Passive mechanics of canine internal abdominal muscles

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Hwang, Willy, Jason C. Carvalho, Isaac Tarlovsky, and Aladin M. Boriek. Passive mechanics of canine internal abdominal muscles. J Appl Physiol 98: 1829–1835, 2005; doi:10.1152/japplphysiol.00910.2003.—The internal abdominal muscles are biaxially loaded in vivo, and therefore length-tension relations along and transverse to the directions of the muscle fibers are important in understanding their mechanical properties. We hypothesized that 1) internal oblique and transversus abdominis form an internal abdominal composite muscle with altered compliance than that of either muscle individually, and 2) anisotropy, different compliances in orthogonal directions, of internal abdominal composite muscle is less pronounced than that of its individual muscles. To test these hypotheses, in vitro mechanical testing was performed on 5 × 5 cm squares of transversus abdominis, internal oblique, and the two muscles together as a composite. These tissues were harvested from the left lateral side of abdominal muscles of eleven mongrel dogs (15–23 kg) and placed in a bath of oxygenated Krebs solution. Each tissue strip was attached to a biaxial mechanical testing device. Each muscle was passively lengthened and shortened along muscle fibers, transverse to fibers, or simultaneously along and transverse to muscle fibers. Both transversus abdominis and internal oblique muscles demonstrated less extensibility in the direction transverse to muscle fibers than along fibers. Biaxial loading caused a stiffening effect that was greater in the direction along the fibers than transverse to the fibers. Furthermore, the abdominal muscle composite was less compliant than either muscle alone in the direction of the muscle fibers. Taken together, our data suggested that the internal abdominal composite tissue has complex mechanical properties that are dependent on the mechanical properties of internal oblique and transversus abdominis muscles.

THE ABDOMINAL WALL CONTAINS the four most powerful expiratory muscles in mammals; the rectus abdominis, the external oblique (EO), the internal oblique (IO), and the transversus abdominis (TA). Anatomically, the IO lies internal to the EO muscle in the lateral abdominal wall, whereas the TA, the most internal abdominal muscle, lies in the lateral and ventral abdominal wall between the internal surface of the IO and the costal cartilage (16). Abdominal muscles contribute to protective reflexes (such as cough, sneeze, and vomiting), generate intra-abdominal pressures necessary for expiratory efforts, and are active during postural adjustments (10). In dogs, Leevers et al. (11) showed that hypercapnia preferentially recruits internal abdominal muscles (TA and IO) with greater tonic and phasic expiratory shortening than external abdominal muscles (rectus abdominis and EO). In humans, Wakai et al. (20) found that during hypercapnia the internal abdominal muscles are activated at a lower ventilatory threshold. Sanna et al. (18) found that abdominal muscle action accounted for expiratory reserve

respiratory muscles; stress; strain

volume recruitment. In humans, De Troyer et al. (6) demonstrated preferential recruitment of TA to the superficial muscles of the abdominal wall during breathing as well as low threshold for abdominal muscle recruitment during expiration, whereas in dogs, Parkas et al. (8) confirmed that preferential recruitment of the TA occurs in the prone position. Abe et al. (1) showed differential activation of abdominal muscles with TA as the most active during both CO2-stimulated ventilation and postural change from supine to standing. Previous work by Robertson et al. (17) demonstrated that, during inspiratory loading, blood flow increased significantly only to the TA but not to the other three abdominal muscles. Furthermore, during expiratory loading, the TA still received the greatest increase in blood flow. These aggregate data suggest that the TA has the greatest respiratory role among the abdominal wall muscles, and the mechanical properties of this muscle are therefore critical to the understanding of abdominal muscle function.

In vivo, abdominal muscles experience biaxial loading that causes mechanical stress not only in the longitudinal direction of the muscle fibers (AF) but also transverse to the fibers (TF). However, unlike the biaxially loaded diaphragm, the abdominal muscles are arranged in multiple layers with fibers in an individual muscle oriented at an angle to fibers in the adjacent muscle. For example, the IO and EO are oriented in such a way that the direction of muscle fibers in the IO is perpendicular to the direction of muscle fibers of the EO. We wondered how the length-tension relationship of individual abdominal muscle layers differs from that of a composite muscle of two of the individual muscle layers of the abdominal wall. We selected the adjacent IO and TA, separated by a network of fascial connective tissue, because we expected myofascial force transmission between these two internal muscle layers during respiration. Functionally loaded with pressure, the TA and IO respond more to increases in chemical or volume-related drive than do the external abdominal muscles as discussed previously (10, 11, 17, 20).

During inspiration, the diaphragm descends, the abdominal pressure increases, passive abdominal wall tension increases, and the abdominal wall lengthens passively. Contraction of abdominal muscles during expiration causes an inward displacement of the abdominal wall and an increased abdominal pressure, which displaces the diaphragm into the thorax and decreases lung volume (7). Understanding how abdominal muscles function physiologically during respiration requires knowledge of their length-tension relationships in the AF and TF since the abdominal muscles are loaded biaxially in vivo. Because fascia tightly binds IO to TA, these length-tension relationships must be investigated in the context of an intact composite of IO and TA. We hypothesize that 1) the IO and the TA muscles form an internal abdominal composite muscle with

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less compliance than that of either muscle individually and 2) anisotropy, different compliances in the orthogonal directions, of the internal abdominal composite muscle is less pronounced than that of the individual muscles due to the 45° angle in fiber orientation of composite muscle layers.

**METHODS**

**Muscle strip preparation.** Following approval of the institutional review board, 11 adult mongrel dogs, weighing from 15 to 23 kg each, were killed by pentobarbital sodium overdose (1 ml/kg) in accordance with American Physiological Society guidelines of animal treatment. The chest was opened by a bilateral thoracotomy extending across the sternum, and the abdominal wall was opened by a midline laparotomy. Within 15–20 min of death, both the IO and TA muscles were excised from the left lateral side of each animal. For testing of individual muscle layers, six IO muscles and six TA muscles were excised from the left lateral side of six dogs, with careful separation of connective fascia between the two muscle layers. For the internal abdominal muscle composite testing, a total of five IO and five TA muscles were excised from the left lateral side of five dogs with careful preservation of connective fascia that connect the IO to the TA. In the latter five dogs, the internal abdominal muscle was excised as intact muscle composed of the IO, TA, and the connective fascia between the IO and TA.

The excised abdominal muscles were immediately immersed in a muscle bath containing modified Krebs-Ringer solution (in mM: 137 NaCl, 5 KCl, 1 NaHPO4, 24 NaHCO3, 2 CaCl2·2H2O, 1 MgSO4·7H2O, pH 7.4) bubbled with 95% O2-5% CO2 at room temperature. For muscle testing, a 5 × 5 cm square of tissue was dissected from the medial section of each muscle with the muscle insertions intact. For testing of individual muscle layers, the muscles were cut along the fibers to minimize the lateral muscle fiber damage. For the internal abdominal composite muscle testing, the muscles whose strain would be measured was cut along the fiber direction while the underlying muscle had its muscle fibers oriented at 45° to the direction of the overlying muscle fibers. Four markers (size 4-0 black suture thread) were placed in a 1 × 1 cm square configuration on the surface of the abdominal muscle and positioned in the center away from the boundaries.

**Biaxial testing equipment.** The passive lengthening of muscle tissue was executed using biaxial testing apparatus described in detail previously (2). Briefly, the apparatus consists of stepper motors aligned directly opposite to force transducers (Grass model FT10) with the two motor transducer pairs at right angles to each other. A muscle bath, through which oxygenated Ringer solution was circulated, was situated between the motor transducer pairs. Each muscle was transferred to the muscle bath, and 10 small fish hooks were attached at ~5-mm intervals along the edges of the muscle sheet. Threads from the hooks along each side of the muscle were led to a carriage, and lines from each of the four carriages were connected to the motor or force transducer that faced the edge. The attachments were adjusted to remove slack from all lines.

Each abdominal muscle was preconditioned with three stretch-release cycles at 6% of maximal tetanic stress applied biaxially. Each individual muscle layer was then passively lengthened uniaxially along the fibers and released when the peak tension reached ~50% of maximal tetanic stress. A second preconditioning was done as described previously. Subsequently, each muscle was passively lengthened transverse to the fiber orientation and passively shortened when tension reached ~70% of maximal tetanic stress. Biaxial passive lengthening was applied to the TA in the AF and TF and released when peak tension reached 70% of maximal tetanic stress. The IO and TA were tested as an internal abdominal composite muscle. In these experiments, the internal abdominal composite muscle was tested while recording either the IO strain or the TA strain. We used protocols of uniaxial and biaxial passive lengthening similar to those applied to the individual layers of the internal abdominal muscle. To compute stress from tension, we measured the thickness of the medial section of the IO and TA muscles using published methods (4, 14). Maximal tetanic stress was assumed to be the standard value of 22 N/cm² for respiratory muscles (15).

A strain rate of 1.5 mm/s was used during all passive lengthening and shortening protocols. Force data were simultaneously collected at a sampling rate of 5 Hz from each force transducer using an analog-to-digital acquisition board (National Instruments) and recorded with LabView software (version 3.0). Marker displacement was monitored by a closed-circuit television video camera (Hitachi HV-720U, Edmund Scientific) and recorded on tape by a video cassette recorder (Sony SLV-620HF). Force data were amplified (Validyne C019A system), collected at 10 Hz using a data acquisition board (Lab-PC1200/AI, National Instruments), recorded using LabVIEW version 5.0 software, and stored in a desktop computer (Dell Pentium 200 MMX).

The video of marker displacement was digitally captured with capturing software (Video Work version 1.5 and VidEdit version 1.1) and a video capture card (Captivator PCI version 9.0, Video Logic) using a frame grabber at a sampling rate of 2 Hz. Precise marker coordinates on a Cartesian coordinate plane were obtained using an image processing and analysis software (ImageTool version 2.00; http://ddsdx.uthscsa.edu/dig/iditesc.html). Changes in muscle length were computed from the markers’ coordinates.

**Computation of two-dimensional strains.** The strains in the plane of the IO, TA, and internal abdominal muscle composite were computed by the following procedure. The square region is divided into triangles with markers at each apex. In the unstressed plane of the tissue, coordinates of these points are denoted $x_i$ and $y_i$ ($i = 1, 2$). The displacements in the local coordinate system of the markers from their reference positions to their positions at a deformed state are denoted by $u_i$ and $v_i$. These are assumed to be a linear function of position in the plane of the triangle and they are computed as follows:

$$u_i = a_1 x_i + a_2 y_i + a_3$$

$$v_i = a_4 x_i + a_5 y_i + a_6$$

This equation with known values of the displacements and the position of three markers substituted for $u_i$, $x_i$, and $y_i$ provides a set of three equations for the three coefficients: $a_1$, $a_2$, and $a_3$. Similarly, the data provide the information required for determining the coefficients ($a_4$, $a_5$, and $a_6$) in the following equation:

$$v_i = a_1 x_i + a_2 y_i + a_3$$

The values of the coefficients $a_1$, $a_2$, etc. were used to find the partial derivatives, which were substituted into the following equations:

$$\varepsilon_x = \delta u/\delta x$$

$$\varepsilon_y = \delta v/\delta y$$

$$\varepsilon_{xy} = \delta u/\delta y + \delta v/\delta x$$

where $\delta u$ and $\delta v$ denote the marker’s displacement in the $x$ (AF) and $y$ (TF) directions, respectively, defined to calculate strains. The strains $\varepsilon_x$ and $\varepsilon_y$ are computed for each triangle. $\varepsilon_{xy}$ is in the direction of muscle fibers, whereas $\varepsilon_{xy}$ is in the TF direction.

$$\lambda = 1 + \varepsilon$$

where $\lambda$ is the extension ratio and $\varepsilon$ is strain in either the AF or TF direction. $\varepsilon$ is computed for the IO, TA, and internal abdominal muscle composite.

**Compliance and compliance ratio.** Compliance is defined as the ratio of mechanical strain to mechanical stress. Compliance ratio (CR) was computed as the ratio of mechanical strain in the TF in response to an applied mechanical stress (e.g., $S_{TF}$) to mechanical strain in the AF in response to the same applied stress $S_{AF}$. For example, for the TA, at a specific mechanical stress, $S_{TF}$ (10% of maximal tetanic stress), mechanical strain in the TF was 0.35 whereas mechanical strain in the
longitudinal fiber direction was 0.58. Therefore, CR was computed as 
\( \frac{0.35/S1}{(0.58/S1)} = 0.6 \).

Statistical analysis. Differences between groups were assessed by ANOVA with use of the SAS Procedure “Mixed” Program. The model was a two-factor fixed or random effects model for three groups of tissue (IO vs. TA; IO vs. composite IO; TA vs. composite TA) and two treatments (passive mechanics: uniaxial stretch along the muscle fibers vs. uniaxial stretch transverse to fibers; type of loading: uniaxial loading vs. biaxial loading). A \( P \) value of 0.05 was chosen as the acceptable level of significance throughout the analysis of all data.

RESULTS

Representative length-tension relationships for the TA as a single muscle layer passive lengthened uniaxially are shown in Fig. 1A. We computed the \( \lambda \) at a tension of 10% of maximal tetanic stress and found \( \lambda \) to be 1.35 and 1.58 in the TF and AF, respectively, yielding a CR of 0.6. The \( \lambda \) at a tension of 30% of maximal tetanic stress and found \( \lambda \) to be 1.44 and 2.02 in the TF and AF, respectively, yielding a CR of 0.43. Representative length-tension relationships for the TA as a single muscle layer are shown in Fig. 1A. The TA was passively lengthened uniaxially either along the muscle fibers or transverse to the fibers. We computed \( \lambda \) at a tension of 10% of maximal tetanic stress and found \( \lambda \) to be 1.25 and 1.51 in the TF and AF, respectively, yielding a CR of 0.49. We computed \( \lambda \) at a tension of 30% of maximal tetanic stress was found to be 1.38 and 1.6 in the TF and AF, respectively, yielding a CR of 0.63. Passively lengthened either uniaxially or biaxially, TA muscle demonstrates an anisotropic behavior with greater compliance in the AF than in the TF (uniaxial loading: TA: CR = 0.65 \pm 0.04; \( P < 0.05 \); biaxial loading: TA: CR = 0.64 \pm 0.03, \( P < 0.05 \)). Although both length-tension curves are shifted to the left during biaxial passive lengthening, indicating decreased muscle extensibility, the difference in extensibility between AF and TF becomes less pronounced compared with uniaxial passive lengthening. Furthermore, during uniaxial passive lengthening along the muscle fibers, the muscle exhibited hysteresis. That is, at the same tension, the muscle exhibited lower mechanical strain on lengthening than on shortening. Simultaneous mechanical loading in the AF and TF (biaxial loading) appeared to diminish this hysteresis.

Representative length-tension relationships for the uniaxial passively lengthened IO are shown in Fig 2. We computed \( \lambda \) at a tension of 10% of maximal tetanic stress and found it to be 1.19 and 1.52 in the TF and AF, respectively, yielding a CR of 0.37. We computed \( \lambda \) at a tension of 30% of maximal tetanic stress and was found to be 1.36 and 1.82 in the TF and AF, respectively, yielding a CR of 0.44. Similar to TA, the IO also demonstrates anisotropic behavior with less compliance in the TF than in the AF (IO: CR = 0.45 \pm 0.04; \( P < 0.05 \)). However, these data suggest that the TA is more compliant than the IO (TA: CR = 0.65 \pm 0.04; \( P < 0.05 \) vs. IO: CR = 0.45 \pm 0.04; \( P < 0.05 \)). Furthermore, in both AF and TF, the IO has a greater amount of hysteresis in response to uniaxial passive lengthening and passive shortening.

Representative length-tension relationships for the entire internal abdominal muscle composite including both the IO and TA are shown in Fig. 3. This internal abdominal composite muscle was mechanically tested intact as in vivo. We passively stretched the composite tissue either uniaxially in the AF of the IO muscle sheet or uniaxially in the TF of the IO muscle sheet.

Fig. 1. A: representative data set of length-tension relationships for the transversus abdominis as a single muscle layer that is passively lengthened and shortened uniaxially either along the muscle fibers or transverse to the fibers. The muscle illustrates an anisotropic behavior. Extensibility in the direction transverse to the fiber is significantly less than that along the fiber. For example, in the range of 25 to 45% of the maximal tetanic stress, the transversus abdominis passively lengthens along the fibers from 1.95 to 2.1 times the unstressed length compared with 1.42 to 1.5 times in transverse passive lengthening. Furthermore, at a muscle length of \( >130\% \) of unstressed length, compliance ratio (CR) is smaller in the direction transverse to the fiber than in the direction along the fiber. For example, at stress of \( \sim 10\% \) of maximal tetanic stress, CR is \( 0.35/0.58 \), whereas at stress of \( \sim 30\% \) of maximal tetanic stress, CR is \( 0.44/0.12 \). The TA muscle is therefore much less compliant in the transverse fiber direction than in the direction along the fiber. The amount of hysteresis appears to be greater along the fibers, whereas transverse to the fibers there is essentially no hysteresis. B: representative data set of length-tension relationships for the transversus abdominis as a single muscle sheet that is passively lengthened and shortened simultaneously biaxially along and transverse to the muscle fibers. The muscle sheet is simultaneously stretched in the direction of the muscle fibers and transverse to the fibers. The muscle illustrates anisotropy: the muscle is more extensible in the along-fiber direction than in the transverse direction to the muscle fibers. Compared with uniaxial passive lengthening, compliance of the muscle along the fiber direction is decreased during biaxial mechanical loading. For example, in the muscle fiber direction and during biaxial loading at stress of \( \sim 30\% \) of maximal tetanic stress, muscle extensibility was \( \sim 1.6 \), whereas the muscle sheet’s extensibility in the fiber direction reached \( \sim 2.0 \). In the transverse direction, the extensibility of the muscle was 1.58, whereas the muscle sheet’s extensibility in the same direction reached \( \sim 1.44 \) during uniaxial loading. At a stress of \( \sim 10\% \) of maximal tetanic stress, CR is \( 0.25/0.51 \), whereas at stress of \( \sim 30\% \) of maximal tetanic stress CR is \( 0.38/0.6 \). However, the compliance is nearly isotropic in the range of 30 to 65% of the maximal tetanic stress. It appears that the amount of hysteresis along the fiber orientation is reduced during biaxial loading compared with uniaxial loading data shown in A.
At a tension of 10% of maximal tetanic stress, muscle length as a fraction of unstressed length in the direction of the IO muscle fibers was 1.33 and 1.16 in the TF and AF of the IO muscle fiber direction, respectively, yielding a CR of 2.06. At a tension of 30% of maximal tetanic stress, muscle length as a fraction of unstressed length in the direction of the IO muscle fibers is 1.42 and 1.50 in the TF and AF of the IO muscle fiber direction, respectively, yielding a CR of 0.84. The internal abdominal composite muscle exhibits an anisotropic behavior with greater compliance in the AF than in the TF of the IO (CR = 0.83 ± 0.06; P < 0.05). This composite tissue also demonstrates more hysteresis in the TF of the IO than in the AF of the IO.

Representative length-tension relationships for the entire internal abdominal muscle composite including both the IO and TA are shown in Fig. 4A. This internal abdominal composite muscle was mechanically tested intact as in vivo. We passively stretched the entire composite muscle uniaxially in either the AF and TF of the TA muscle. We computed λ at a tension of 10% of maximal tetanic stress and found it to be 1.42 and 1.5 in the TF and AF, respectively, yielding a CR of 1.05. The λ at a tension of 30% of maximal tetanic stress and was found to be 1.6 and 1.78 in the TF and AF, respectively, yielding a CR of 0.77. The internal abdominal composite muscle exhibits an anisotropic behavior with greater compliance in the AF than that in the TF of the IO (CR = 0.76 ± 0.04; P < 0.05). In contrast to TA as a single muscle layer, biaxial passive lengthening does not appear to decrease extensibility of the TA/IO internal abdominal composite muscle. The internal abdominal composite muscle shows hysteresis in the AF of the TA but not in the TF of the TA. In contrast to TA as a single muscle layer, biaxial passive lengthening of the internal abdominal composite muscle did not decrease the amount of hysteresis in either direction compared with that of uniaxial passive mechanical lengthening.

**DISCUSSION**

In this study, we found that the TA and the IO muscles form an internal abdominal composite muscle that is less compliant than either muscle alone in the AF, but it is more compliant in the TF. Furthermore, we found that anisotropy of the internal abdominal muscles as a composite muscle is less pronounced than that of the individual muscles. In addition to anisotropy of the internal abdominal muscles, the other major findings of this study include the observation that the abdominal muscle composite is less compliant than either muscle alone in the AF, but it is more compliant in the TF. Both TA and IO muscles demonstrated a smaller compliance in the TF than in the AF. The data are consistent with the existence of myofascial force transmission between IO and TA.
Compliance and extensibility of the TA compared with the IO muscle. Under uniaxial passive lengthening, the TA demonstrates greater compliance in both the TF and AF compared with the IO. To understand this difference in compliance, one must understand morphology of the IO and TA as well as the extracellular matrix. Composed of muscle fibers held together by connective tissue, skeletal muscle has mechanical properties dependent on the contribution of both the fibers and connective tissue (19). The abdominal muscles are arranged in multiple layers, each with unique fiber architecture dictating the mechanical properties of the muscle. We previously found that essentially none of the TA muscle fibers span the entire length of the muscle, whereas the IO consists of 90% nonspanning and 10% spanning muscle fibers (3). The nonspanning fibers are tapered at one or both ends of the fiber to a very fine strand, and force transmission within each layer of the muscle is therefore expected to be essentially in shear. Loeb et al. (12) raised an interesting point that if the individual fibers insert diffusely into an epimysial extracellular matrix, then the extracellular series elasticity in the muscle can change the distribution of stretch within the muscle. This would result in increased compliance because it makes possible the sliding of discontinuous muscle fibers with respect to each other. This mechanism may explain the contribution of discontinuous fiber architecture to increased compliance of TA compared with IO.

Compliance and extensibility of the individual IO and TA muscles compared with the composite muscle. The measured length-tension relationships of the IO, TA, and the two muscles together as an internal abdominal composite muscle showed that, in the AF, the composite muscle of the IO and TA muscles is less extensible than either the IO or TA muscle alone. That is, the length-tension relationship of the internal abdominal composite muscle in the AF was shifted to the left compared with either IO or TA individually. In contrast, measured length-tension relationships in the TF demonstrate that the composite muscle of the IO and TA muscles is more extensible than either the IO or TA muscle alone. That is, the length-tension relationship of the internal abdominal composite muscle in the TF was shifted to the right compared with that of IO or TA individually.

As discussed previously, the abdominal muscles are arranged in multiple layers, each with muscle fibers oriented along a different axis from that of the adjacent layer. The IO has muscle fiber orientation at a 45° angle from that of the TA, whereas the EO has muscle fiber orientation at a 90° angle from that of the IO. In the presence of extracellular connective tissue matrix, this arrangement of muscle layers allows for transmission of muscle forces between adjacent muscle layers. Therefore, rather than bearing a transverse stress with increased abdominal pressure during inspiratory activity, the IO or TA can transmit this transverse stress to the adjacent abdominal muscle layer. Compared with single muscle layers, the internal abdominal composite muscle showed both decreased extensibility in the AF and increased extensibility in the TF, and muscle anisotropy was less pronounced in the composite than in the individual muscles. These data are consistent with the presence of myofascial passive force transmission between the IO and TA via the interfascial connective tissue during inspiration (9, 13).

Muscle extensibility in the internal abdominal composite does not appear to be decreased during biaxial loading as it...
does in individual muscle layers of either TA or IO. The internal abdominal composite muscle is less compliant and less extensible compared with either IO or TA muscle alone. Teleologically, the compliance of abdominal musculature must remain within its normal physiological range to permit efficient muscle contraction and muscle relaxation. During inspiration, descent of the diaphragm, lengthening of abdominal wall musculature, and subsequent increase of intra-abdominal pressure occur. Our data demonstrate that biaxial passive lengthening does not decrease compliance of the internal abdominal muscle composite, and preventing such a decrease in compliance avoids elevated intra-abdominal pressure that would oppose descent of the diaphragm. In contrast, during expiration, the abdominal muscles contract, and excessive extensibility could dissipate this pressure work through deformation of the abdominal muscle sheets. In the latter case, the internal abdominal muscle composite’s contribution to decreased extensibility maintains an appropriate level of compliance to generate abdominal pressure. The effect of biaxial passive lengthening on passive mechanical properties of the internal abdominal muscle composite is therefore consistent with its physiological role.

**Anisotropy of internal abdominal composite muscle vs. individual muscle layers.** When activated during expiration, each abdominal muscle contracts along the direction of its muscle fibers to increase abdominal pressure and consequently mechanical stress in both the AF and TF directions. The anisotropic behavior of uniaxial passively lengthened internal abdominal composite muscle is less pronounced than either of the individual muscle layers, and this results from greater extensibility in the TF of the internal abdominal composite muscle than of either the IO or TA. A single muscle layer with excessive extensibility in the TF would tend to expand in the TF as it contracts in the AF and thus dissipate pressure work. However, possible myofascial force transmission in abdominal musculature may prevent such deformation of the individual muscle layers. The nonlinear behaviors in the AF and TF differ greatly, however, between each individual layer. The length-tension relation in the AF is only mildly nonlinear over the sizable range of strains that our data cover, whereas in the TF nonlinear stiffening is more pronounced than in the AF.

**Comparison of internal abdominal muscles vs. diaphragm.** Excessive extensibility in the TF of a single muscle layer such as the diaphragm would allow expansion in the TF as it contracts in the AF and thus dissipate pressure work. Anatomically, fascia tightly binds the IO to the TA, and myofascial force transmission among the layers of abdominal musculature therefore prevents such deformation. A previously published length-tension relationship of the diaphragm (2) shows that at a stress of 2.2 N/cm² (10% maximal tetanic stress for respiratory muscles) in the AF of the diaphragm, a strain of 0.64 occurs. In comparison, at a stress of 2.2 N/cm² in the AF of IO and TA, respective strains of 0.45 and 0.65 occur. These data suggest compliance in the AF of diaphragm similar to that in the AF of the TA but greater than that in the AF of the IO. Unlike the diaphragm in which fibers are arranged in a single muscle layer, the abdominal muscles are arranged in multiple layers, each with unique fiber architecture, as discussed previously.

**Myofascial force transmission between IO and TA.** Our data are consistent with the existence of myofascial force transmission between the IO and TA via the connective tissue network separating the two muscles. In other words, a mechanical linkage exists between the IO and TA, with muscle force generated by the contracting TA readily transmitted directly to the adjacent IO muscle via connective tissue network and vice versa. Furthermore, during inspiratory efforts, a stretched TA muscle may pass passive muscle tension to the IO muscle via the interfascial connective tissue and vice versa. Our data show that the extensibility of the internal abdominal composite muscle to be much less than any of the individual IO or TA muscle layers, consistent with a mechanism of myofascial force transmission between the IO and TA.

In summary, the major finding of this study includes the observation that, in general, the internal abdominal muscles are anisotropic. Both TA and IO muscles demonstrated less extensibility TF than AF. The abdominal muscles are much less extensible during biaxial than uniaxial passive lengthening, particularly AF. Furthermore, the anisotropy of the internal abdominal muscles as composite tissue is less pronounced than the individual muscles during uniaxial passive lengthening. In addition, the internal abdominal composite muscle is less compliant than either muscle alone in the AF direction. Taken together, the data are consistent with the possibility of myofascial force transmission between IO and TA. Mechanical linkage between the IO and TA is responsible at least in part for the decrease in muscle compliance of the internal abdominal muscle compared with either IO or TA.

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