ± SD	(Range)	Mean ± SD	(Range)
Plantar intrinsic foot muscles	9.14 ± 1.31	(6.61–11.42)	92.64 ± 15.95	(63.82–126.59)
Intrinsic great toe flexors	7.04 ± 1.27	(4.43–9.01)	48.46 ± 8.69	(33.36–68.58)
FHB	3.05 ± 0.65	(1.94–4.65)	12.44 ± 2.55	(7.60–17.12)
ABH	3.01 ± 0.55	(2.26–4.10)	21.76 ± 4.58	(15.35–32.41)
ADDH-OH	3.42 ± 0.59	(2.19–4.40)	12.76 ± 2.27	(8.08–18.06)
ADDH-TH	1.01 ± 0.29	(0.50–1.64)	1.51 ± 0.54	(0.79–2.90)
Intrinsic lesser toes flexors	6.20 ± 0.90	(4.32–7.89)	44.17 ± 8.21	(30.42-58.02)
QP	1.97 ± 0.44	(1.35–2.88)	11.49 ± 2.54	(7.76–16.51)
FDB	2.48 ± 0.41	(1.76–3.19)	16.62 ± 3.58	(10.07–23.16)
ABDM	2.90 ± 0.55	(1.95–3.85)	16.06 ± 2.92	(9.73–19.94)
Extrinsic toe flexors	5.33 ± 0.89	(4.10–7.02)	88.6 ± 13.74	(72.02–114.57)
FHL	4.74 ± 0.65	(3.63-5.63)	67.93 ± 13.01	(49.37–94.51)
FDL	1.55 ± 0.22	(1.20–2.00)	20.66 ± 3.22	(15.76–27.06)

ABDM: abductor digit minim; ABH: abductor hallucis; $ACSA_{max}$: maximal anatomical cross-sectional area; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FDL: flexor digitorum longus; FHB: flexor hallucis brevis; FHL: flexor hallucis longus; MV: muscle volume; QP: quadratus plantae.

Associations between $ACSA_{max}$ or MV of toe flexor muscle and TGS

Pearson's correlation coefficients between TGS and $ACSA_{max}$ or MV of individual muscles or muscle groups are summarized in Table 5-1-2. TGS was positively correlated with the $ACSA_{max}$ for each of the ADDH-OH, ADDH-TH, and FDB, and also with the MV of the ADDH-OH. The magnitudes of the correlation coefficients with TGS were not statistically different between $ACSA_{max}$ and MV (i.e., the r value of $ACSA_{max}$ and TGS vs that of MV and TGS) in any muscles of the ADDH-OH, ADDH-TH, and FDB ($z = -1.443 – -0.562$, $p = 0.149 – 0.599$). The $ACSA_{max}$ of the intrinsic great toe flexors was positively associated with TGS, but those of any functional muscle groups (whole plantar intrinsic foot muscle, intrinsic lesser toes, and extrinsic toe flexors) were not. Moreover, MV of any other functional muscle groups was not significantly correlated with TGS.

Stepwise multiple liner regression analysis using $ACSA_{max}$ as independent variable selected the $ACSA_{max}$ of the ADDH-OH as an explainable factor for TGS: TGS (N) = 10.61 × [$ACSA_{max}$ of ADDH-OH (cm^2)] + 40.26 (adjusted $R^2 = 0.418$). Similarly, using MV as an independent variable selected the MV of the ADDH-OH as an explainable factor for TGS: TGS (N) = 8.94 × [MV of ADDH-OH (cm^3)] + 34.04 (adjusted $R^2 = 0.294$).

Table 5-1-2. Correlations coefficients between TGS and $ACSA_{max}$ or MV of the individual muscles or functional muscle groups

	$ACSA_{max}$			MV		
	r		p	r		p
Plantar intrinsic foot muscles						
Whole plantar Intrinsic foot muscles	0.361		0.154	0.385		0.127
Intrinsic great toe flexors	0.604	*	0.010	0.454		0.067
FHB	0.442		0.076	0.430		0.085
ABH	0.364		0.151	0.277		0.282
ADDH-OH	0.674	**	0.003	0.582	*	0.014
ADDH-TH	0.523	*	0.031	0.474		0.054
Intrinsic lesser toes flexors	0.244		0.345	0.267		0.300
QP	0.115		0.660	0.126		0.631
FDB	0.492	*	0.045	0.271		0.293
ABDM	0.366		0.149	0.310		0.226
Extrinsic toe flexors	0.401		0.111	0.376		0.137
FHL	0.333		0.191	0.399		0.112
FDL	0.106		0.687	-0.009		0.974

Significance of Pearson's correlations coefficients is indicated as follows: *p < 0.05, **p < 0.01. ABDM: abductor digit minim; ABH: abductor hallucis; $ACSA_{max}$: maximal anatomical cross-sectional area; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FDL: flexor digitorum longus; FHB: flexor hallucis brevis; FHL: flexor hallucis longus; MV: muscle volume; QP: quadratus plantae.

5-1-4. Discussion

This Chapter is the first case that determined the $ACSA_{max}$ and MV for each constituent of the plantar intrinsic foot muscles and extrinsic toe flexors and examined their associations with TGS. The major findings obtained here were that 1) TGS was significantly correlated with the $ACSA_{max}$ of the ADDH-OH, ADDH-TH, and FDB, as well as with the MV of the ADDH-OH, and 2) the $ACSA_{max}$ and MV of the ADDH-OH alone explained 42% and 29%, respectively, of the variance in TGS by stepwise multiple linear regression analysis. These results indicate that among the plantar intrinsic foot muscles and extrinsic toe flexors, the ADDH-OH primarily contributes to TGS production.

At the start of the present study, it is hypothesized that the muscle(s) mainly act on great toe flexion would primarily contribute to the magnitude of TGS. However, the current results refuted this. The reason why the ADDH-OH was selected as the primary contributor to TGS may be attributable to a unique characteristic of this muscle having multiple functions of adduction and flexion of the great toe. The participants in this Chapter were asked to grip a solid straight bar for the TGS measurement. In general, it is recognized toe gripping action requires the combined movement of flexion at the MTP and IP joints (Soysa et al., 2012). On the other hand, this action is also observed in the plantar grasp reflex, which is one of the primitive reflexes and consists of the combination of flexion and adduction of the toes (Futagi et al., 2012). Taken together, the toe gripping on the toe grip dynamometer for producing TGS can be considered as a complex multiple movement consisting of flexion at the MTP and IP joints and adduction at the MTP joint rather than simple flexion at the MTP and IP joints. Therefore, the ADDH-OH, which acts on both adduction and flexion of the great toe (at the MTP joint), appears to contribute to TGS production more strongly than the muscles specialized in great toe flexion (i.e., FHB and FHL).

It is worth noting that among the plantar intrinsic and extrinsic foot muscles, not only

the ADDH-OH but also ADDH-TH acts on both the flexion and adduction at the MTP joint of the great toe (Neumann, 2017). However, the ADDH-TH was not selected as the determinant for TGS. This may be due to the morphological differences between the two muscles. First, the $ACSA_{max}$ and MV of the ADDH-OH were about 2.4 and 7.5 times, respectively, larger than those of the ADDH-TH (Table 5-1-1). Second, the ADDH-OH runs along the longitudinal direction of the foot and contracts closely parallel to the direction of the great toe movement during TGS production. On the other hand, the running direction of the ADDH-TH is perpendicular to the longitudinal axis of the foot, and this muscle contracts transversely and orthogonally to the direction of the great toe movement during TGS production. Thus, it is likely that the morphological features of the ADDH-OH would be suited for producing TGS more than that of the ADDH-TH, and consequently the ADDH-OH alone might have been selected as the contributor to TGS.

In general, the force generation capacity of a muscle is theoretically best related to its PCSA (Haxton, 1944). Thus, adopting PCSA rather than $ACSA_{max}$ and MV as independent variables would be desirable to examine the association of muscle size with TFS. However, the determination of PCSA in vivo needs data concerning pennation angle and fascicle length in addition to MV (Fukunaga et al., 2001), and the procedure determining the PCSA of foot muscles has not been established likely due to their complex architecture. On the other hand, a previous study revealed that the correlation coefficients of $ACSA_{max}$ and MV with muscle strength are comparable to that of PCSA (Balshaw et al., 2021; Bamman et al., 2000). In the current results as well, both $ACSA_{max}$ and MV of the ADDH-OH were selected as explainable factors for TGS, without a significant difference between $ACSA_{max}$ and MV in their correlation coefficients with TGS. Thus, this study supports the previous studies (Balshaw et al., 2021; Bamman et al., 2000) and recommends future studies adopt either $ACSA_{max}$ or MV as a representative muscle size index for examining the association between muscle size and TGS

in vivo.

5-1-5. Conclusions

Among the plantar intrinsic and extrinsic foot muscles, the ADDH-OH primarily contributes to TFS production by using the toe grip dynamometer (i.e., TGS). The $ACSA_{max}$ and MV of the ADDH-OH alone explained 42% and 29%, respectively, of the variance in TGS.

Section 2 Strength and size relationships of toe flexor muscles with special reference to the toes intended for force production

5-2-1. Introduction

The magnitude of TFS differed depending on the toe(s) intended for force production: the great toe alone can produce TFS twice as great as the lesser toes can (Abe et al., 2016), while the latter is about one-third of the TFS produced by all toes (Mickle et al., 2016). Taking these findings into account together with the differences in the anatomical function of individual toe flexor muscles (section 1-5-1-3), it is likely that the muscle(s) that specifically contribute to the TFS production may differ depending on the toes intended for force production. However, it is unknown how the strength and size relationships of the toe flexor muscles vary depending on the toes intended for force production. This section aimed to elucidate this subject by examining the association of $ACSA_{max}$ of each toe flexor muscle with three types of TFS production measured by using the custom-made toe push dynamometer: TPS produced by all toes (TPS-All), great toe (TPS-Great), and lesser toes (TPS-Lesser). It is hypothesized that both TPS-All and TPS-Great associate with $ACSA_{max}$ of the muscles specialized in the great toe flexion (i.e., FHB and FHL), while TPS-Lesser relates to $ACSA_{max}$ of the muscles specialized in lesser toes flexion (i.e., FDB and FDL).

5-2-2. Methods

Participants

Fifteen male university students (age, 22.6 ± 2.7 yrs; height, 170.8 ± 5.1 cm; body mass, 64.4 ± 4.7 kg; mean ± SD) who had no history of a diagnosed neuromuscular disorder or

lower limb injury voluntarily participated in this Chapter. All participants provided prior written informed consent based on the guidelines of the Declaration of Helsinki.

Experimental procedure

At the beginning of this study, all participants attended physical characteristic measurements (body mass and height). Then, the foot and lower leg images were obtained using MRI. After the completion of the morphological and MRI measurements, three types of the maximum voluntary isometric TPS were measured using a custom-made toe push dynamometer: TPS-All, TPS-Great, and TPS-Lesser. Each TPS measurement was conducted in a randomized order in a single session of a day.

Determination of $ACSA_{max}$

T1-weighted MR images of the right foot and lower leg were scanned using a 3.0 T MR system. The scanning of T1-weighted MR images of the whole foot and lower leg were performed in accordance with the procedure in Chapter 2 and section 1 of Chapter 5, respectively. This section only determined $ACSA_{max}$ of each individual toe flexor muscle, because the results of section 1 of Chapter 5 showed that the correlation coefficient of TGS was not statistically differed between MV and $ACSA_{max}$.

Measurements of TPS

A custom-made toe push dynamometer (T.K.K. 1268, Takei Scientific Instrument Co, Niigata, Japan), previously used to measure the TPS-All produced in previous studies (Kurihara et al., 2021; Rowley et al., 2015; Yuasa et al., 2018) was applied to determine each maximum voluntary isometric TPS (Fig. 5-2-1). This section modified this device to measure the TPS-Great and TPS-Lesser separately (detailed below). The overall procedure of measuring each

TPS was in accordance with previous studies (Kurihara et al., 2021; Yuasa et al., 2018). First, the participants sat upright on the chair and their right foot was fixed on the ground of the device, with the hip and knee joints flexed at 90° and the ankle joint in a neutral position (i.e., 90° plantarflexed) (Fig. 5-2-2 A). The toe(s) intended for force production were then placed on a fixed angle-adjustable sensor plate. As such, all toes were placed on the angle-adjustable sensor plate for TPS-All (Fig. 5-2-2 B), only the great toe only for TPS-Great (Fig. 5-2-2 C), and the lesser toes for TPS-Lesser (Fig. 5-2-2 D). For the latter two measurements, the toe(s) not intended to produce force (lesser toes for TPS-Great and great toe for TPS-Lesser) were placed on another metallic plate mounted outside of the device to avoid touching the sensor plate (Fig. 5-2-2 C and D). In all TPS measurements, the angle-adjustable sensor plate was placed at 45° of dorsiflexion at the MTP joint, in accordance with previous studies (Kurihara et al., 2021; Yuasa et al., 2018). Previous reports have shown that the highest TPS values were determined at 45° of dorsiflexion at the MTP joint and 90° of dorsiflexion at the ankle joint angles in all cases when TPS was produced by all toes (Goldmann & Brüggemann, 2012), the great toe, and lesser toes (Saeki et al., 2021). To avoid extraneous movements, the ankle and forefoot were fixed on the ground of the device using Velcro straps. To measure each TPS, the participants were instructed to cross their arms in front of their chest and press down the sensor plate as strongly as possible with the toes defined above, without any extraneous movements. During the measurements of the TPS-great and TPS-Lesser, the participants were required to pay attention only to the toe(s) intended for force production and not to produce force with the non-intended toes. They were further instructed not to lift any toes not intended for force production from the metallic plate in all the tests. Two or three trials of submaximal force outputs for the familiarization procedures were conducted before the measurements. After familiarization trials with at least a 3-minute rest period, the participants performed the task with the maximal force for at least 3 seconds. The maximum effort trials were repeated twice, with a rest period of at

least 1 minute. In the case that any extraneous movements other than the instructed ones or visually obvious contraction of the calf muscles were observed, the trial was determined as a failed trial. Moreover, when the difference between the two values was more than 10% of the higher one, the measurement was measured 1 more time. The test trial was repeated up to 5 times, and the largest value was used for further analysis. The ICC of the two test trials in which the largest values were obtained among all test trials were calculated to assess the inter-rater repeatability of each TPS measurement. The ICC (1, 2) values were 0.98 for TPS-All, 0.98 for TPS-Great, and 0.97 for TPS-Lesser. In addition, the ICC of each TPS measurement, which was performed three times at 2-5 days apart with the same procedure, was examined in another experiment participated in 11 healthy young males. The ICC (1, 3) values were 0.81 for TPS-All, 0.79 for TPS-Great, and 0.87 for TPS-Lesser, confirming good repeatability according to the classification reported in a previous study (Koo & Li, 2016).

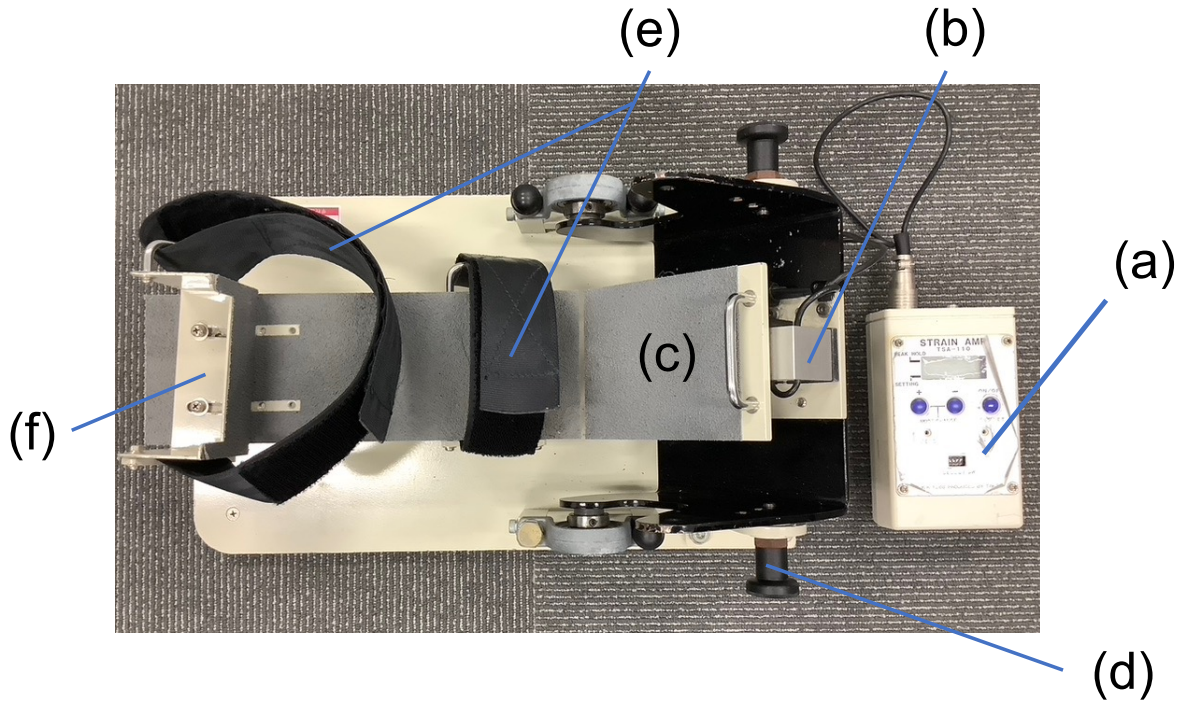

Figure 5-2-1. Toe push dynamometer. Panel A shows the toe push dynamometer. (a): strain amplifier, (b): strain gauge load cell; (c): fixed and angle-adjustable sensor plate; (d): angle adjustment knob; (e): Velcro straps; (f): heel stopper. The measurement range and accuracy of the strain amplifier are 0 – 980 N and ± 0.5 % f.s., respectively. The rated output current and coupling repeatability of the strain gauge load cell is 1.0197 mV V + 15 – 0 % and 0.015 % of RQ. Dimensions of the device: 275 (width), 450 (depth), 165 (height) mm and 14.3 kg.

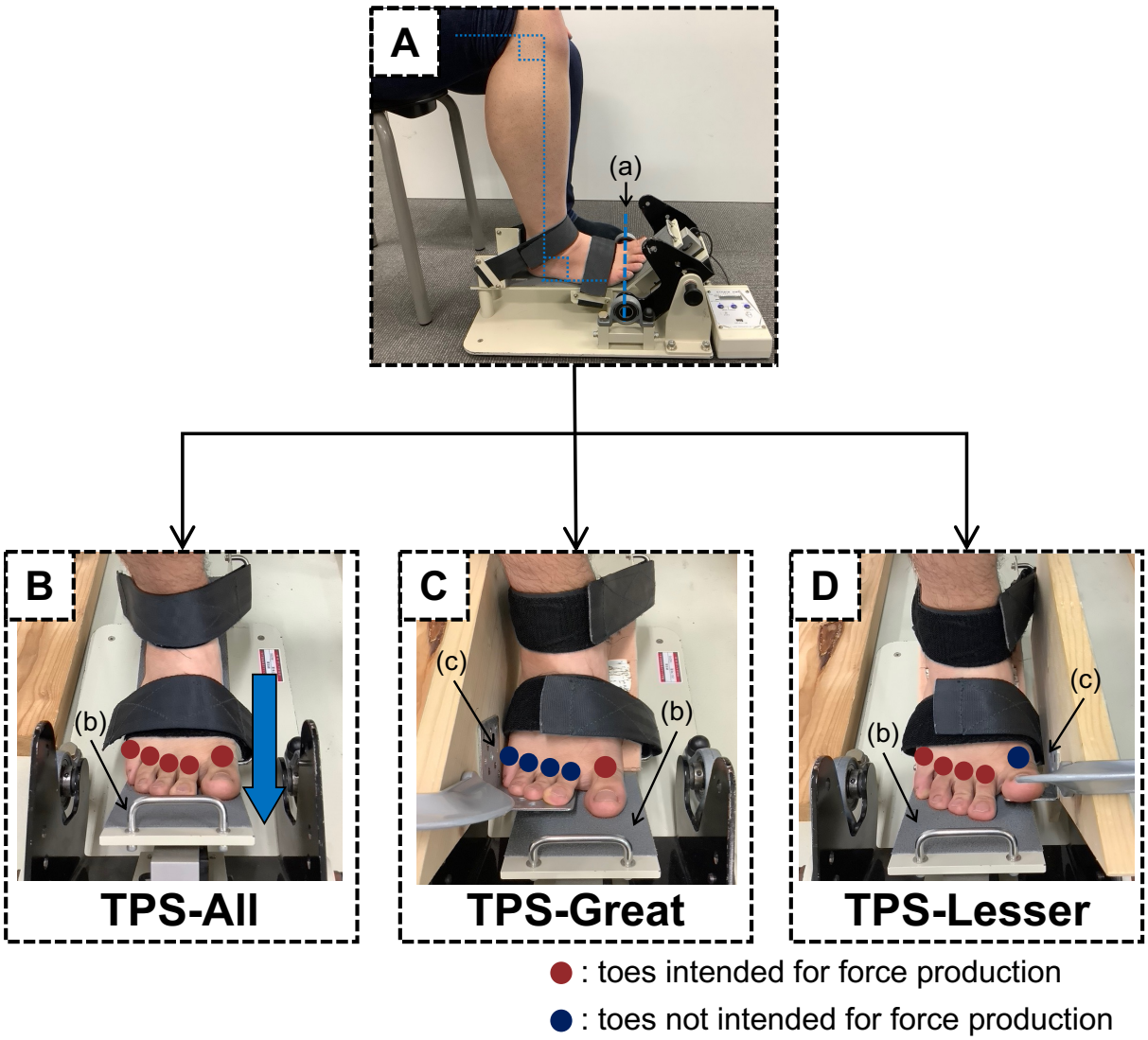

Figure 5-2-2. Measurement of three types of toe push strength (TPS). Panel A: lateral view of the TPS measurement. Panel B, C, and D indicate the toes setting for measuring TPS produced by all toes (TPS-All), great toe (TPS-Great), and lesser toes (TPS-Lesser), respectively. (a): horizontal axis of the metatarsophalangeal (MTP) joint; (b): fixed and angle-adjustable sensor plate; (c) metallic plate for the toes not intended for force production. Blue arrows in the Panel B indicate the direction of force exertion (i.e., the direction of pushing the sensor plate by each toe intended for force production).

Statistical analysis

Descriptive data are presented as means ± SDs. The normality of each data was tested by the Kolmogorov-Smirnov test and confirmed as a normal distribution. Pearson's correlation coefficients were computed to examine the relationships between TPS and $ACSA_{max}$ of each individual muscle or functional muscle group. The level of significance was set at $p < 0.05$. All statistical analysis was conducted using statistical software (SPSS version 27.0, IBM Co., USA).

5-2-3. Results

Descriptive data on the $ACSA_{max}$ and TPS are shown in Table 5-2-1. Table 5-2-2 summarizes Pearson's correlation coefficients between TPS and $ACSA_{max}$ of each individual muscle or functional muscle group. Only the $ACSA_{max}$ of FHB was significantly correlated to TPS-All ($r = 0.570$, $p = 0.026$). No significant correlations were found between either value of TPS-Great and TPS-Lesser and the $ACSA_{max}$ of any individual muscles or functional muscle groups ($r = -0.220 – 0.393$, $p = 0.165 – 0.993$ for TFS-Great and $r = -0.037 – 0.500$, $p = 0.069 – 0.900$ for TFS-Lesser).

Table 5-2-1. The descriptive data on $ACSA_{max}$ and TPS.

	Mean ± SD	Range
$ACSA_{max}$ (cm^2)		
Plantar intrinsic foot muscles		
Whole plantar intrinsic foot muscles	8.36 ± 1.21	6.61 – 10.22
Intrinsic great toe flexors	6.92 ± 0.78	5.84 – 8.37
FHB	3.25 ± 0.56	2.66 – 4.66
ABH	2.90 ± 0.63	1.73 – 4.13
ADDH-OH	3.50 ± 0.45	2.81 – 4.14
ADDH-TH	0.95 ± 0.16	0.71 – 1.17
Intrinsic lesser toes flexors	5.55 ± 0.79	4.32 – 6.37
QP	1.74 ± 0.30	1.37 – 2.28
FDB	2.40 ± 0.40	1.77 – 3.09
ABDM	2.70 ± 0.52	2.03 – 3.74
Extrinsic toe flexors		
FHL	4.79 ± 0.65	3.93 – 6.22
FDL	1.78 ± 0.33	1.14 – 2.50
TPS (N)		
TPS-All	193.3 ± 43.2	111.7 – 289.1
TPS-Great	134.4 ± 27.5	93.1 – 187.2
TPS-Lesser	89.5 ± 24.1	45.1 – 129.4

ABDM: abductor digiti minimi; ABH: abductor hallucis; $ACSA_{max}$: maximal anatomical cross-sectional area; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FDL: flexor digitorum longus; FHB: flexor hallucis brevis; FHL; flexor hallucis longus; QP: quadratus plantae; TPS: toe push strength; TPS-All: TPS produced by all toes; TPS-Great: TPS produced by the great toe; TPS-Lesser: TPS produced by lesser toes.

Table 5-2-2. Pearson's correlation coefficients between toe push strength (TPS) and $ACSA_{max}$ of each individual muscle or functional muscle groups.

	TPS-All		TPS-Great	TPS-Lesser
	r		r	r
Plantar intrinsic foot muscles				
Whole plantar intrinsic foot muscles	0.359		-0.133	0.423
Intrinsic great toe flexors	0.353		0.143	0.169
FHB	0.570	*	0.201	0.280
ABH	0.314		-0.137	0.367
ADDH-OH	-0.075		-0.048	0.104
ADDH-TH	0.403		0.101	0.322
Intrinsic lesser toes flexors	0.345		-0.211	0.489
QP	-0.005		-0.137	0.147
FDB	0.468		-0.006	0.298
ABDM	0.370		-0.156	0.140
Extrinsic toe flexors				
FHL	0.026		0.150	-0.103
FDL	0.273		0.073	0.184

Significance of Pearson's correlations coefficients are indicated as follows: *$p < 0.05$.

ABDM: abductor digiti minimi; ABH; abductor hallucis; ADDH-OH: adductor hallucis oblique head; ADDH-TH: adductor hallucis transverse head; FDB: flexor digitorum brevis; FDL: flexor digitorum longus; FHB: flexor hallucis brevis; FHL: flexor hallucis longus; QP: quadratus plantae; TPS-All: TPS produced by all toes; TPS-Great: TPS produced by the great toe; TPS-Lesser: TPS produced by lesser toes.

5-2-4. Discussion

Contrary to our expectations, only the $ACSA_{max}$ of FHB was significantly associated with TPS-All. The TFS production by the great toe and lesser toes was found to be independent of the size of muscles specializing in each of the two types of toe flexions.

The current result that only the $ACSA_{max}$ of FHB significantly associated with TPS-All (Table 5-2-2) differed from our hypothesis that the corresponding relationship would be found in the $ACSA_{max}$ of muscles specialized in the great toe flexion, that is, FHB and FHL. This may be explained by the consistency between the toe action for force production depending on the device utilized and the anatomical function of each of the specific muscles. Using the toe push dynamometer in this section, flexion at the MTP joint with minimum flexion of the IP joint was required for force production (Soysa et al., 2012). Based on the difference in the anatomical insertion of FHB and FHL, the former flexes the first MTP joint only, whereas the latter acts on the flexion at the first MTP joint as well as IP joints (Neumann, 2017). Thus, the current result may be attributable to the fact the anatomical function of FHB would be the most suitable for the toe pushing action.

TPS-Great and TPS-Lesser were not significantly associated with $ACSA_{max}$ of any individual muscles and functional muscle groups (Table 5-2-2). The reasons for these unexpected results are unknown but might involve two possibilities. First, it is possible that plantar intrinsic foot muscles could not be fully activated during the TPS-Great and TPS-Lesser production. Olivera et al. (Perez Olivera et al., 2022) examined the magnitude of the activation level of ABH during maximal force output by the combination of abduction and flexion of the great toe. They reported that only a limited number of the participants (23%) could voluntarily activate ABH at more than 90 % of the maximum activation level determined by the twitch interpolation technique, whereas the others (77%) voluntarily activated this muscle at approximately 70% on average (range 36–83%) (Perez Olivera et al., 2022). This suggests that

under voluntary contractions, the plantar intrinsic foot muscles cannot be fully activated during TPS production by the great toe and lesser toes with the related muscles. Second, the mechanical coupling of the tendons would be involved to explain the present results. A cadaveric study with 55 specimens and 110 legs observed mechanical connections between the tendons of the extrinsic toe flexors (i.e., FHL and FDL) in all cases (Edama et al., 2016). Thus, it is likely that FHL and FDL do not act selectively on the flexion of the great toe and lesser toes, respectively, and consequently, when producing TPS-Great and TPS-Lesser, muscle tension produced by the muscle relating to the toes intended for force production may be distributed to the other toes not intended for force production. In fact, it has been observed that when producing force by a finger with peripheral tendon connections of finger muscles, other fingers, especially the adjacent finger not intended to produce force involuntarily, also produced a substantial amount of force (Zatsiorsky et al., 2000). Considering these aspects, the difficulty in voluntarily activating the individual plantar intrinsic foot muscles and separately contracting the extrinsic toe flexors during the TFS-Great and TFS-Lesser productions could explain the unexpected results regarding their associations with the $ACSA_{max}$ values of the corresponding muscles.

5-2-5. Conclusions

The current results indicate that the magnitude of TFS depending on the toes intended for force production is not associated with the size of the muscles specialized in each toe flexion. This result may be attributable to the difficulty in separately producing TFS by the great toe and lesser toes, potentially due to the decreased voluntary activation and/or mechanically connected tendons of the toe flexor muscles.

Chapter 6 General Discussion

In this Chapter, first, the main findings of each Chapter (section 6-1) were summarized. And then, the contribution of plantar intrinsic foot muscles to the maintenance of the foot structure and TFS production was discussed (section 6-2). Moreover, the difference in the muscle that mainly contributes to force production between TGS and TPS-All (section 6-3), the significance of strengthening TFS to physical performance and rehabilitation (section 6-4), and limitations and future perspectives were also discussed (section 6-5). Finally, the conclusions of this thesis were described (section 6-6).

6-1. Summary of the main findings

The main findings of each Chapter are summarized as follows.

Chapter 2: The results showed that muscle size (MV and $ACSA_{max}$) varied among individual plantar intrinsic foot muscles. Moreover, the ACSA distribution along the FL and the position where $ACSA_{max}$ was observed differed among individual muscles.

Chapter 3: Individual plantar intrinsic foot muscles were assigned to each of the four clusters by K-means clustering analysis with PCSA and fiber length as attributes, which were estimated by using data obtained from the living subject in Chapter 2 and cadavers in previous studies (Kura et al., 1997; Ledoux et al., 2001). The involved muscles in each cluster and the contractile properties, estimated from the relationship between PCSA and fiber length, are as follows: cluster 1) high force production at slow shortening velocity, ADDH-OH and FHB; cluster 2) high force production at moderate shortening velocity, ABDM, ABH, FDB, and

FHB; cluster 3) very small force production at moderate shortening velocity, ADDH-TH only; cluster 4) moderate force production at high shortening velocity, QP only**.**

Chapter 4: The MV of the whole plantar intrinsic foot muscles, especially those specialized in toe flexion, relates to the forefoot width and circumferential parameters involved in forming anterior and posterior transverse arches. However, the association between MLA height and the MV of any plantar intrinsic foot muscle could not find.

Chapter 5: The results showed that ADDH-OH was consistently selected as a major contributor to TGS production when either MV or $ACSA_{max}$ was adopted as parameters representing muscle size (section 1). The significant association of TPS-All was only found with the $ACSA_{max}$ of FHB. TPS-Great and TPS-Lesser were not significantly associated with the $ACSA_{max}$ of any toe flexor muscles (section 2).

6-2. The contribution of plantar intrinsic foot muscles to the maintenance of the foot structure and TFS production

This thesis attempted to elucidate how the morphological profiles of individual plantar intrinsic foot muscles associate with foot structure and TFS by adopting the following two approaches. Chapter 3, which adopted an approach based on morphological parameters reflecting the contractile properties, showed that the function of plantar intrinsic foot muscles, especially the maintenance of foot arch structure and force production at the toes, can be estimated by the contractile properties of each cluster (detailed in the discussion section of Chapter 3). Chapters 4 and 5 determined associations of the size of individual plantar intrinsic foot muscles with the foot morphological profile and TFS, respectively as an approach based on the muscle size and its relation to foot structure and TFS. Whether the function predicted by the contractile properties of each cluster in Chapter 3 coincided with the findings on

associations of the size of plantar intrinsic foot muscles with foot structure and TFS in Chapters 4 and 5, respectively, were undefined. In the subsequent subsections, therefore, the contribution of individual plantar intrinsic foot muscles to foot structure (section 6-2-1) and TFS (section 6-2-2) is discussed by combining the findings obtained from these approaches.

6-2-1. The maintenance of the foot structure

The results of Chapter 4 showed that the MLA height was not associated with the size of individual plantar intrinsic foot muscles. In Chapter 3, the involved muscles of cluster 1 (i.e., ADDH-OH and FHB) would be assumed to produce stabilizing forces for the MLA because they are located beneath this arch (Neuman. 2017), and those of cluster 2 (i.e., ABDM, ABH, FDB, and FHB) would contribute to stabilizing the MLA, lateral longitudinal arch, and sole because they lie covering the exoskeleton from the sole of the foot (Neuman. 2017). However, the results obtained in Chapter 4 deny these assumptions. Whether the plantar intrinsic foot muscles contribute to the maintenance of MLA is still in debate. For example, a study reported that those with a flat foot, characterized by lowered MLA, had smaller ACSA and muscle thickness of ABH and FHB compared to a population with a normal foot (Angin et al., 2014). On the other hand, the other observed a large muscle thickness of ABH in a flat foot (Taş et al., 2018). The MLA height indices measured in Chapter 4 were determined in the bilateral standing condition. Therefore, there is a possibility that the magnitude of the postural demand adopted in Chapter 4 might have been insufficient to evaluate MLA height indices, and consequently could not find significant associations between the indices and muscle size, being supposed from the results of Chapter 3. Further study is needed to determine how the muscles involved in clusters 1 and 2 contribute to maintaining the arch structure of the foot under conditions with high postural demands.

As opposed to MLA height indices, the size of the whole and several plantar intrinsic

foot muscles positively correlated to width and circumferential parameters that are assumed to be involved in forming the anterior/posterior transverse arches (Chapter 4). In Chapter 2, it was speculated that cluster 3 functions as stabilizing the anterior transverse arch because there is consistency between the running direction of this arch and that of the ADDH-TH, which is a major constituent of cluster 3. However, the results in Chapter 4 contradict this speculation in Chapter 2. Rather, significant associations of the parameters that are involved in forming the anterior/posterior transverse arches were found in the size of the whole muscles and in individual muscles within clusters 1, 2, and 4 (FDB, FHB, ad QP). Considering these, it seems that the plantar intrinsic foot muscles as a whole (except for ADDH-TH, which is the main constituent of cluster 3) may contribute to forming the transverse arches rather than the MLA regardless of the difference in anatomical profiles and contractile properties derived from the morphological profiles. Therefore, strengthening the whole plantar intrinsic foot muscles will be beneficial for stabilizing the transverse arches. Furthermore, this eventually may contribute to the stiffening of the MLA since the formation of the posterior transverse arch as adequate curvature has been suggested to be one of the key factors in the stiffening of the longitudinal structures of the foot (Venkadesan et al. 2020).

6-2-2. The TFS production

In Chapter 5, the association between TFS and the size of toe flexor muscles was examined with the hypothesis that the muscles that specialized in toe flexion would mainly contribute to TFS production. However, the results in Chapter 5 differed from this hypothesis predicted by the anatomical perspective. Specifically, the ADDH-OH, which mainly acts on the adduction and assists with flexion at the great toe was selected as the primary contributor to TGS production (section 1), and only FHB, which specialized in great toe flexion was significantly associated with TPS-All production (section 2). It is worth noting that based on

the morphological classification in Chapter 3, ADDH-OH and FHB were the muscles involved in cluster 1. The involved muscles of cluster 1 (ADDH-OH and FHB) act on the great toe flexion. Thus, it is likely that the function of cluster 1 is the primary force generator in the great toe. In other words, it can be said that the results obtained from actual measurements of muscle strength and muscle size in Chapter 5 may be rephrased by a morphological perspective that the muscles involved in cluster 1 contribute to TFS. Taken together, these aspects would be the evidence to support the potential utility of estimating the function of plantar intrinsic foot muscles, particularly the force production at the toes, on the basis of morphological information beyond the perspective derived from the anatomical profiles such as depth of presence and site of attachment.

6-3. The difference in the muscle that mainly contributes to force production between TGS and TPS-All

The results of Chapter 5 showed that the muscle that mainly contributes to TFS production differed depending on the toe actions required device utilized. The major contributor to TGS, which was determined using the toe grip action, was the size of ADDH-OH. On the other hand, the significant association for TPS-All, which was determined using the toe pushing action, was only observed in the size of FHB. This inconsistency may be explained by the following two aspects.

First, the toe action required for force production differed between TGS and TPS-All. The TGS measurement adopted in section 1 of Chapter 5 was performed using the toe grip dynamometer, which requires toe gripping action for force production. In this case, the anatomical function of ADDH-OH, which mainly acts on adduction and assists in the flexion of the great toe (Neumann, 2017) is considered to coincide with the toe gripping action. On the

other hand, TPS-All determined in section 2 of Chapter 5 was measured using a custom-made toe push dynamometer. This device requires the toe pushing action for force production, which is consisted of the flexion at the MTP joint with minimum flexion of the IP joint (Soysa et al., 2012). FHB is specialized in the flexion at the first MTP joint (Neumann, 2017) and therefore the anatomical function of this muscle would be most suitable for joint movement of the toe pushing action. Thus, the muscle that primarily contributes to force production differed between TGS and TPS-All may be explained by the difference in the joint movements of the toe action for force production depending on the device utilized.

In addition, the MTP joint position on the sagittal plane during force production differed between TGS and TPS-All. Goldmann et al., (2012) examined the influence of the MTP joint angle on the TFS magnitude and found that TFS increased with the increment of dorsiflexion angle, with the largest values observed at MTP joint 25–45° dorsiflexed. Kurihara et al. (2022) also found that the value of TFS was greater in the MTP joint dorsiflexed position (i.e., TPS-All) than in the MTP joint plantarflexed position (i.e., TGS). It is considered that this increment of the TFS magnitude with the MTP joint dorsiflexed angle is due to the force-length relationship of both extrinsic toe flexors and plantar intrinsic foot muscles (Goldmann & Brüggemann, 2012). However, based on the results of Chapter 5, it would be suitable to interpret the differences in the major contributors between TGS and TPS-All from the force-length relationship of the plantar intrinsic foot muscles. FHB inserts beneath the plantar surface of medial and lateral sesamoid bones of the first metatarsal, while ADDH-OH distally attaches to the lateral side of medial sesamoid bones (Neumann, 2017). According to this, it seems that the magnitude of the change in muscle length with the MTP joint dorsiflexion is greater in FHB and relatively smaller in ADDH-OH. Thus, it is possible that in the TPS-All measurement, which requires force production in the MTP joint dorsiflexed position, the FHB may be approached the ascending limb of the length-force relationship, and thus could produce higher

force than the ADDH-OH. On the other hand, in the TGS measurement that requires force production at the MTP joint plantarflexed position, the ADDH-OH, which is less affected by the change of muscle length due to the MTP joint, may be able to produce greater force than the FHB, which seems to be approached descending limb. Taken together, the reason why the muscle that primarily contributes to force production differed between TGS and TPS-All may be further explained by the changes in the force-length relationship of FHB depending on the MTP joint position required for the device utilized.

It is also worth noting that, in Chapter 5, significant associations of the TFS were not found in the size of the muscles with relatively larger MV, specifically ABH and ABDM. The magnitude of TFS was influenced by the ankle joint position: the highest TFS value was observed at 0º–20º of the ankle joint dorsiflexed, while the magnitude of TGS gradually decreased toward the ankle joint angle plantarflexed (Goldmann & Brüggemann, 2012; Yamauchi & Koyama, 2019a). This may be associated with the force-length relationship of extrinsic toe flexors. The fascicle length of FHL changes by 0.5 mm per 1 degree of ankle joint rotation occurred (Refshauge et al., 1995). Thus, the TFS produced in the neutral position adopted in Chapter 5 seems to involve the contribution of the extrinsic toe flexors more than the plantar intrinsic foot muscles. Therefore, the contribution of the plantar intrinsic foot muscles, which did not find significant associations, to TFS might have been found by adopting dependent variables such as TFS produced in the ankle joint plantarflexed position. Furthermore, Chapter 5 measured TFS only to determine the force-generation capacity of plantar intrinsic foot muscles. Therefore, when the relationship between the size and strength of the plantar intrinsic foot muscles can be determined by adopting the toe strength produced by other directions of movement, such as the toe abductor strength of the great or fifth toe, it may be possible to clearly find the contribution of the ABH and ABDM, which mainly act on the abduction, to the toe strength.

6-4. Significance of strengthening TFS to physical performance and rehabilitation

This thesis provides detailed insight into the role of the individual toe flexor muscles in producing TFS. The size of plantar intrinsic foot muscles primarily contributes to TPS-All and TGS production. Specifically, ADDH-OH was selected as the major contributor to TGS production (section 1 of Chapter 5), while only FHB was significantly associated with TPS-All production (section 2 of Chapter 5). However, the size of any toe flexor muscles was not significantly correlated with the TFS produced by separating toes intended for force production (i.e., TPS-Great and TPS-Lesser) (section 2 of Chapter 5). Such novel evidence may provide useful information on designing strategies or exercises for the enhancement of physical performance and for the rehabilitation of several foot and ankle pathological conditions.

6-4-1. Enhancement and/or improvement of physical performance

It has been well documented that TGS significantly relates to the scores of physical performances in various populations. For example, higher TGS in adolescents to young adults relates to greater athletic performances such as sprinting and jumping (Kurihara et al., 2021; Otsuka et al., 2015; Yamauchi & Koyama, 2020). Furthermore, in older adults, reduced TGS associates with impairment of the dynamic balance ability (Suwa et al., 2016) and mobility (Uritani et al., 2016). On the other hand, the influence of the TPS-All on physical performance has only been examined in a limited population. In collegiate competitive athletes, a significant association of the change of direction performance (pro-agility and 3-cone tests) was observed in TPS-All, but not in TGS (Yuasa et al., 2018). Collegiate competitive athletes also had a significant association between TPS-All and jumping performance (Yuasa et al., 2019). Moreover, in the basketball players who belong to junior and junior high schools, the height of vertical jump was significantly related to TPS-All and TGS, but the association was weaker in the former than in the latter as a whole result (Kurihara et al., 2021). Combining these previous

findings with the differences in the primary contributors to the production between TGS and TPS-All, it is recommended that strengthening of TGS and its determinant, ADDH-OH, should be incorporated into exercise programs aimed at improving and/or enhancing physical performance in a wide-range population. On the other hand, for competitive athletes, it would be recommended to strengthen the TPS-All and its determinant, FHB, to enhance athletic performance.

6-4-2. Rehabilitation for several foot and ankle pathological conditions

Plantar fasciitis is one of the most common running-related musculoskeletal injuries (Kakouris et al., 2021), which is characterized by plantar heel pain (Dyck & Boyajian-O'Neill, 2004). The populations that suffered from plantar fasciitis showed atrophy of the plantar intrinsic foot muscles in the forefoot region compared to healthy populations (Chang et al., 2012). In addition, previous studies have reported the characteristics of plantar intrinsic foot muscle size in populations with chronic ankle instability (Feger et al., 2016), which is reported to develop in 40% of initial lateral ankle sprains (Doherty et al., 2016). From their findings, compared to healthy populations, those with chronic ankle instability had reduced MV of FHB and ADDH-OH (Feger et al., 2016). Therefore, employing TGS and TPS-All strengthening exercises in rehabilitation programs for these ankle and foot pathological conditions may be useful to improve atrophy in the plantar intrinsic foot muscles.

In addition, it has been suggested that one of the reasons for the occurrence of hallux valgus, which is characterized as a static subluxation of the first MTP joint with laterally deviated great toe and medially deviated 1st metatarsal (Mann & Coughlin, 1981) is the muscle imbalance in the abductor and adductor muscles of the great toe (Arinci Incel et al., 2003). Silver. (1923) specifically noted that the anatomical action of ADDH (i.e., adduction and assistance with flexion at the first MTP joint) and its tendon naturally tends to increase hallux

valgus deformity. In fact, middle to older populations with hallux valgus decreased muscle thickness and ACSA of ABH (abductor) as well as those of intrinsic toe flexors (FDB and FHB) (Taş & Çetin, 2019). Considering these aspects, it would be recommended to incorporate TPS rather than TGS as improving muscle atrophy of the abductor and flexor muscle of the great toe and weakness of TFS if conservative therapy is chosen for the treatment of hallux valgus. The reason for this recommendation is that TGS may induce severe deformity of the great toe by strengthening ADDH-OH. Nevertheless, there has been no case that tested the effectiveness of TGS or TPS-All as rehabilitation for these pathological conditions, and further study is needed to clarify this subject.

6-5. Limitations of this thesis and future perspectives

This thesis has the following limitations. First, each Chapter of this thesis examined male university students only. The reason for this was to avoid potential confounding influences of sex differences in the magnitude of MLA height (Zhao et al., 2020) and TFS (Kurihara et al., 2014) and of age-related reduction in the size of plantar intrinsic foot muscles (Mickle et al., 2016) and TFS (Mickle et al., 2016; Uritani et al., 2014). Thus, it is unclear whether the current findings can be applied to other populations, such as females, older adults, and those with abnormal foot postures. A further study is warranted to determine whether the current findings can be generalized to other populations. Nevertheless, in particular, the data on MV and $ACSA_{max}$ of individual plantar intrinsic muscles obtained in Chapter 2 would be useful information to clarify such population differences.

Second, Chapter 3 estimated PCSA and muscle fiber length by combining the data obtained from Chapter 2 and from previous cadaveric studies by Kura et al., (1997) and Ledoux et al., (2001). The cadaveric data were obtained from a limited number of samples (N = 2–11)

(Kura et al., 1997; Ledoux et al., 2001) and/or from much older samples than the present study (50–80 yrs) (Kura et al., 1997), and were measured approximately 20 years before the experiment of Chapter 3 was conducted (Kura et al., 1997; Ledoux et al., 2001). Thus, the possibility that the morphological profiles of the subjects in this study and those of the samples in previous cadaveric studies (Kura et al., 1997; Ledoux et al., 2001) are dissimilar cannot be ruled out. In addition, Ledoux et al., (2001) mentioned that based on data obtained from their limited samples (N = 2), the influence of the pennation angle on the force produced by the plantar intrinsic foot was not great, because the cosines of the angles range from 0.993 to 0.945. Recently, an attempt to quantify the magnitude of muscle fiber length and pennation angle of gastrocnemius in vivo using magnetic resonance diffusion tensor imaging (Takahashi et al., 2022). A further study applying such methods for determining muscle fiber length and pennation angle of individual plantar intrinsic foot muscles may enable the characterization of the contractile properties of these muscles in vivo more precisely from data obtained from the same sample.

Third, Chapter 3 categorized individual plantar intrinsic foot muscles into four clusters depending on their morphological information (PCSA and muscle fiber length) and estimated the function of each cluster. In addition to such a morphological perspective, it is necessary to consider the moment arm to determine the function of a specific muscle during physical activities. However, no studies have reported data on the moment arm of the plantar intrinsic foot muscles for any joint within the foot from living subjects. On the other hand, a cadaveric study with older samples has provided data on the moment arm of the muscles, which act on the great toe, at the MTP joint only (Tanaka et al., 2008). Based on their limited findings, the average moment arm of these muscles ranged from 4.5 to 8.2 mm (ABH: 6.2 mm; ADDH-OH: 7.0 mm; ADDH-TH: 4.5 mm; FHB medial head: 8.2 mm; FHB lateral head: 8.0 mm) (Tanaka et al., 2008). Thus, except for ADDH-TH with an extremely small moment arm, the influence

of the differences in the moment arm of individual plantar intrinsic foot muscles on MTP joint torque may be small, only about 1.3 times at maximum (based on the values of ABH [6.2 mm] and FHB medial head [8.2 mm]). Combining this with the complex anatomy of the plantar intrinsic foot muscles being closely packed in the small area of the sole, the differences in the moment arm among individual these muscles would be predicted to be small compared to muscles of the lower extremity acting on the ankle and knee joints, and consequently, their influence on foot function to be minimal.

Forth, in Chapter 2 and 3, the FL and muscle length of individual plantar intrinsic foot muscles was determined by MRI. In detail, FL and muscle length were measured as the number of slices between the medial calcaneal tuberosity and the sesamoid bones of the first metatarsal and between the most proximal and most distal MR images where the muscle was visible, multiplied by the slice thickness, respectively. In this thesis, a series of foot MR images was measured with a slice thickness of 3.5 mm (no gap between slices). Therefore, it should be noted that the muscle lengths and FL may contain potential errors of up to 7 mm.

Finally, section 2 of Chapter 5 suggested that the reduced activation level and mechanical tendon connections of toe flexor muscles might be the potential reasons why the size of toe flexor muscles cannot explain the TPS production by the great toe (TPS-Great) and lesser toes (TPS-Lesser). However, this thesis has no data on the differences in the activated muscles during any type of TFS production. Some studies have adopted T2-weighted MRI (Gooding et al., 2016) and positron emission tomography (Kanayama et al., 2022) to determine which muscle(s) were activated during foot exercises with complex movements, such as the short-foot, towel-gathering, and toe-spread-out exercises. Further studies applying such methods may clarify the contribution of individual toe flexor muscles to TFS production, depending on the toe(s) intended for force production.

6-6. Conclusions of this thesis

The general purpose of this thesis was to elucidate how the morphological profiles of individual plantar intrinsic foot muscles associate with foot structure and TFS. The major findings from the two approaches adopted in this thesis were as follows.

The approach based on morphological parameters reflecting the contractile properties

: The involvement of plantar intrinsic foot muscles in the maintenance of foot structure and force production at the toes may vary in each cluster classified by the similarity of the contractile properties.

The approach based on the muscle size and its relation to foot structure and toe flexor strength

: The size of whole plantar intrinsic foot muscles is significantly related to foot width and circumferential parameters which may be involved in forming transverse arches, but not to the medial longitudinal arch height measured in the bilateral standing condition. The size of these muscles also is significantly associated with toe flexor strength, but its primary contributor depends on the toe action required by the device utilized: the primary contributor to toe flexor strength produced by a toe gripping action is adductor hallucis oblique head, while toe flexor strength produced by a toe pushing action for all toes is significantly related to flexor hallucis brevis only.

These indicate that 1) the size of plantar intrinsic foot muscles relates to parameters involved in forming transverse arches as a whole and 2) that these muscles with morphological profiles specialized in producing high force at a slow shortening velocity, primarily contribute to toe flexor strength, depending on the toe action for force production.

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