LICENCIATURA EN FISICA MEDICA

BIOFISICA

CAPITULO 5

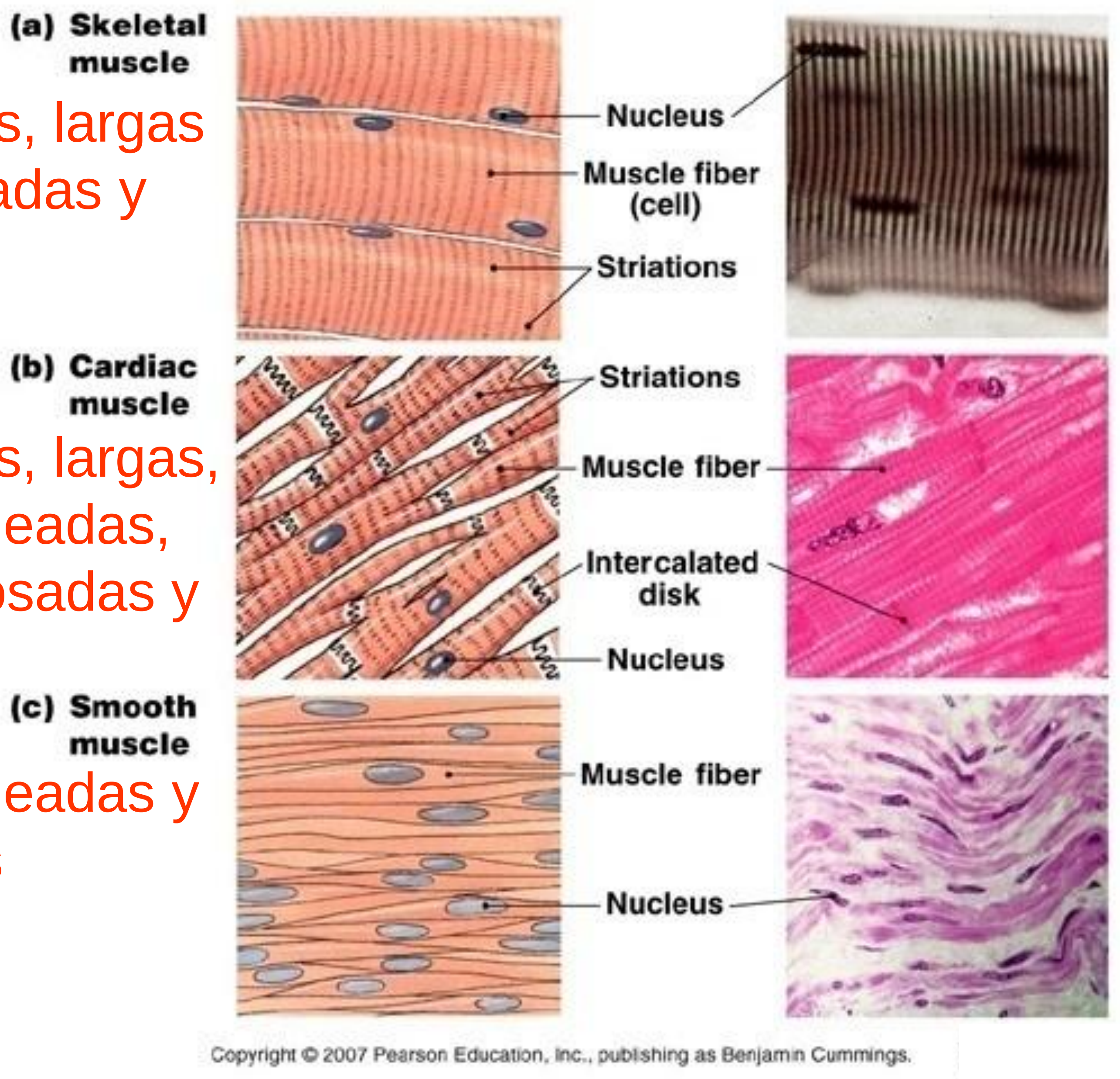
Músculos: Los Motores del Cuerpo Humano. Vistas: Macroscópicas, Microscópicas y Nanoscópicas.

CELULAS DE LOS MUSCULOS I

Células:
Cilíndricas, largas polinucleadas y estriadas.

Cilíndricas, largas, mononucleadas, anastomosadas y estriadas.

Mononucleadas y ahusadas



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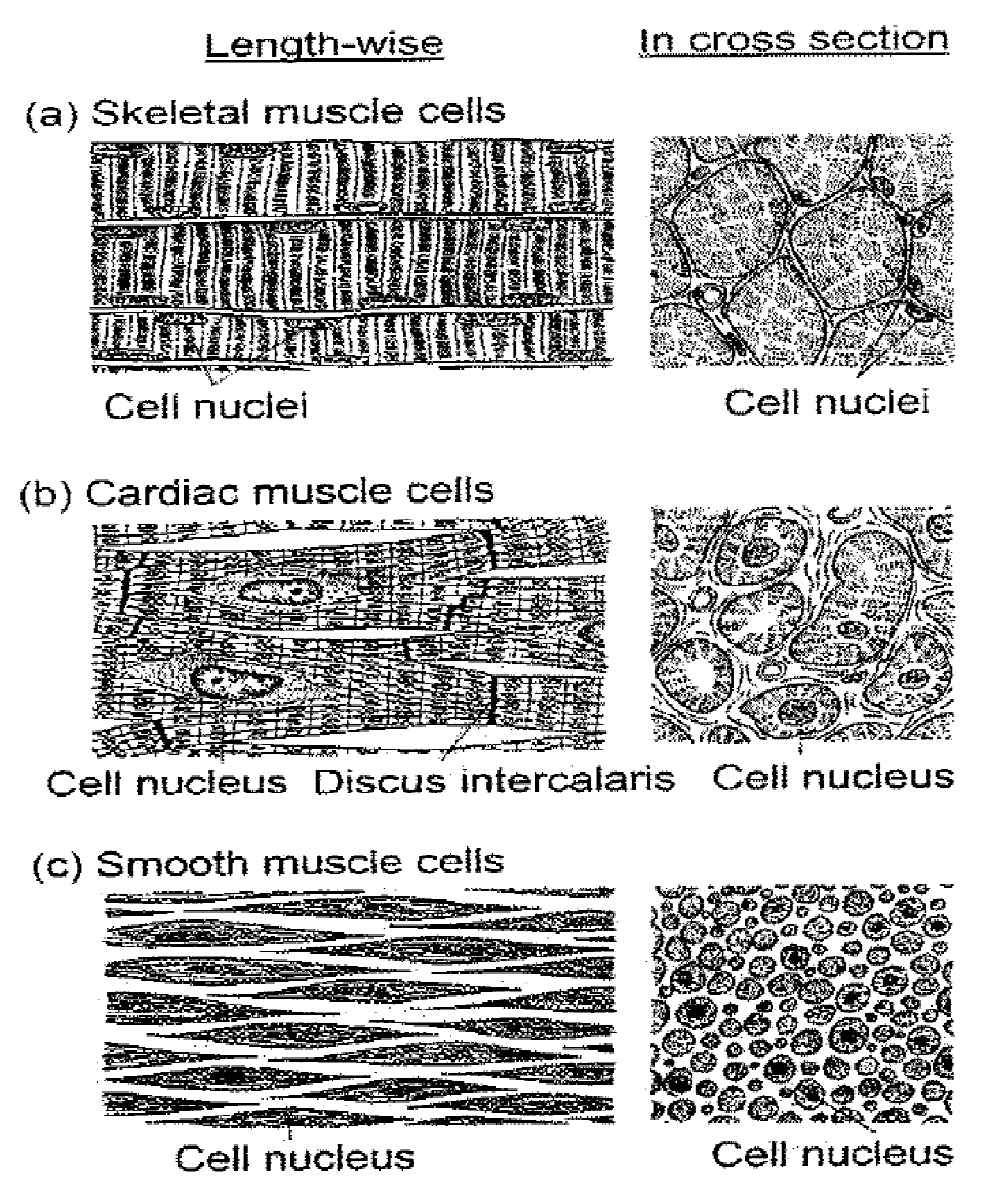
CELULAS DE LOS MUSCULOS II

Cabeza, cuello, tronco, miembros, párpados, ojos. Actúan bajo control consciente, aunque el diafragma durante el hipo no lo hace.

Corazón.
No actúan bajo control consciente.

Adosadas a vasos sanguíneos, y a los sistemas digestivo y urogenital.
No actúan bajo control consciente.



MUSCULOS QUE INTERVIENEN I

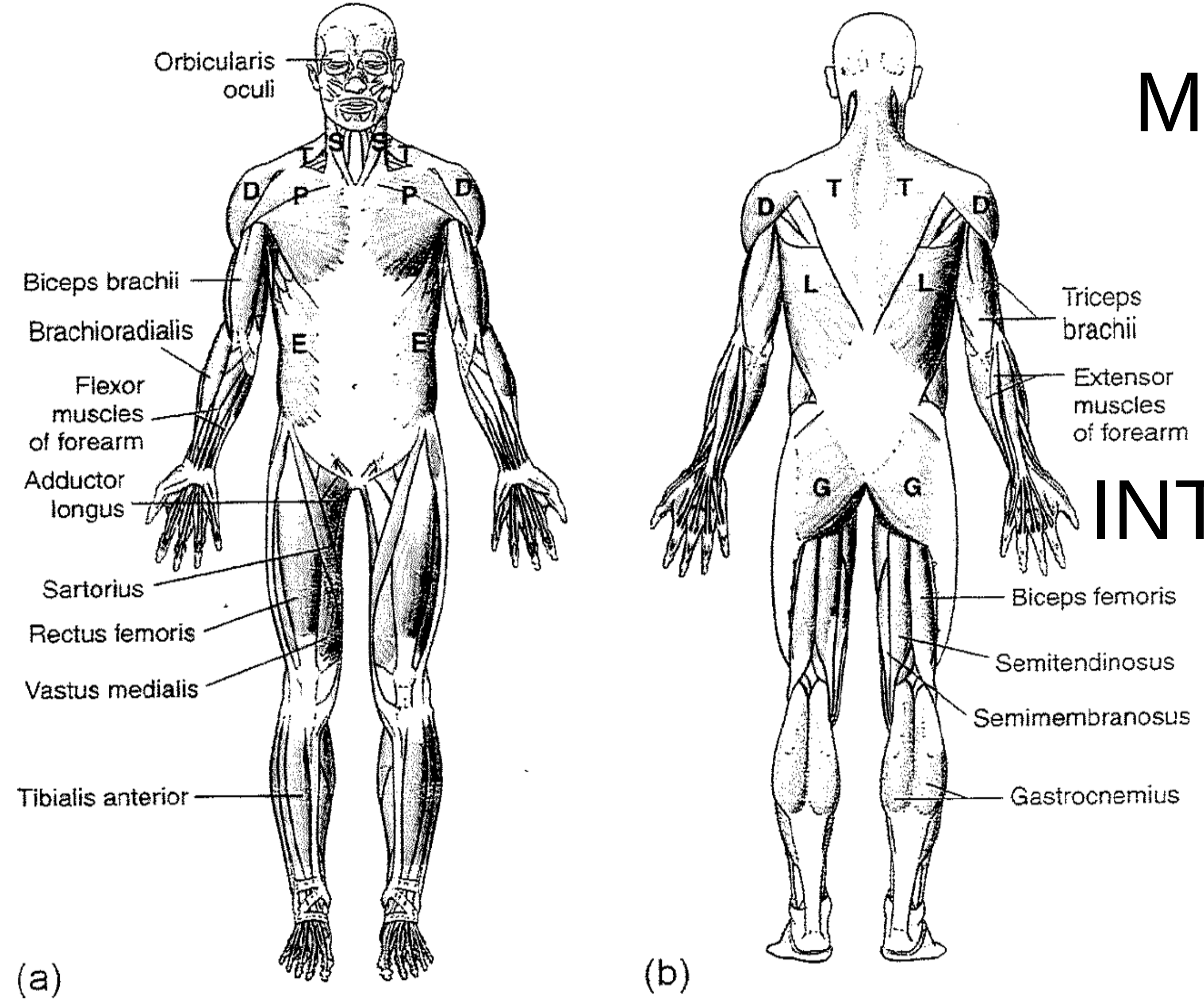


Fig. 1.8. **(a)** Anterior and **(b)** posterior views of some of the larger skeletal muscles in the body. Several muscles are labeled: S, sternocleidomastoid; T, trapezius; D, deltoid;, P, pectoralis major; E, external oblique; L, latissimus dorsi; G, gluteus maximus. In **(b)**, the broad-banded tendon extending from the gastrocnemius and soleus (deep to the gastrocnemius, not shown) muscles to the ankle (calcaneus) is the calcaneal (or Achilles) tendon. (From [49]. Used with permission)

Componen ≈ 43% de la masa corporal. En reposo consumen ≈ 18% de la energía disponible (TMB). Sólo el 25% de esa energía es usada en la acción, el resto, 75%, la liberan como calor.

ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES I

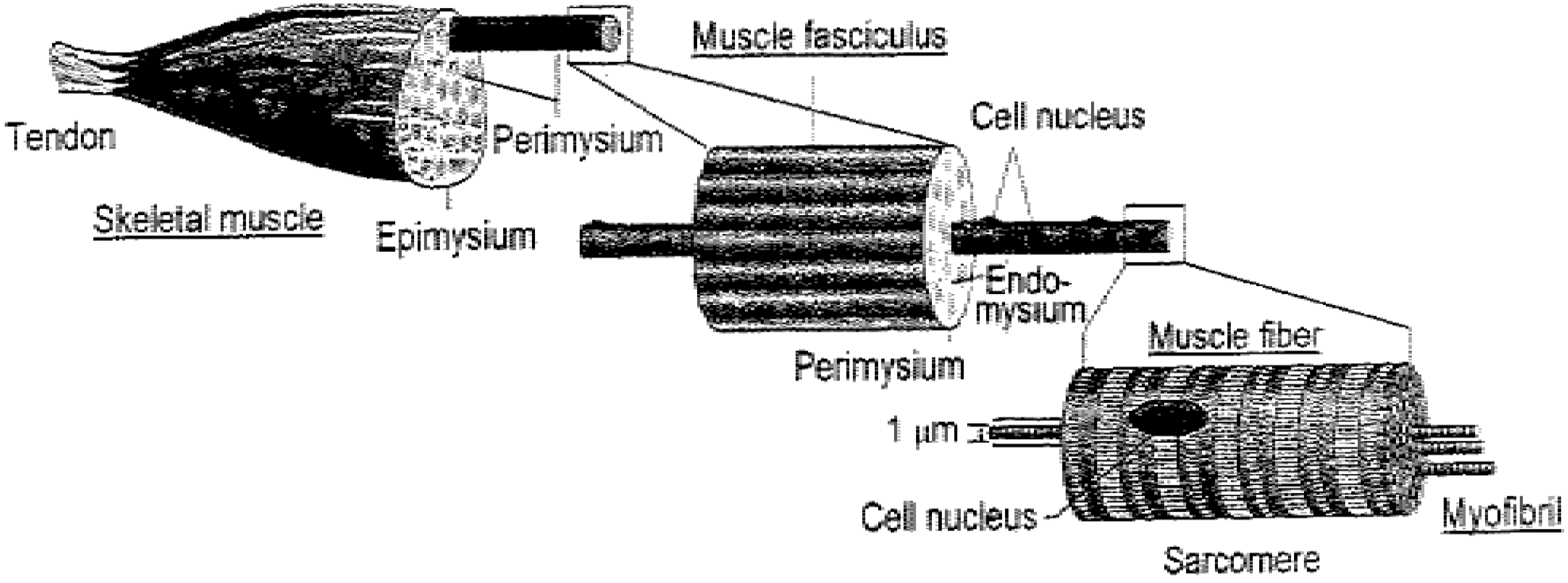
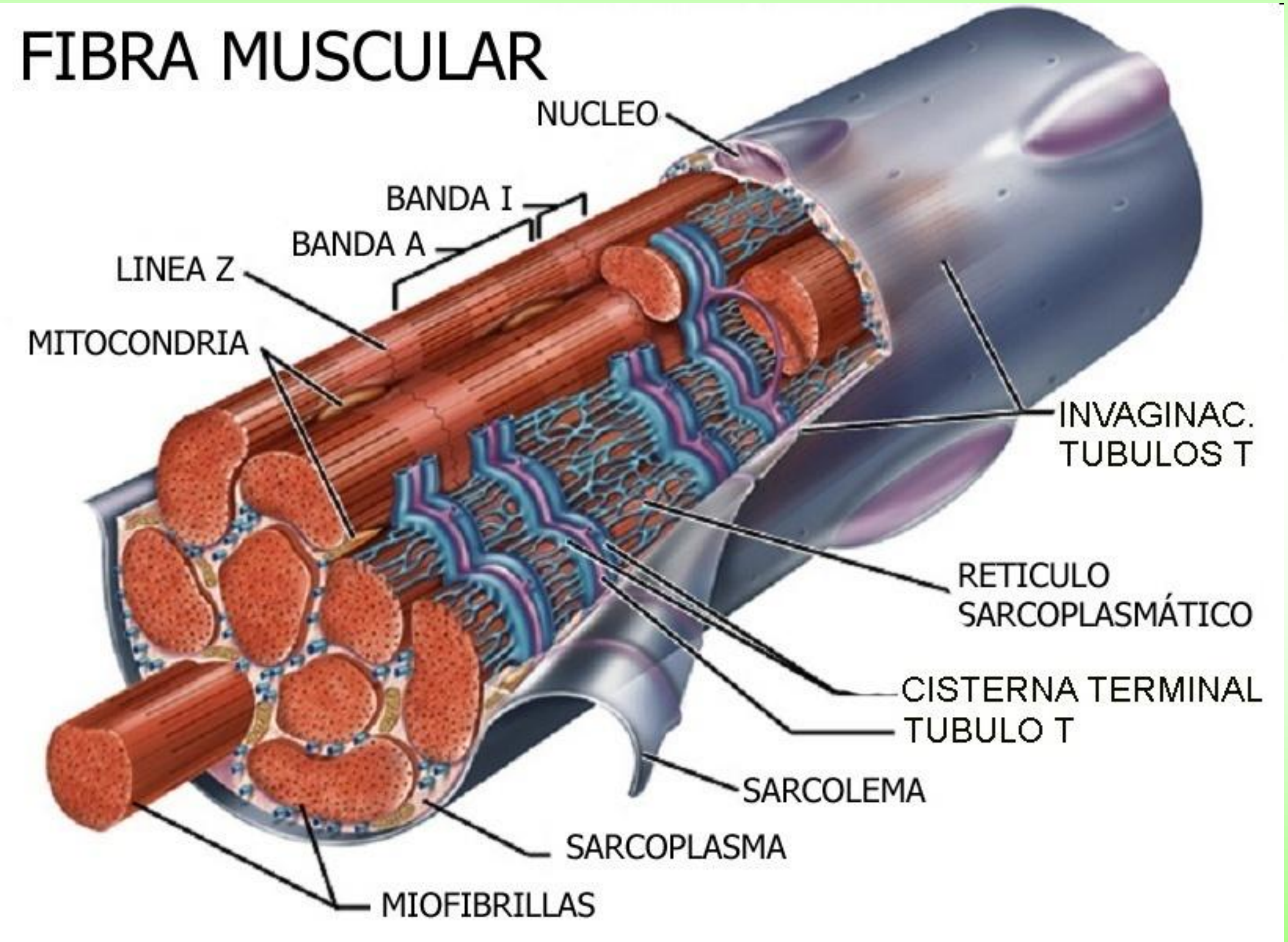
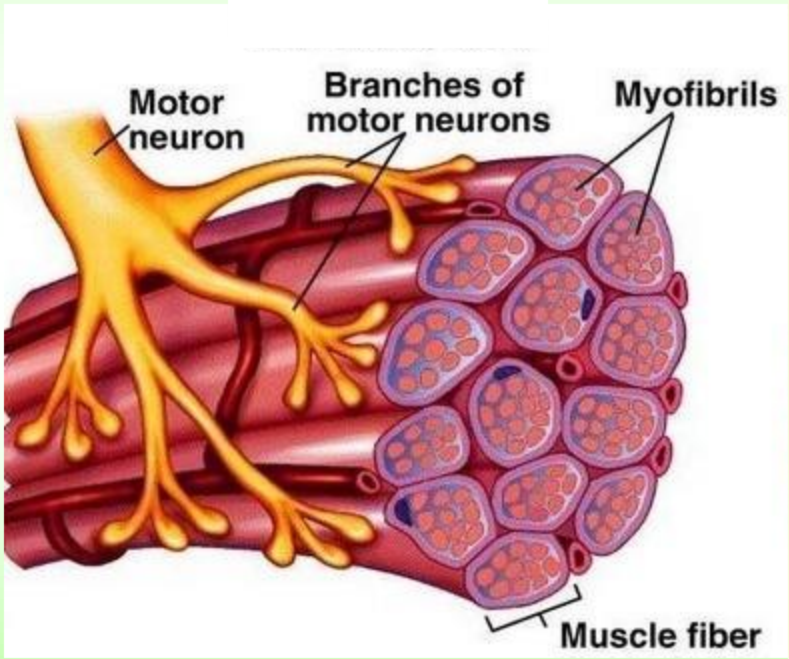


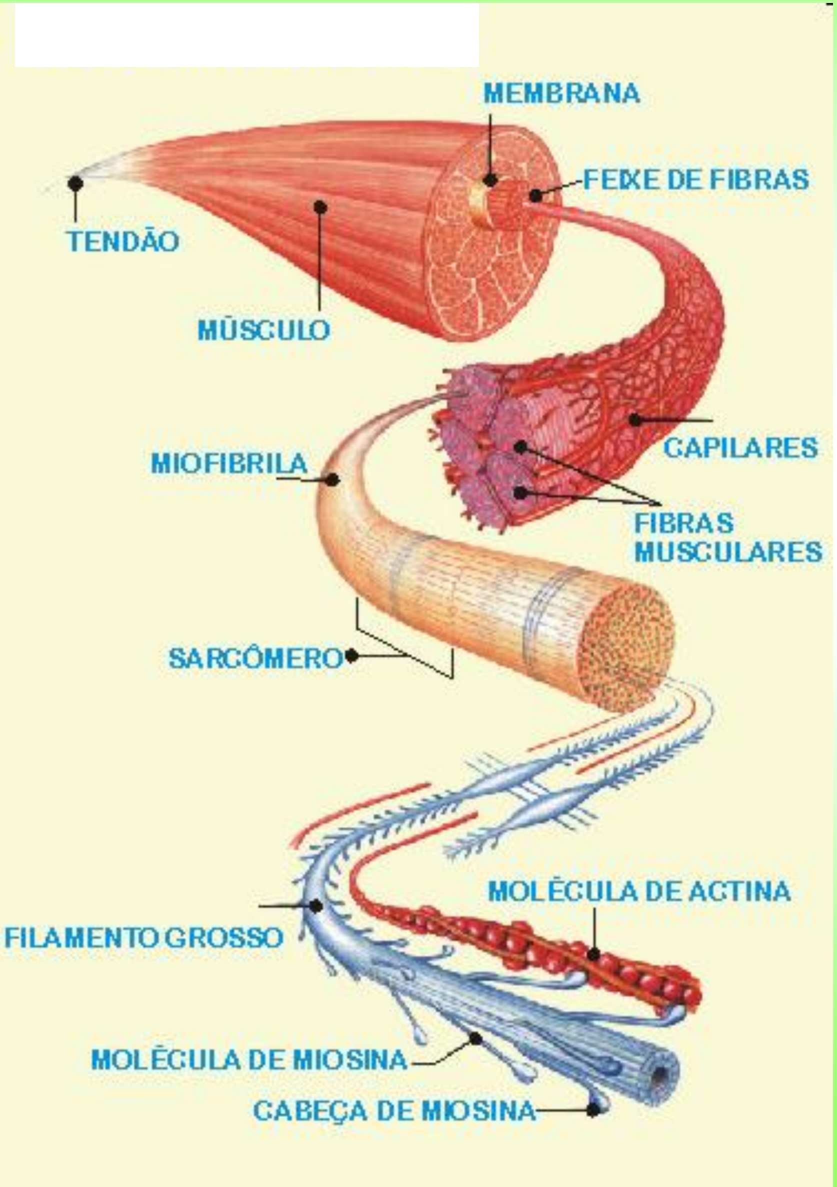
Fig. 5.6. Organization of skeletal muscles, down to the myofibril level. See Fig. 5.7 for the structure of the myofibril. (From [281])

ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES II

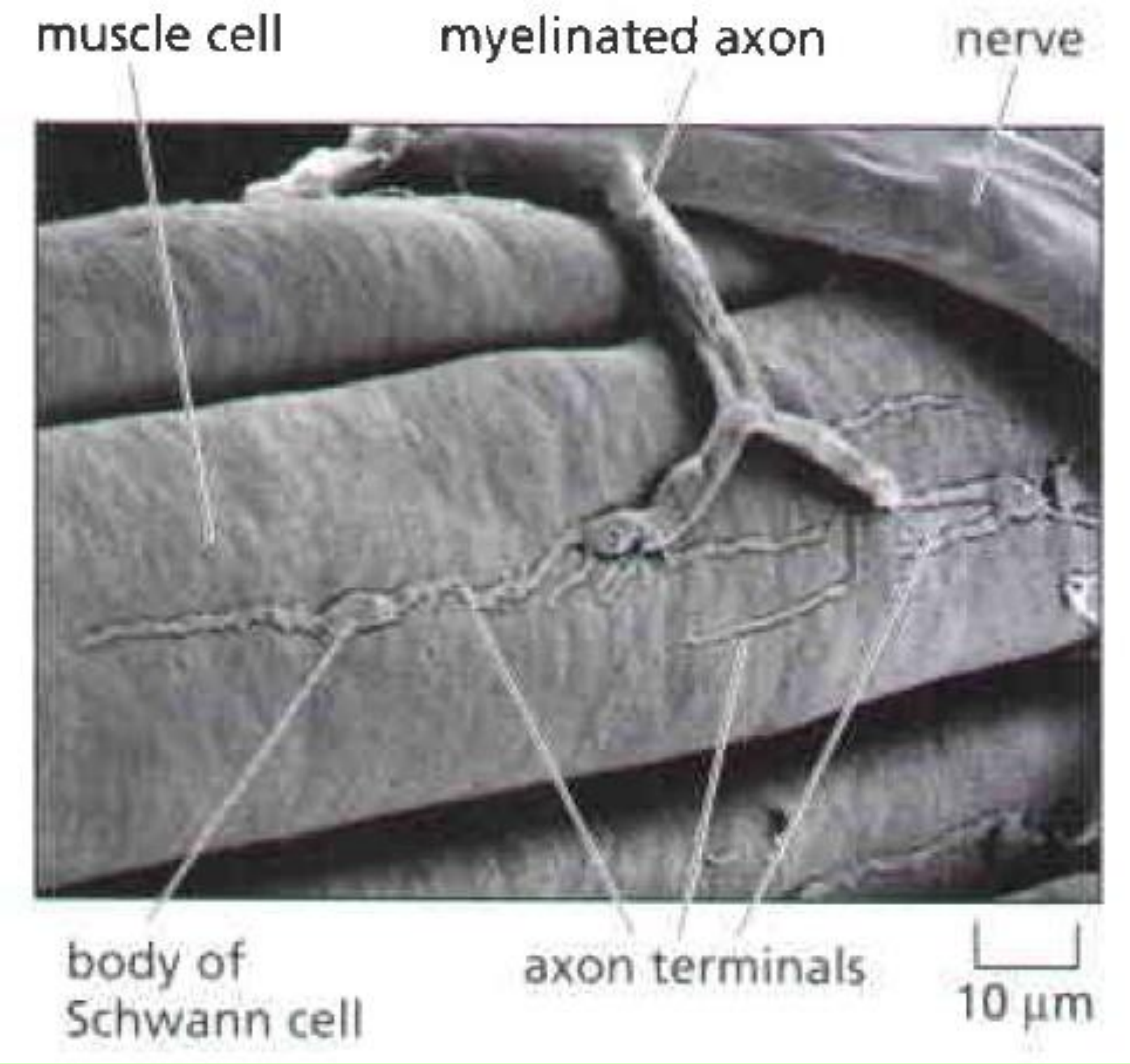


ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES III

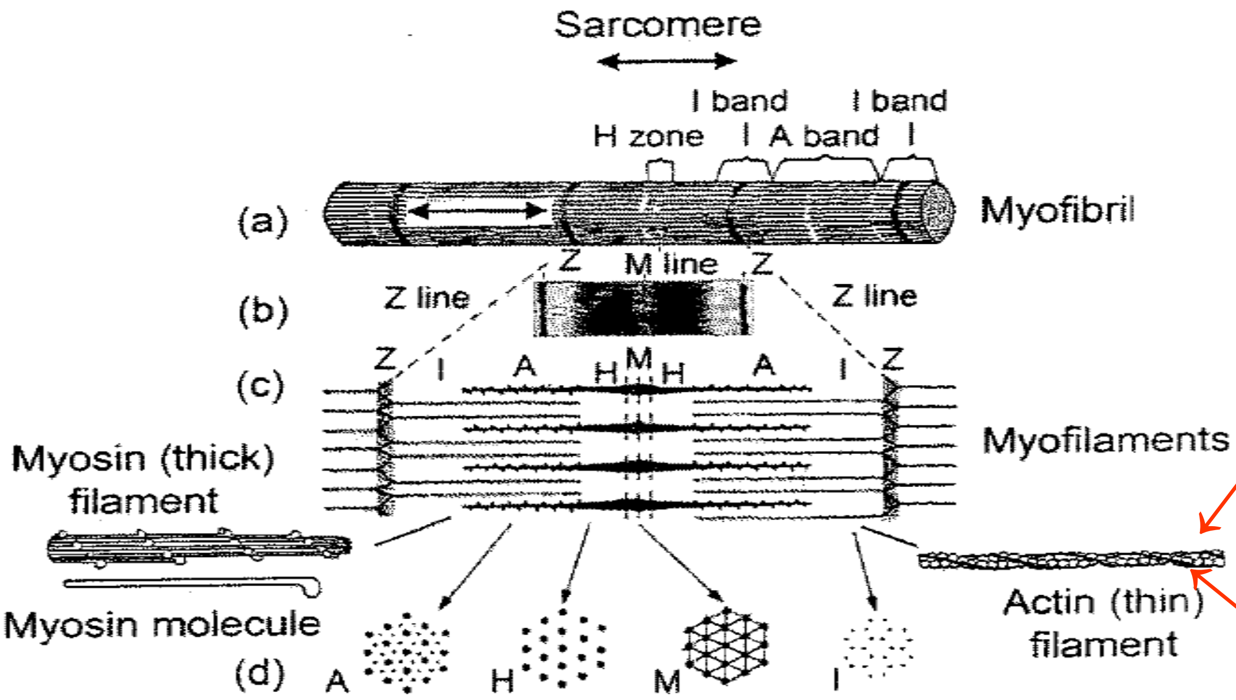




ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES IV



ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES V

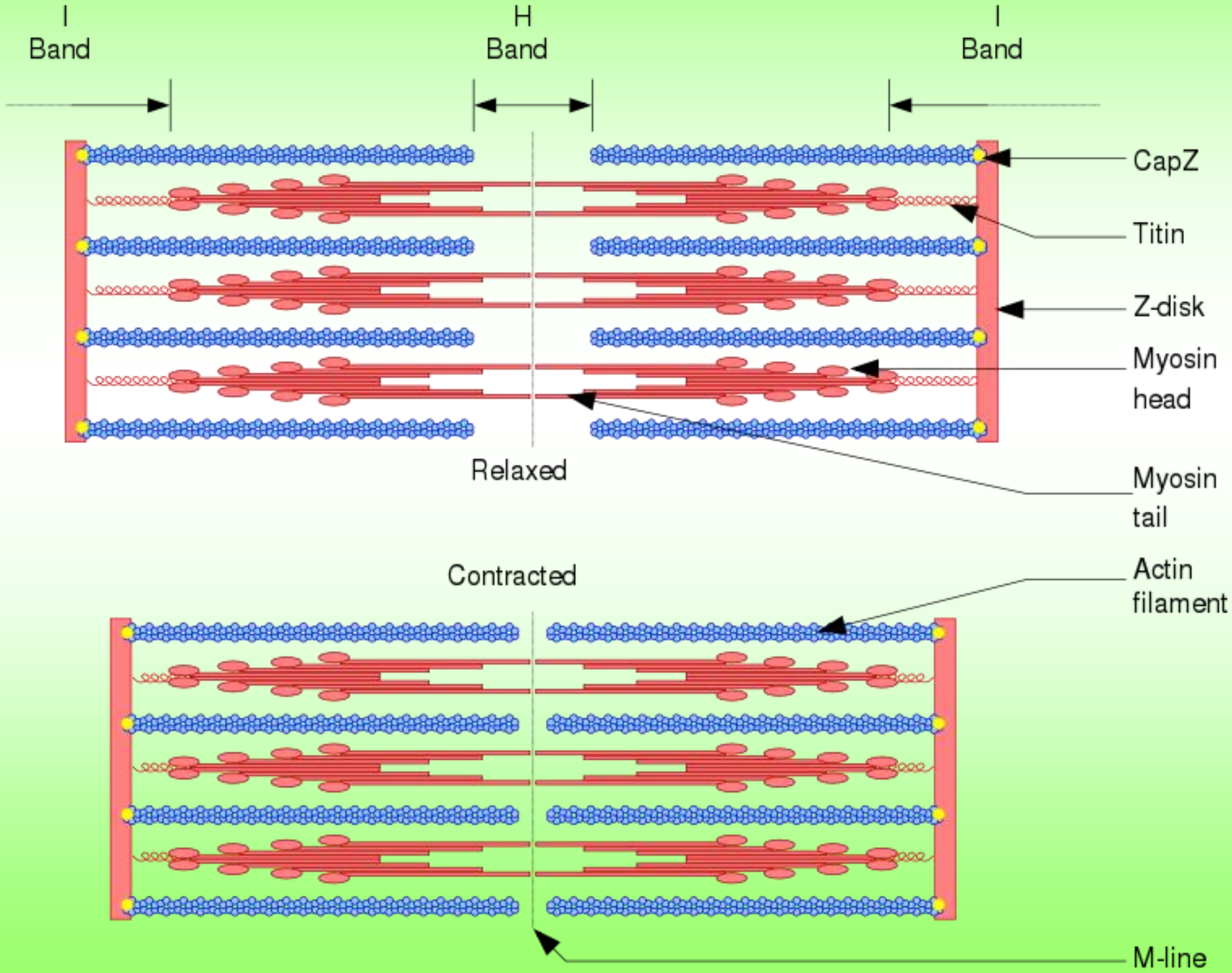


Proteina Tropomiosina enrollada sobre el filamento.

ProteinaTroponina periódicamente localizada

Fig. 5.7. **(a)** Structure and substructure of the myofibril shown in Fig. 5.6, with the banded structure of sarcomeres (whose periodicity is denoted by the arrows). **(b)** The scanning electron micrograph of skeletal muscle shows the structure of bands and lines in sarcomeres. This is associated with the thick and thin filaments in **(c)** from the longitudinal perspective of **(a)** and **(b)**, the transverse cross-section is seen in **(d)**. (From [280])

ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES VI



CANTIDAD DE FIBRAS MUSCULARES EN ALGUNOS MUSCULOS HUMANOS

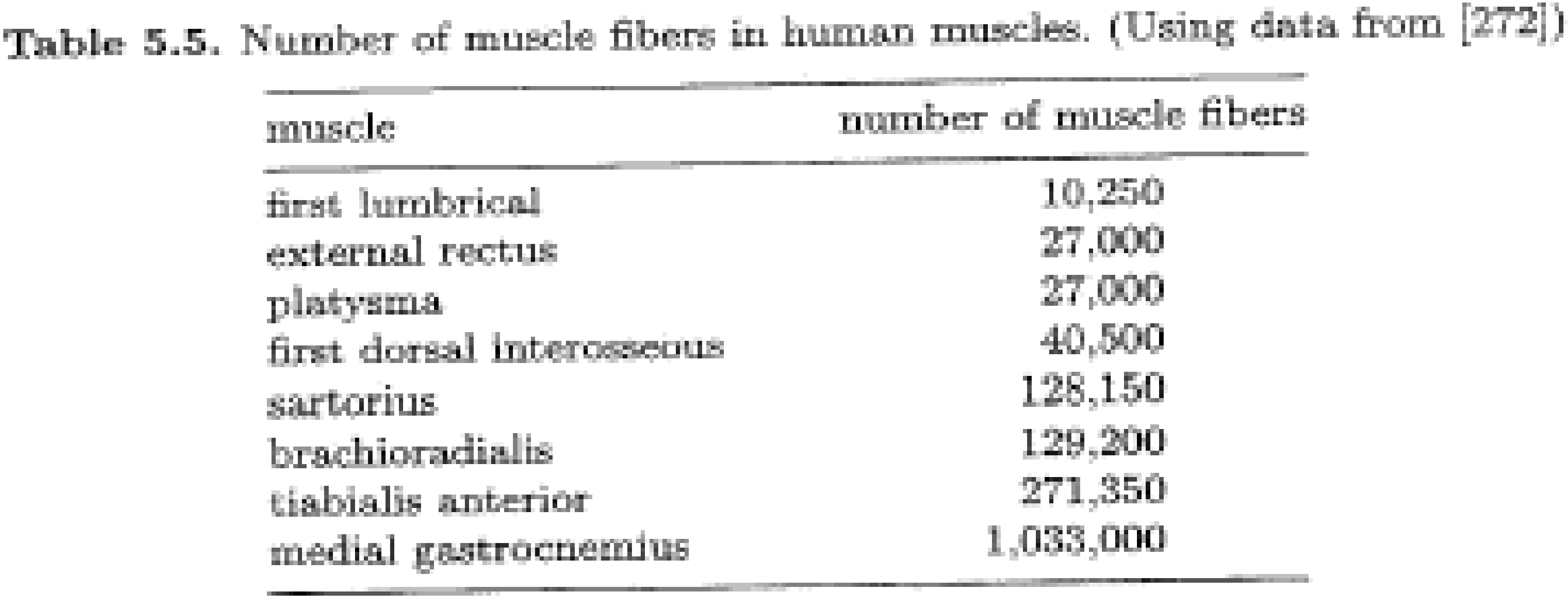
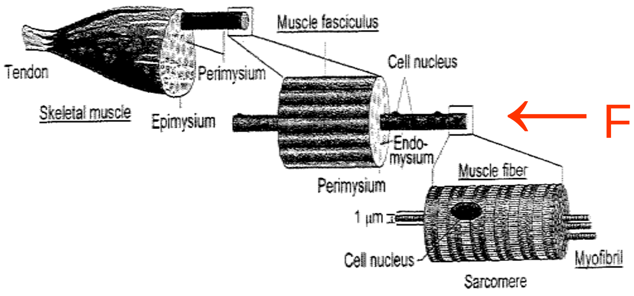


Table 5.5. Number of muscle fibers in human muscles. (Using data from [272])

muscle	number of muscle fibers
first lumbrical	10,250
external rectus	27,000
platysma	27,000
first dorsal interosseous	40,500
sartorius	128,150
brachioradialis	129,200
tiabialis anterior	271,350
medial gastrocnemius	1,033,000



← Fibra muscular

Fig. 5.6. Organization of skeletal muscles, down to the myofibril level. See Fig. 5.7 for the structure of the myofibril. (From [281])

CANTIDAD DE SARCOMEROS EN ALGUNOS MUSCULOS HUMANOS

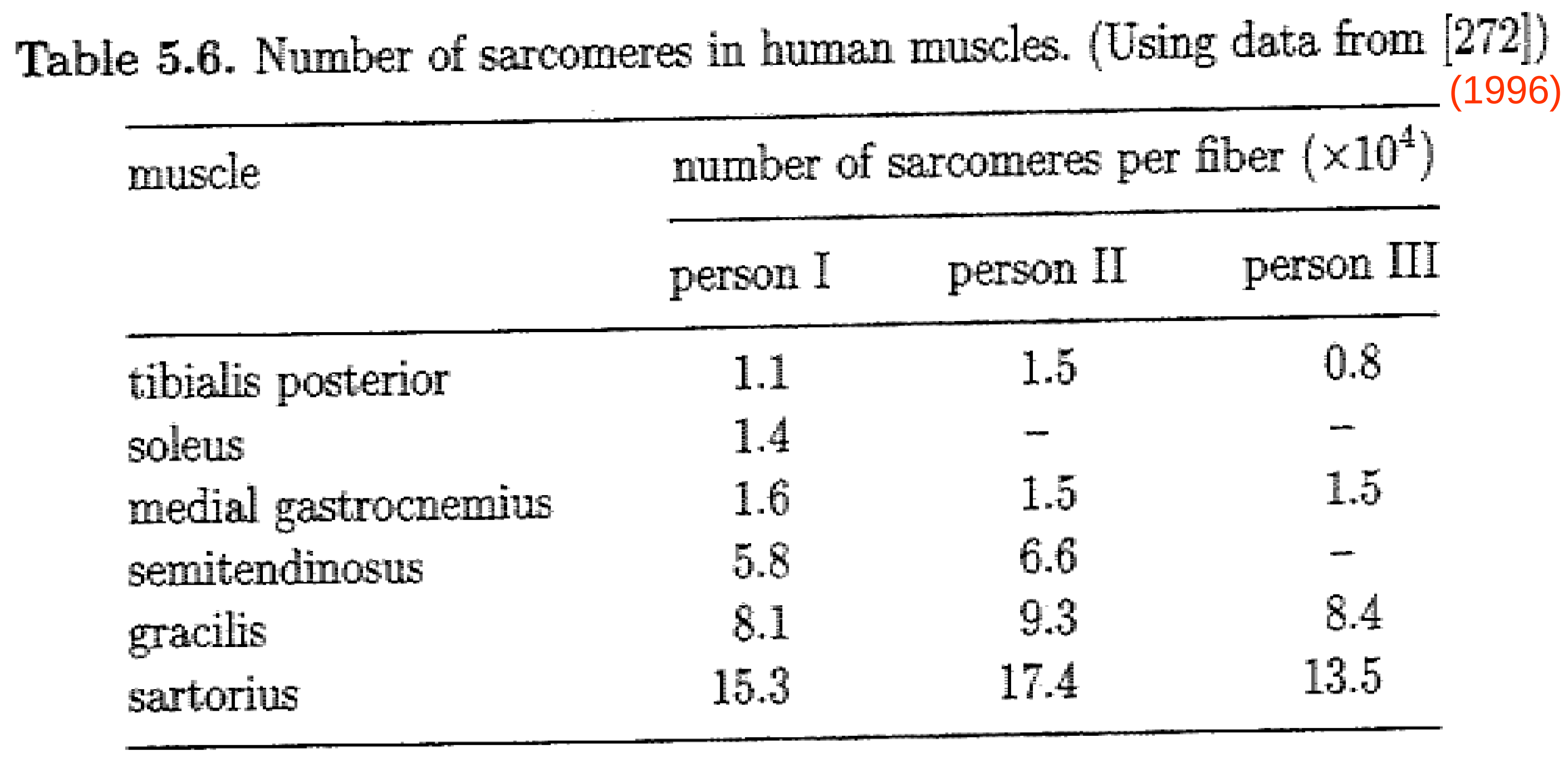
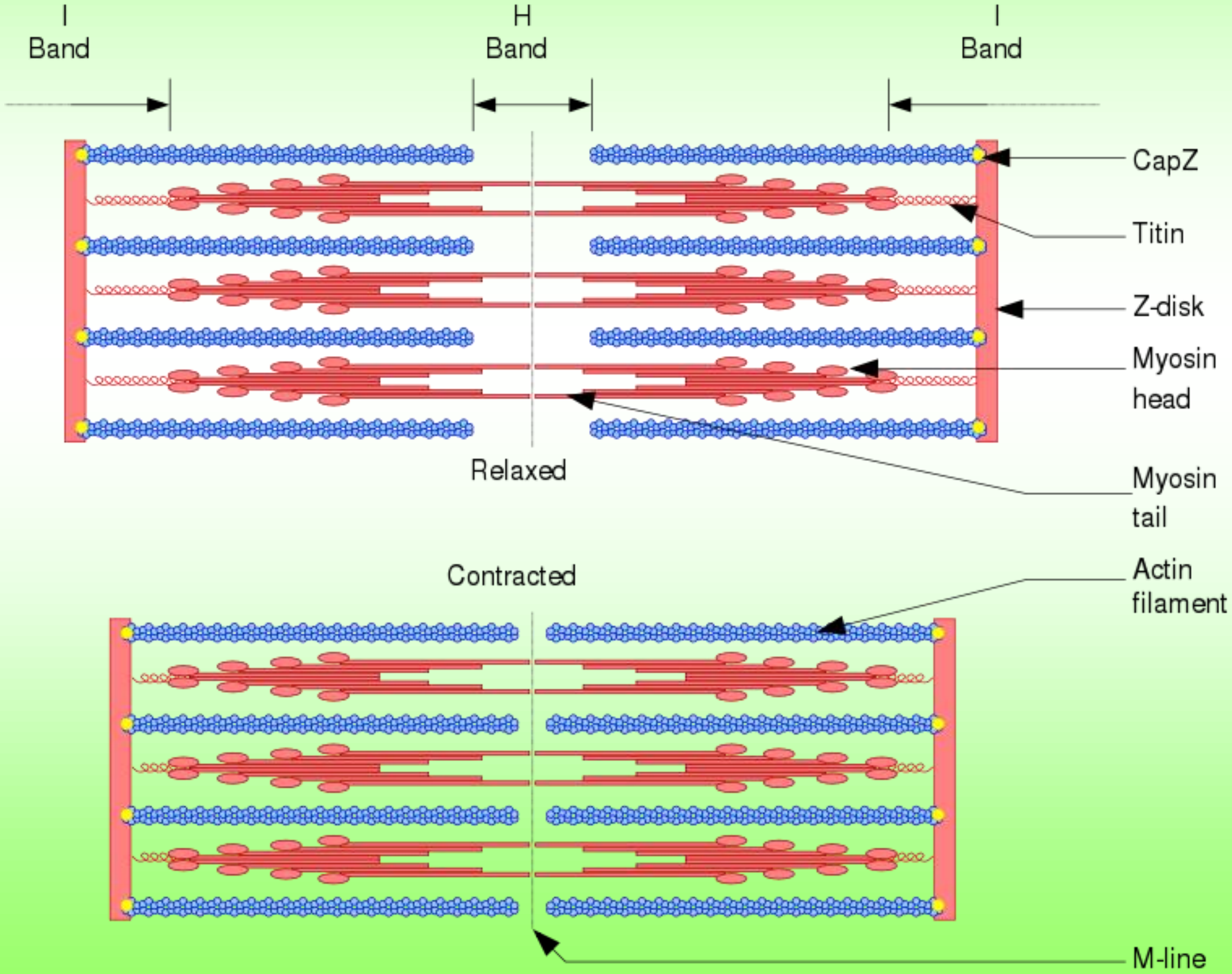


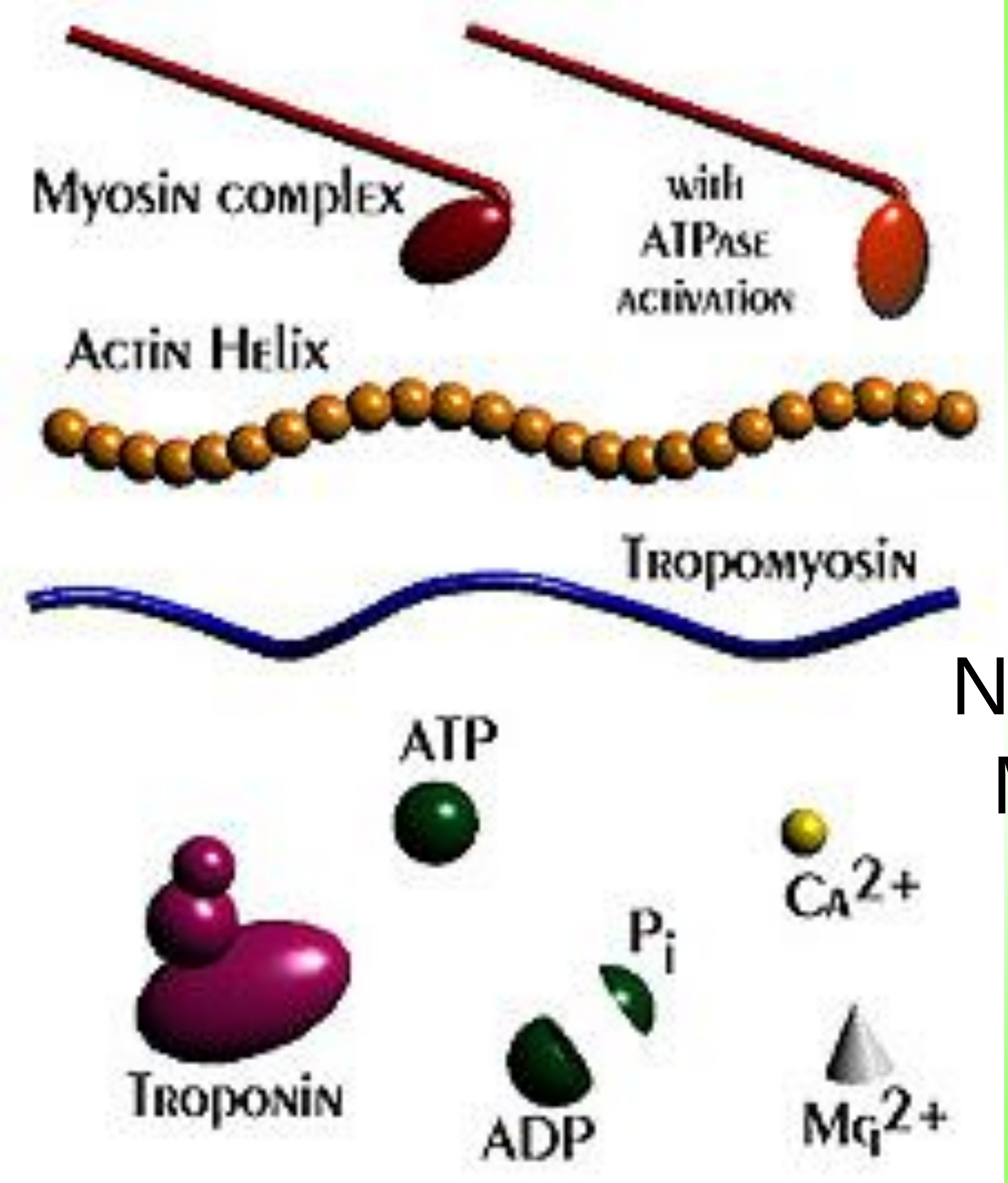
Table 5.6. Number of sarcomeres in human muscles. (Using data from [272])

(1996)

muscle	number of sarcomeres per fiber ($\times 10^4$)		
	person I	person II	person III
tibialis posterior	1.1	1.5	0.8
soleus	1.4	–	–
medial gastrocnemius	1.6	1.5	1.5
semitendinosus	5.8	6.6	–
gracilis	8.1	9.3	8.4
sartorius	15.3	17.4	13.5

FILAMENTOS DESLIZANTES DE MIOSINA Y ACTINA Y RESORTES DE TITINA EN LOS SARCOMEROS





IONES Y MOLECULAS EN LOS NANOMOTORES MUSCULARES

NANOMOTORES MUSCULARES A FILAMENTOS DESLIZANTES I

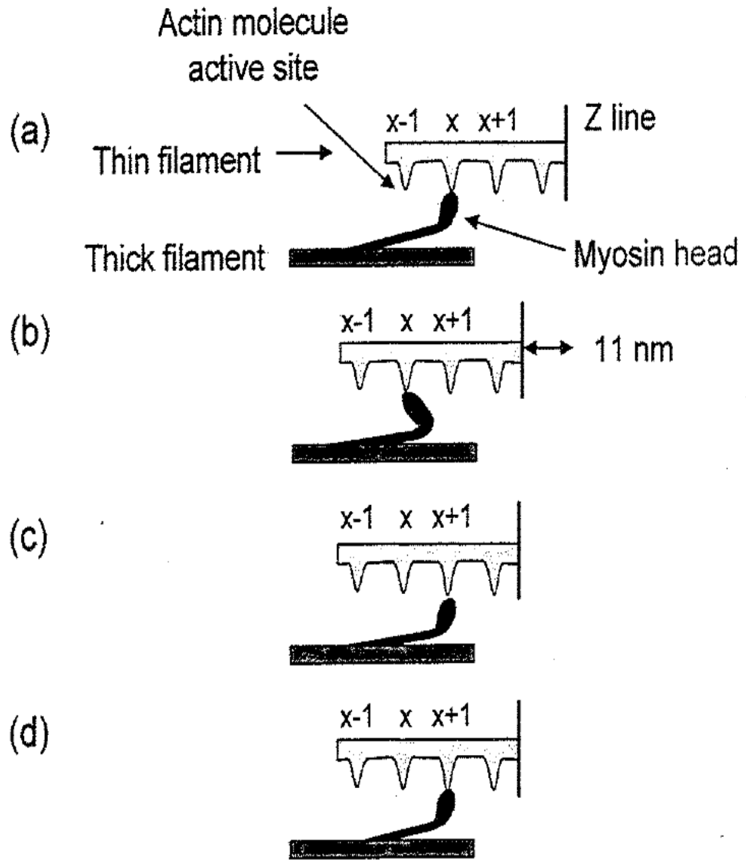
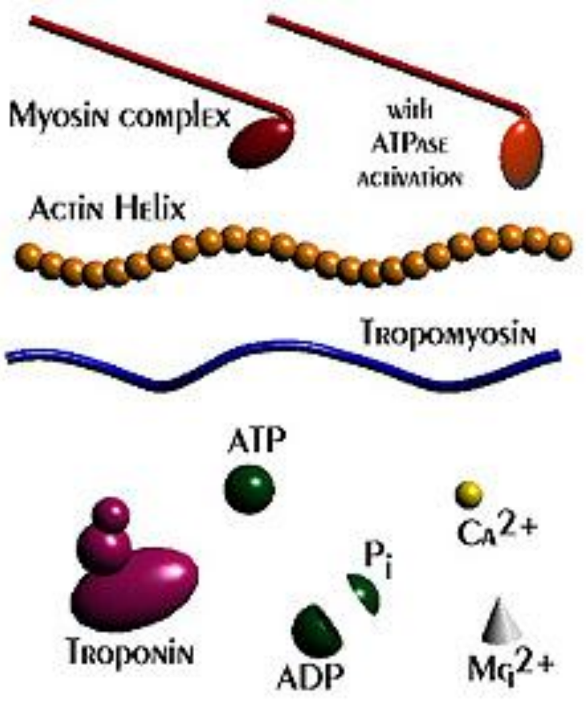


Fig. 5.34. Sliding of myofilaments, with **(a)** binding of the myosin head to an active actin site (site x), **(b)** the power stroke in which the myosin head hydrolyzes ATP and distorts, and moves the thin filament, **(c)** the myosin head detaches and relaxes, and **(d)** the myosin head reattaches to a new actin site $(x+1)$ for a new cycle. (Based on [280] and [284])



NANOMOTORES MUSCULARES A FILAMENTOS DESLIZANTES II

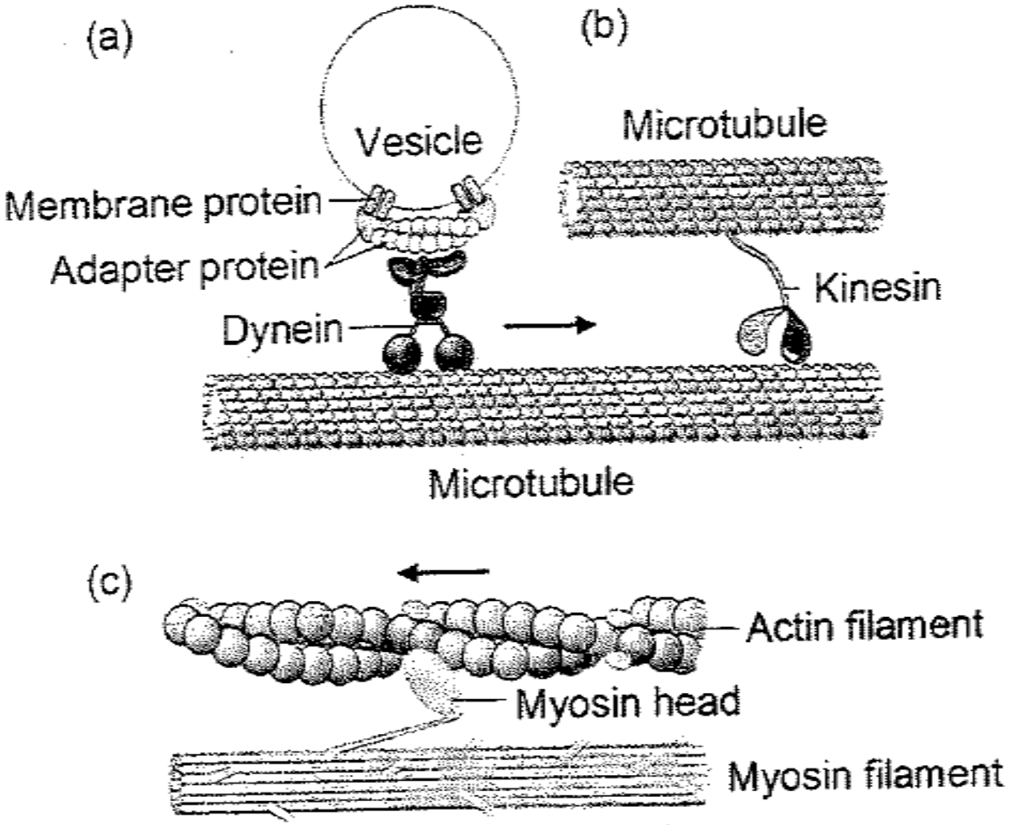
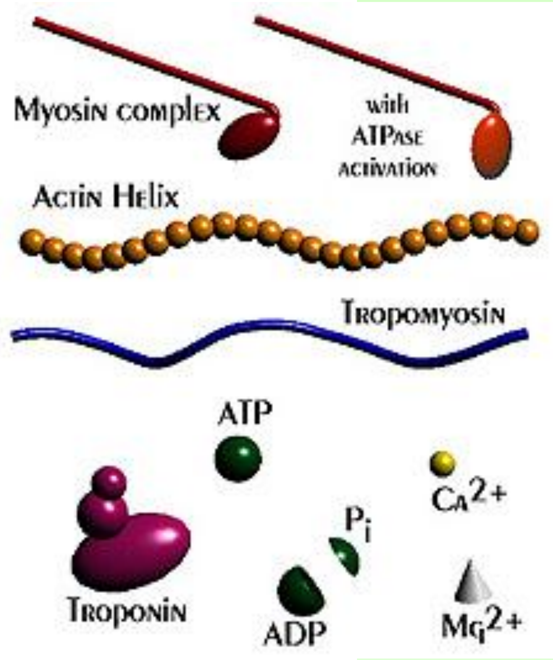
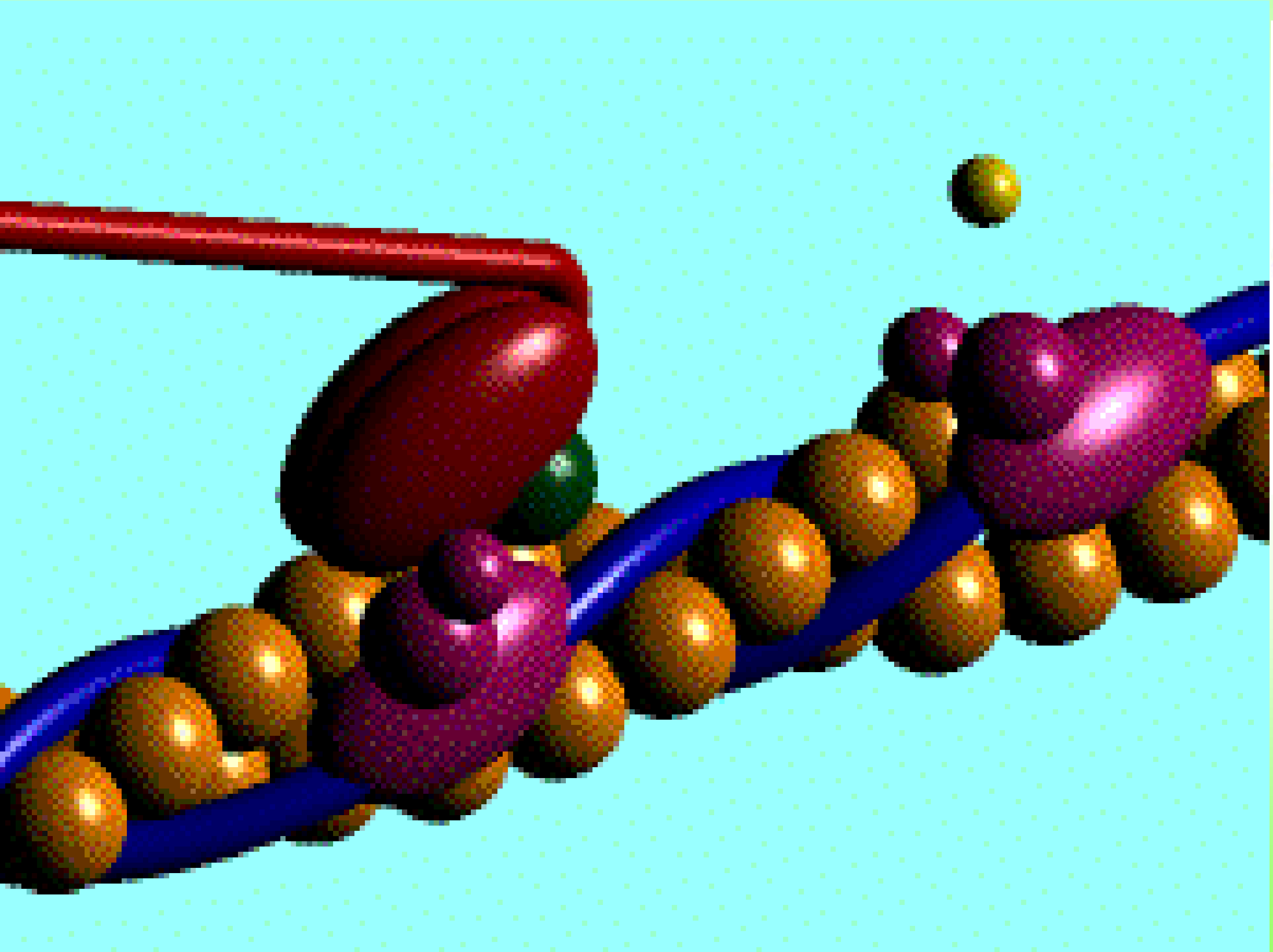
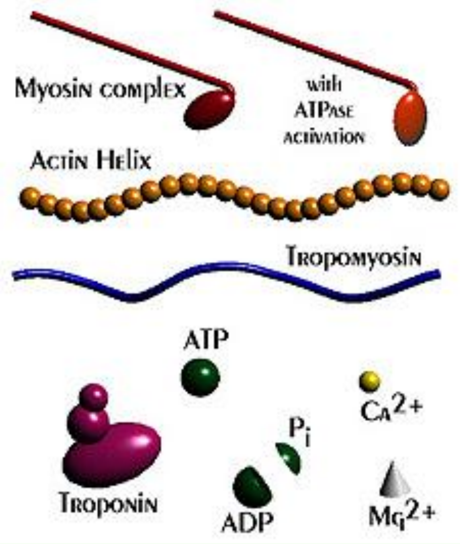


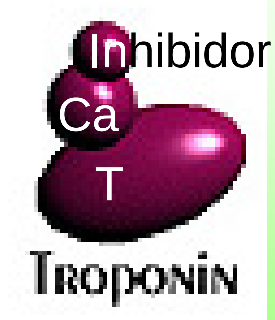
Fig. 5.35. Comparison of motor proteins, with **(a)** transport of a vesicle along a microtubule track by dynein, **(b)** transport of a microtubule on a microtubule track by kinesin, and **(c)** motion of the actin filament by a myosin filament. (From [281])



NANOMOTORES MUSCULARES A FILAMENTOS DESLIZANTES III







NANOMOTORES MUSCULARES A FILAMENTOS DESLIZANTES I

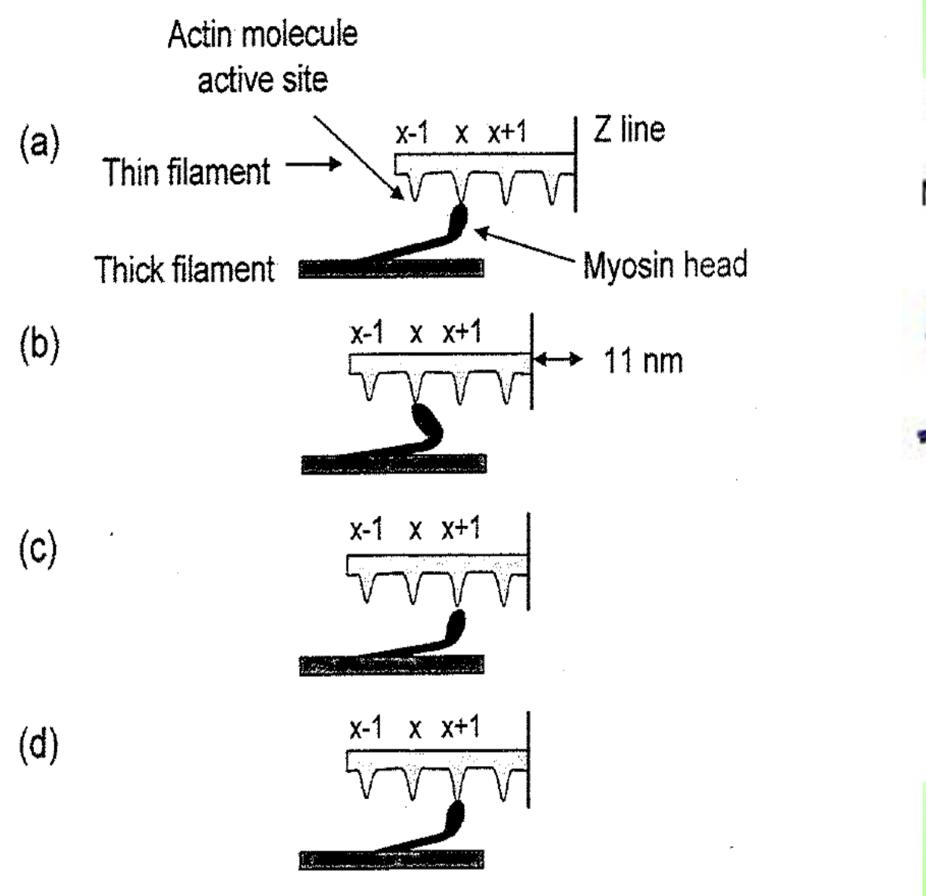
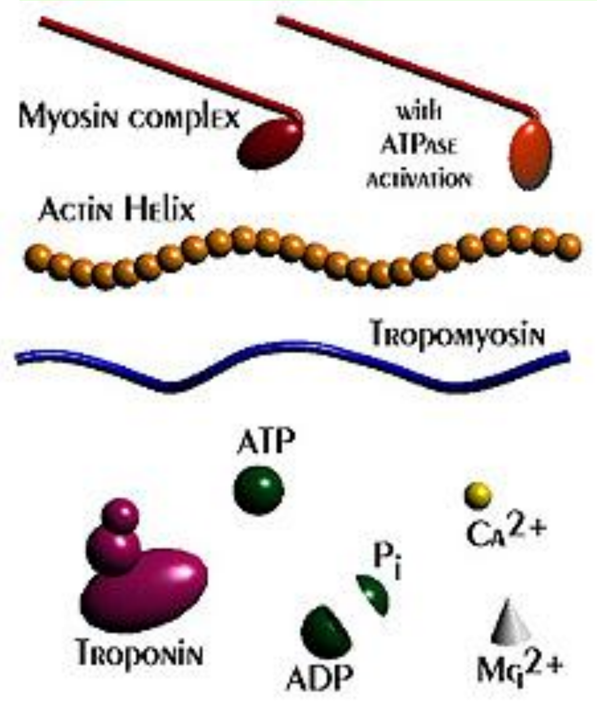
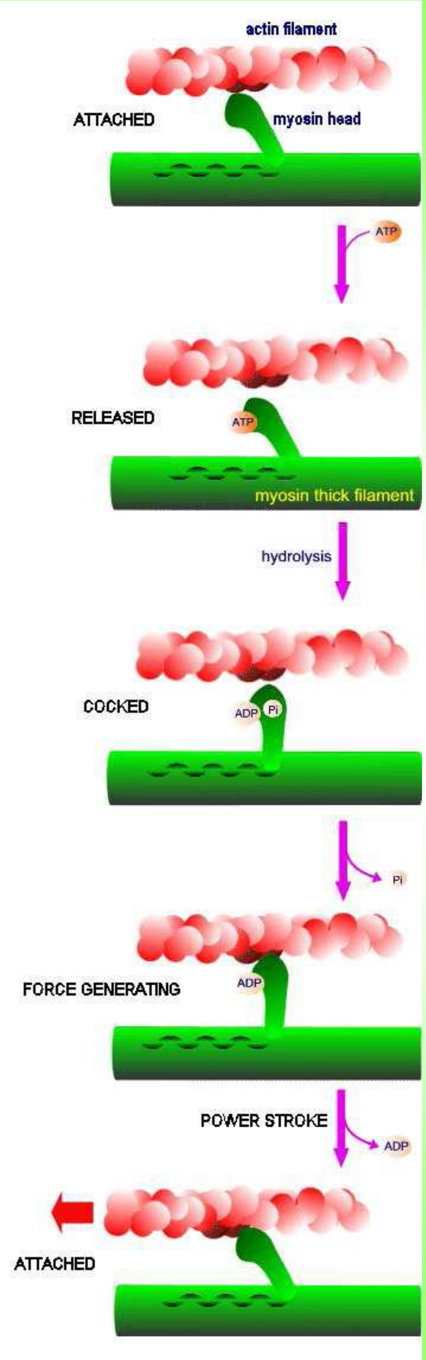


Fig. 5.34. Sliding of myofilaments, with **(a)** binding of the myosin head to an active actin site (site x), **(b)** the power stroke in which the myosin head hydrolyzes ATP and distorts, and moves the thin filament, **(c)** the myosin head detaches and relaxes, and **(d)** the myosin head reattaches to a new actin site ($x+1$) for a new cycle. (Based on [280] and [284])





(MA) + ATP <——> (M-ATP) + A

(M-ATP) <——> (M*-ADP-Pi)

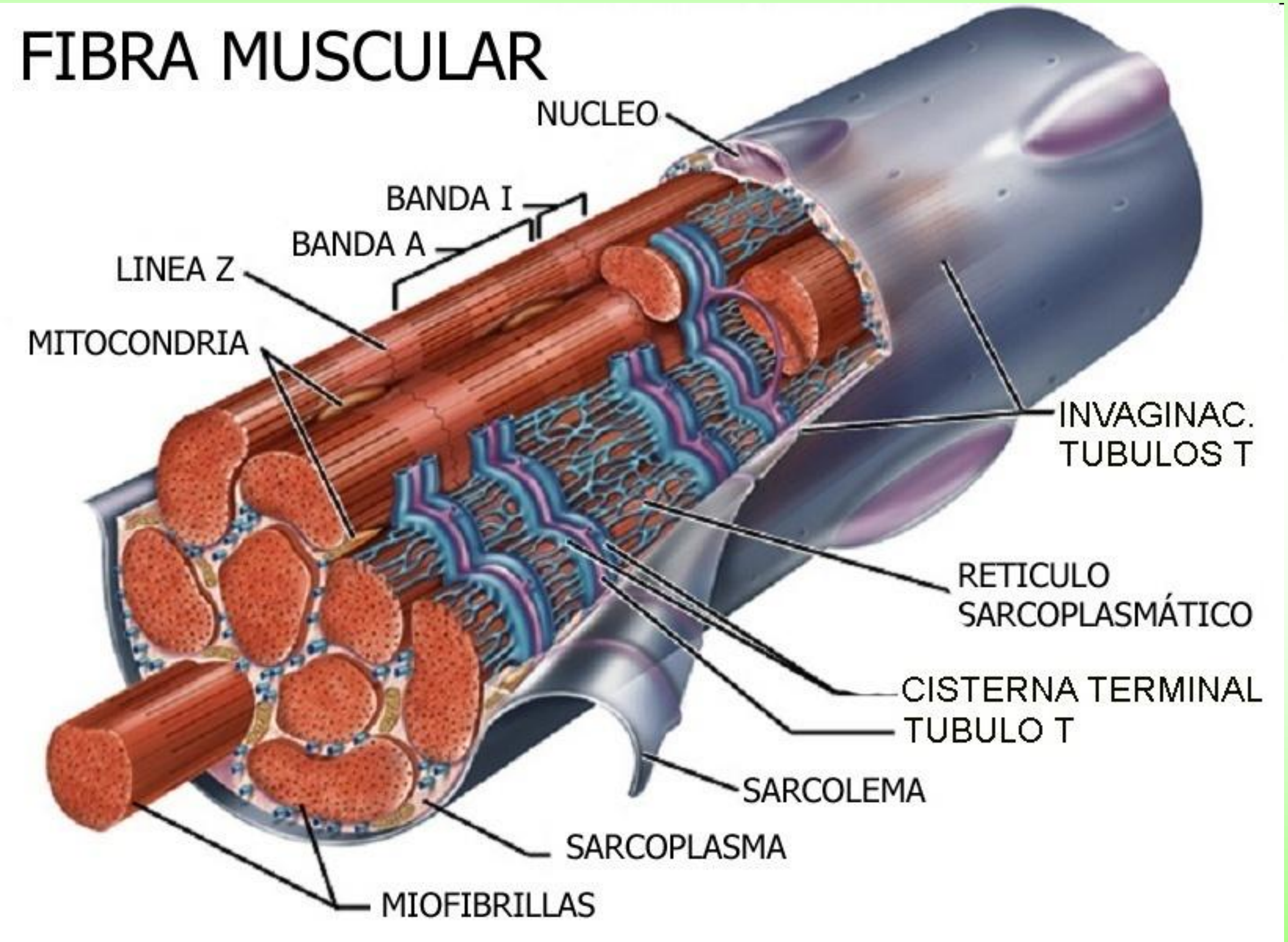
(M*-ADP-Pi) + A <——> (M*-ADP-A) + Pi

(M*-ADP-A) <——> (M-A) + ADP

Regulación del calcio Sarcoplasmático

Los eventos que estimulan la actividad muscular al elevar el calcio sarcoplasmatico empiezan con una excitación neuronal en la unión neuromuscular. La excitación induce despolarización local del sarcolema lo cual se difunde a través del sistema de túbulos T y hacia el interior de la miofibra. La despolarización del túbulo T se difunde al retículo sarcoplasmatico (SR), lo cual causa que se abran los canales de calcio voltaje-dependientes localizados en las membranas del SR. A este evento le sigue un movimiento rápido y masivo de calcio desde las cisternas hasta el sarcoplasma el cual se encuentra cerca de las miofibrillas. Las concentraciones de calcio elevadas influyen en la subunidad Tn-C de la troponina lo cual resulta en múltiples power strokes las cuales se siguen dando siempre y cuando las concentraciones de calcio se mantengan sobre 1 a 5 micromolares.

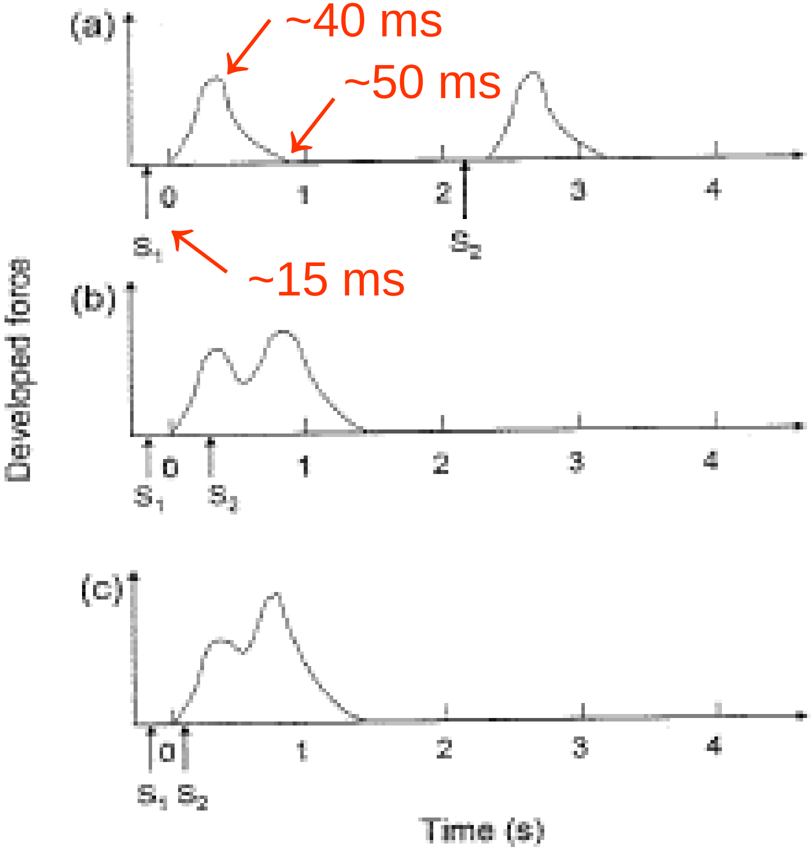
ORGANIZACION JERARQUICA DE LOS MUSCULOS ESQUELETALES II



ESTIMULACION SUCESIVA CON DIFERENTES RETARDOS I

La variación temporal de la fuerza se modela como:

$$F(t) = F_o \frac{t}{T} e^{-t/T}$$



~40 ms

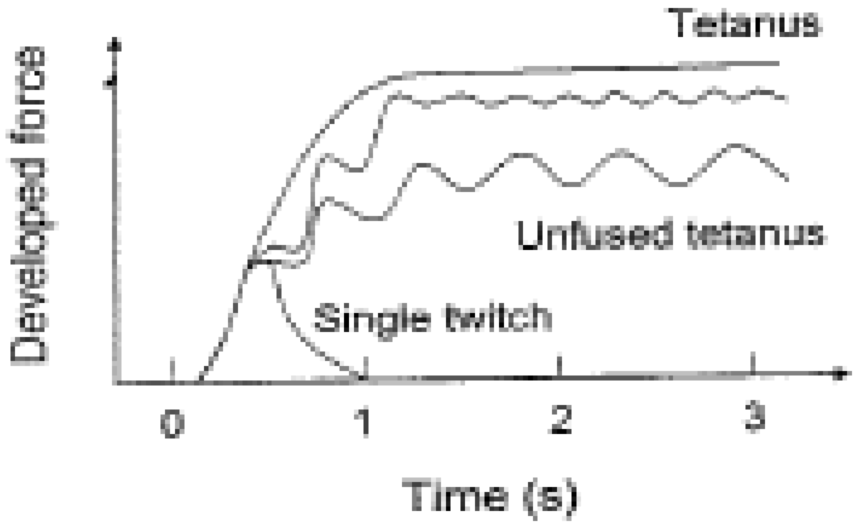
~50 ms

~15 ms

Fig. 5.8. Two twitches stimulated at S_1 and S_2, with various delays. (Based on [271])

Twitch: Contracción muscular brevísima, inesperada e inconsciente que se realiza en el tiempo T .

ESTIMULACION SUCESIVA CON DIFERENTES RETARDOS II



De 50 a 60 pps

Fig. 5.9. A twitch, and then a series of twitches leading to unfused tetanus, and at an even higher frequency leading to tetanus. (Based on [271])

Soleo ~ 30 pps y los músculos del ojo ~ 300 pps.

***Twitch**: Contracción muscular brevísima, inesperada e inconsciente que se realiza en el tiempo T .*

ESTIMULACION SUCESIVA CON DIFERENTES RETARDOS III

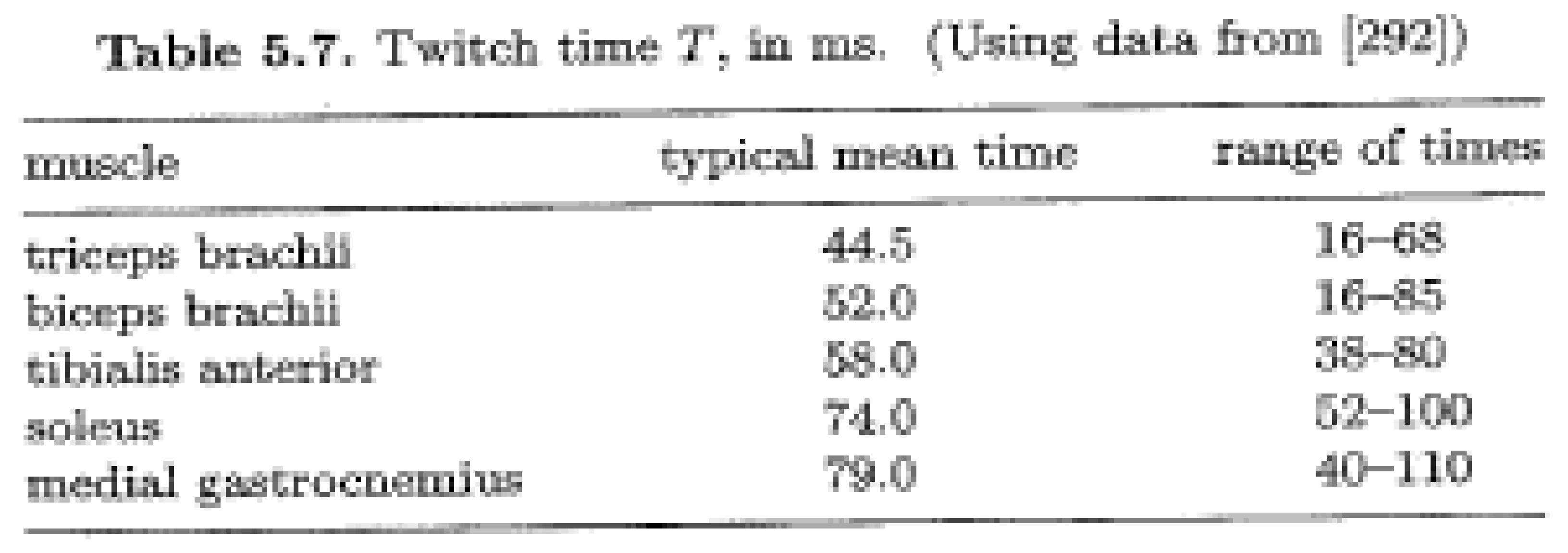
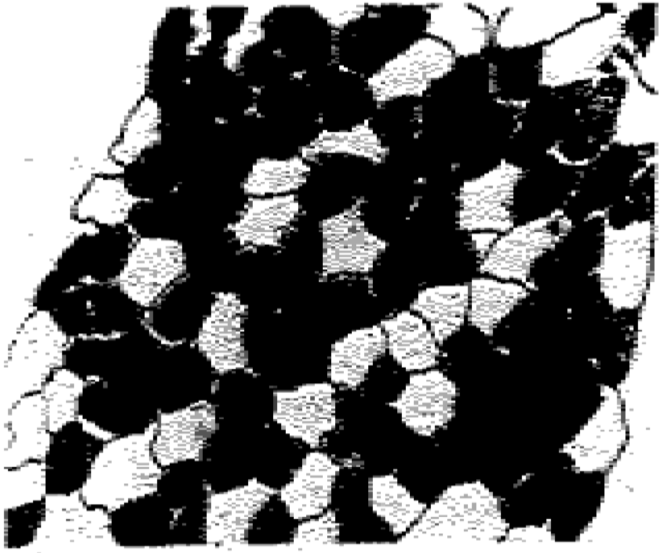


Table 5.7. Twitch time T, in ms. (Using data from [292])

muscle	typical mean time	range of times
triceps brachii	44.5	16–68
biceps brachii	52.0	16–85
tibialis anterior	58.0	38–80
soleus	74.0	52–100
medial gastrocnemius	79.0	40–110

Twitch: Contracción muscular brevísima, inesperada e inconsciente que se realiza en el tiempo T .

CELULAS MUSCULARES AEROBICAS: ST *(Slow-Twitch)*(LENTAS) TIPO I, Y FT *(Fast-Twitch)* (RAPIDAS) TIPO II



~ 110 ms. ST (Lentas). Rojas. Aeróbicas. Tipo I

~ 50 ms. FT (Rápidas). Tipo II:

A) Rojas
B) Blancas

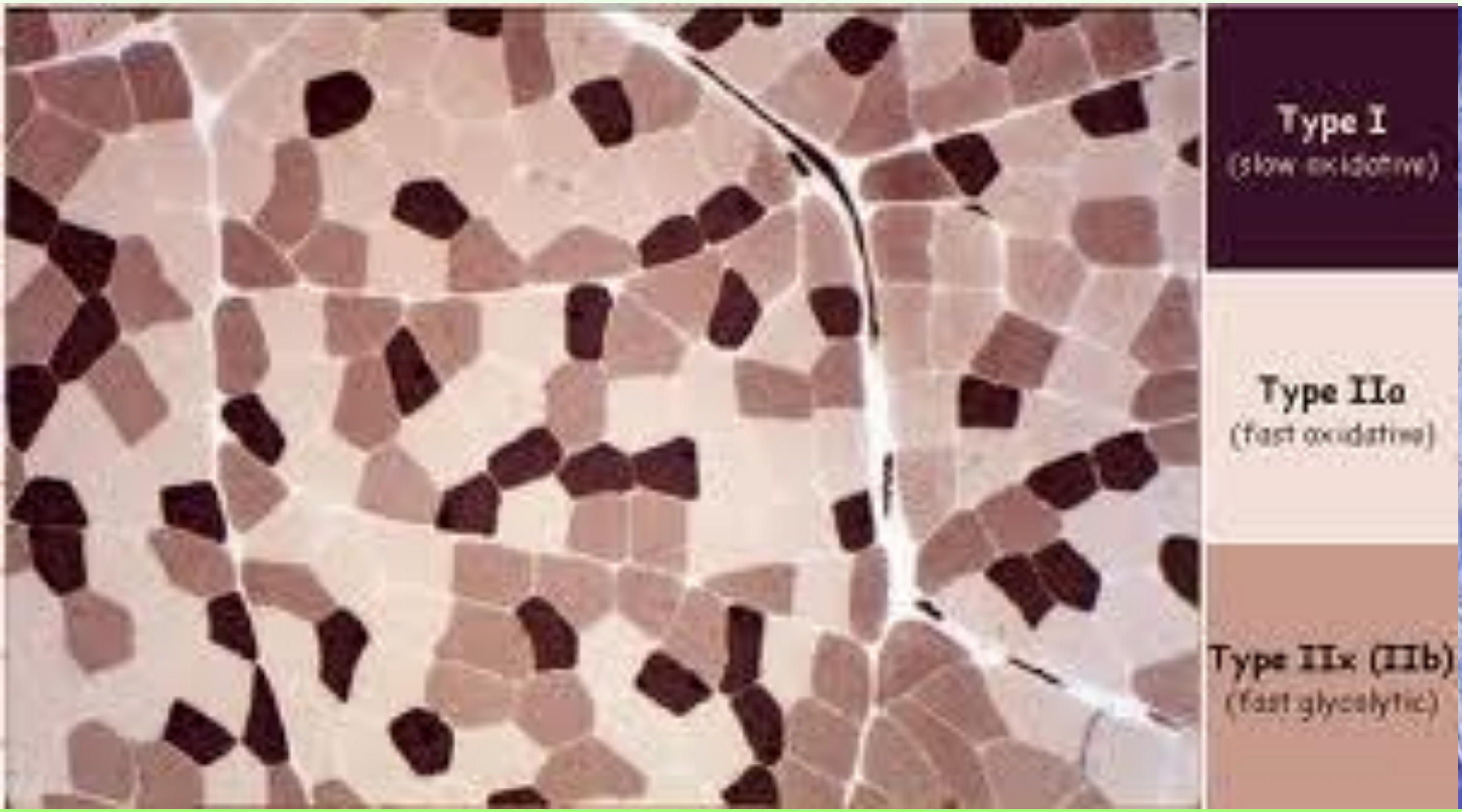
Fig. 5.10. Photomicrograph of stained muscle cells from a human vastus lateralis muscle, showing ST Type I (*dark*) and FT Type II (*lightly stained*) cells, with *fine lines* showing boundaries added. (From [250]. Used with permission)

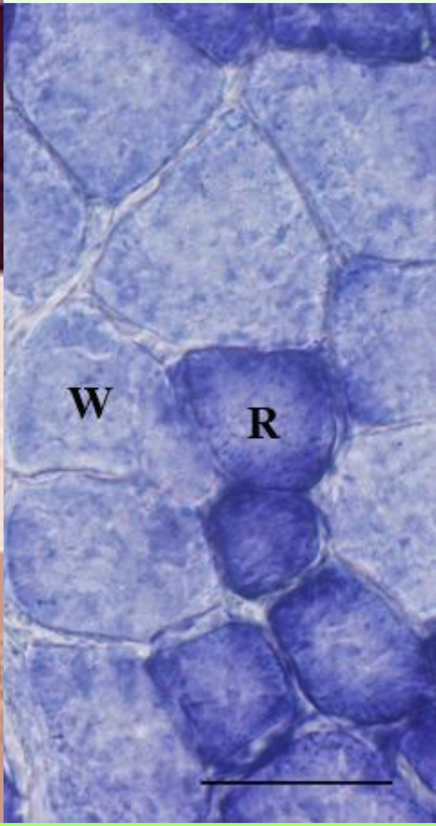
LOS TRES TIPOS DE FIBRAS

50% de Fibras rojas I ~ 110 ms ST

25% de Fibras rojas IIA ~ 50 ms FT

25% de Fibras blancas IIB ~ 10 ms FT #





Anaeróbicas

RESPUESTAS ISOMETRICAS DE ALGUNOS MUSCULOS

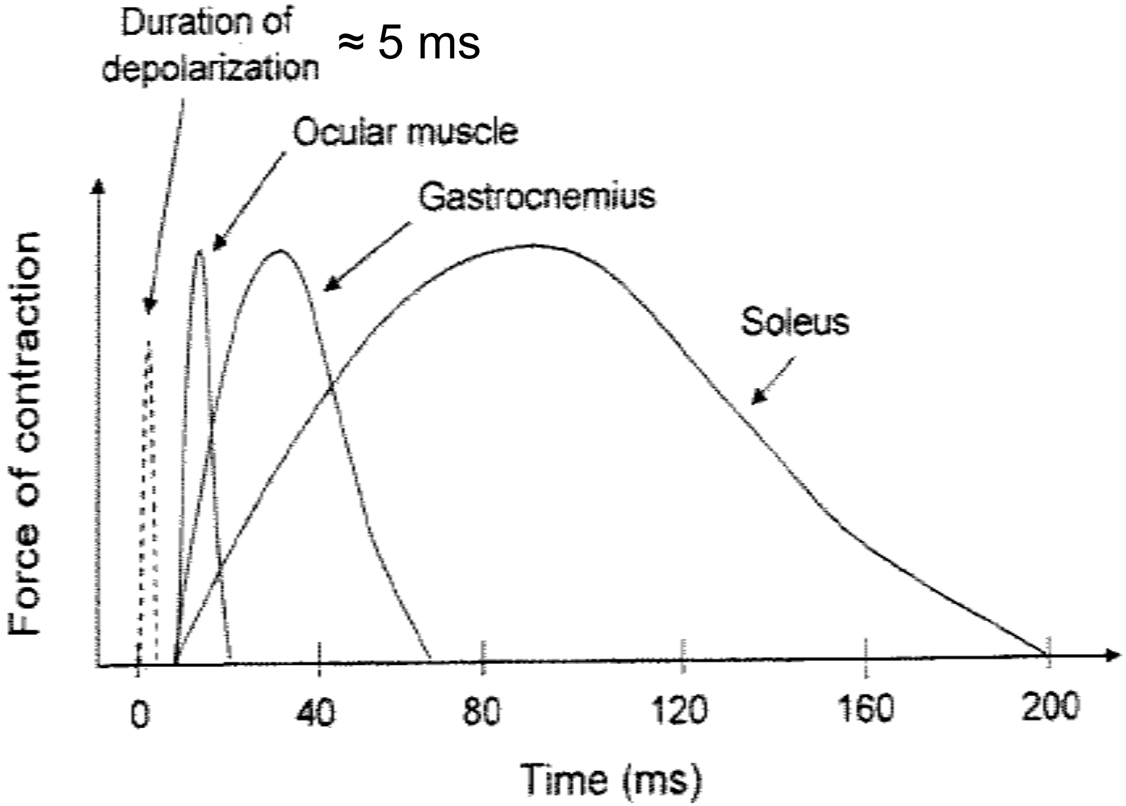


Fig. 5.11. Duration of isometric responses for different muscles with different FT and ST muscle fibers. (Based on [254])

VELOCIDAD DE CONTRACCION vs. PROPORCION DE FIBRAS FT (RAPIDAS)

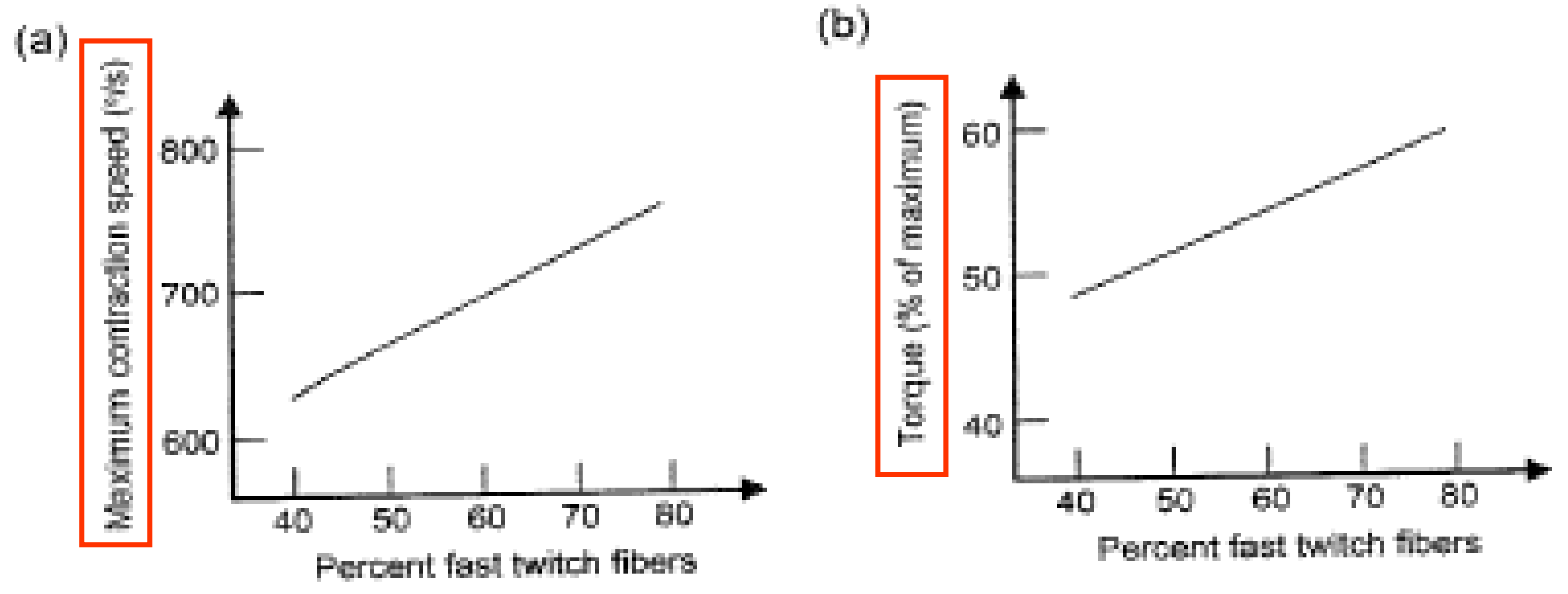


Fig. 5.12. Knee extension performance vs. percentage of FT fibers in the knee. (Based on [251] and [286])

Estos músculos producen **contracciones isocinéticas** generando movimientos con **velocidades angulares constantes**.

PROPIEDADES MUSCULARES EN ATLETAS DE ESPECIALIDADES

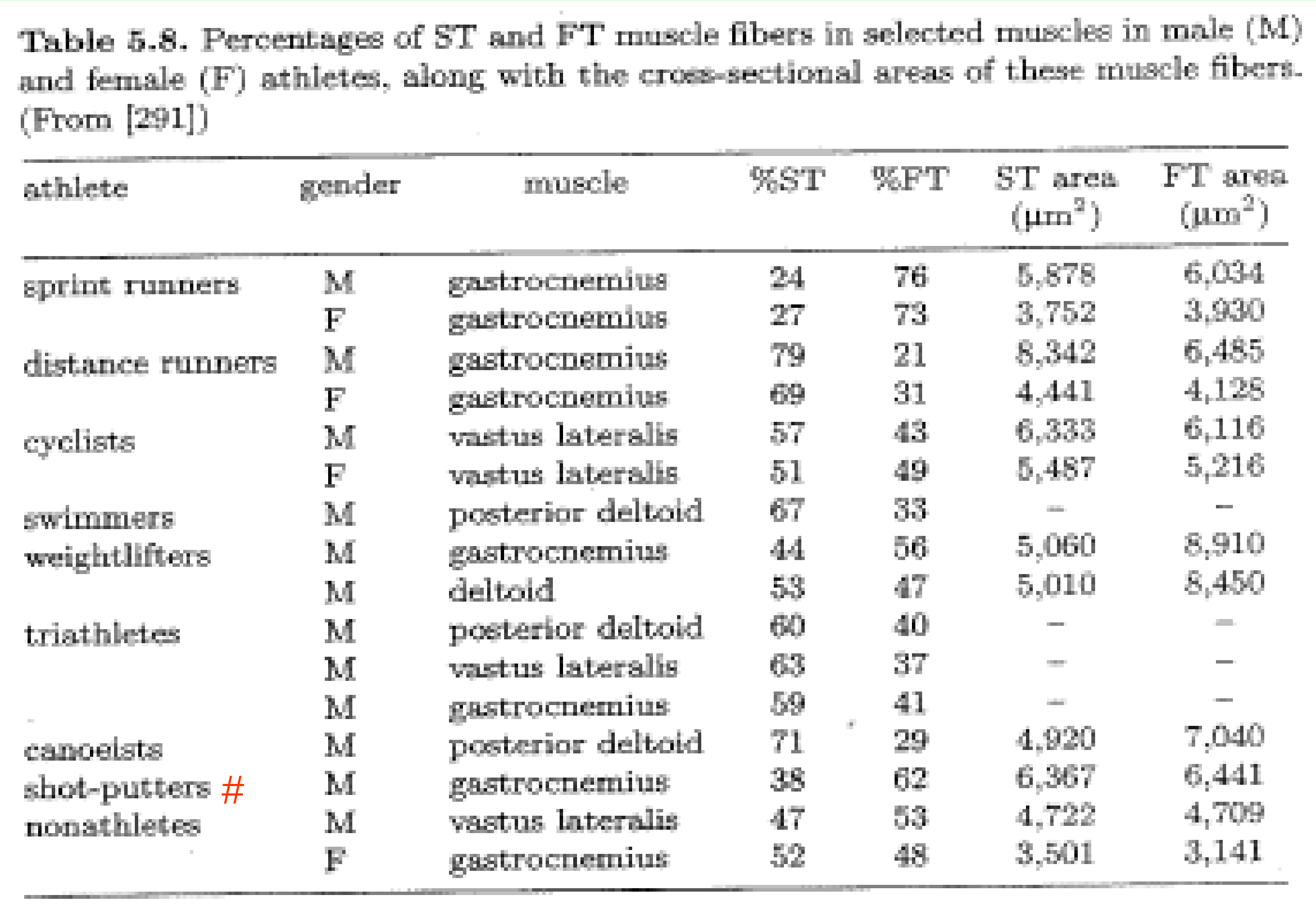
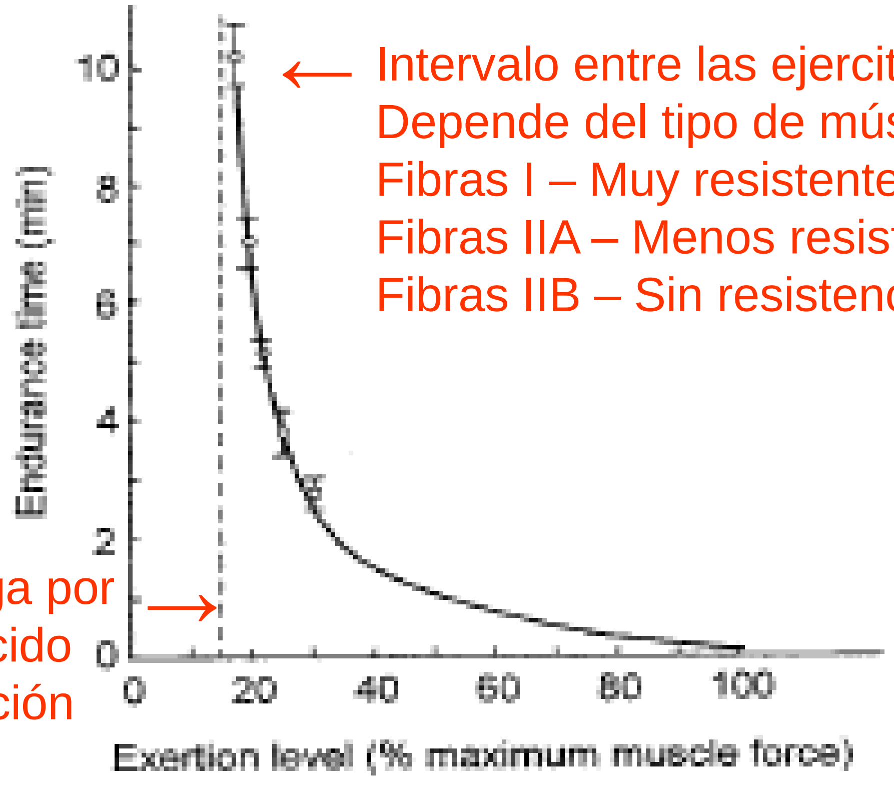


Table 5.8. Percentages of ST and FT muscle fibers in selected muscles in male (M) and female (F) athletes, along with the cross-sectional areas of these muscle fibers. (From [291])

athlete	gender	muscle	%ST	%FT	ST area (μm^2)	FT area (μm^2)
sprint runners	M	gastrocnemius	24	76	5,878	6,034
	F	gastrocnemius	27	73	3,752	3,930
distance runners	M	gastrocnemius	79	21	8,342	6,485
	F	gastrocnemius	69	31	4,441	4,128
cyclists	M	vastus lateralis	57	43	6,333	6,116
	F	vastus lateralis	51	49	5,487	5,216
swimmers	M	posterior deltoid	67	33	–	–
weightlifters	M	gastrocnemius	44	56	5,060	8,910
	M	deltoid	53	47	5,010	8,450
triathletes	M	posterior deltoid	60	40	–	–
	M	vastus lateralis	63	37	–	–
	M	gastrocnemius	59	41	–	–
canoeists	M	posterior deltoid	71	29	4,920	7,040
shot-putters #	M	gastrocnemius	38	62	6,367	6,441
nonathletes	M	vastus lateralis	47	53	4,722	4,709
	F	gastrocnemius	52	48	3,501	3,141

Lanzador de bala.

CURVA DE ROHMERT



← Intervalo entre las ejercitaciones < 90 s.
Depende del tipo de músculo; si posee:
Fibras I – Muy resistente a la fatiga.
Fibras IIA – Menos resistentes que las I.
Fibras IIB – Sin resistencia a la fatiga.

Límite a la fatiga por →
aumento del ácido
láctico y reducción
de la irrigación

Fig. 5.18. Rohmert curve for static muscle endurance, with ±1 SD (standard deviation) points shown. (From [243], adapted from [285]. Reprinted with permission of Wiley)

Endurance: Resistencia muscular al esfuerzo o al ejercicio sostenido

TIPOS DE FIBRAS MUSCULARES I

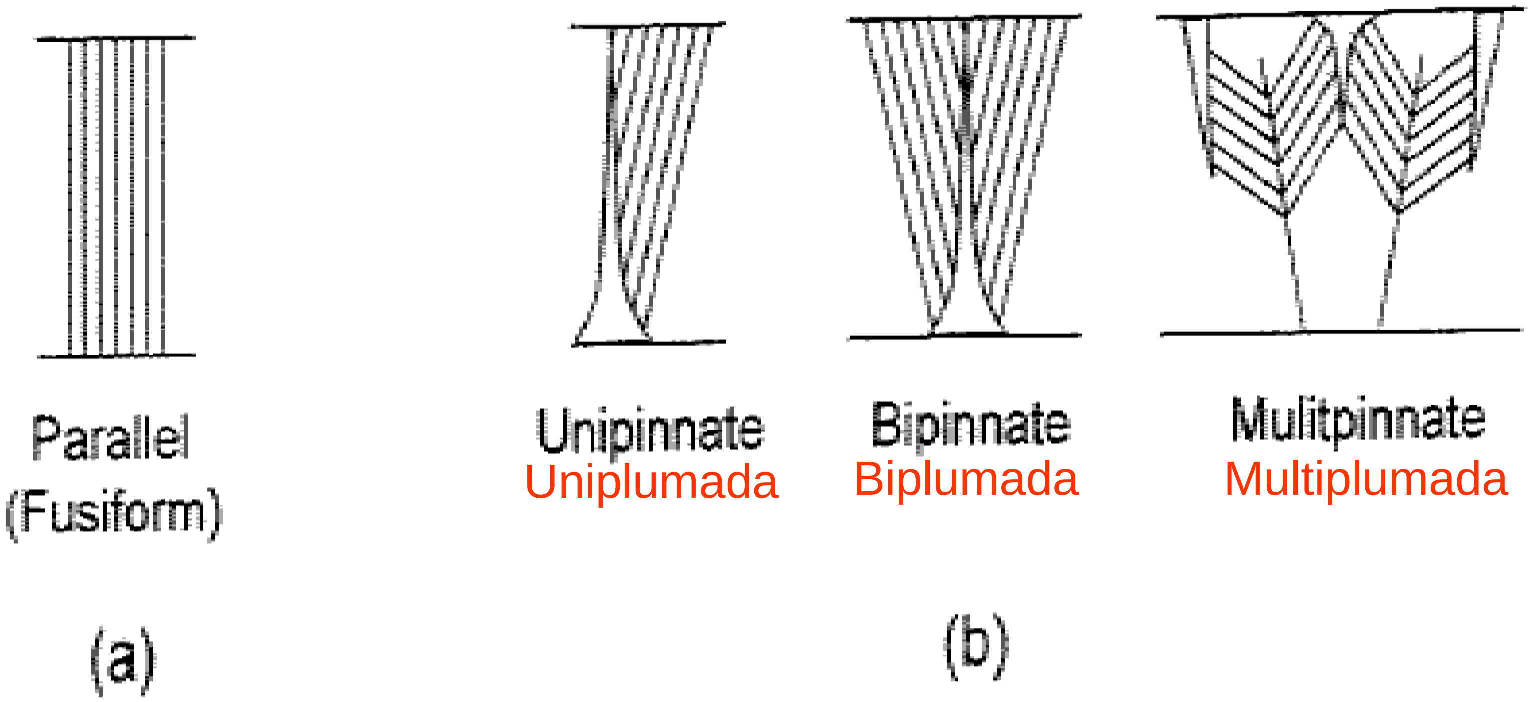


Fig. 5.3. Types of fiber arrangements in skeletal muscles, with (a) parallel and (b) pinnate fibers. (Based on [271])

TIPOS DE FIBRAS MUSCULARES II

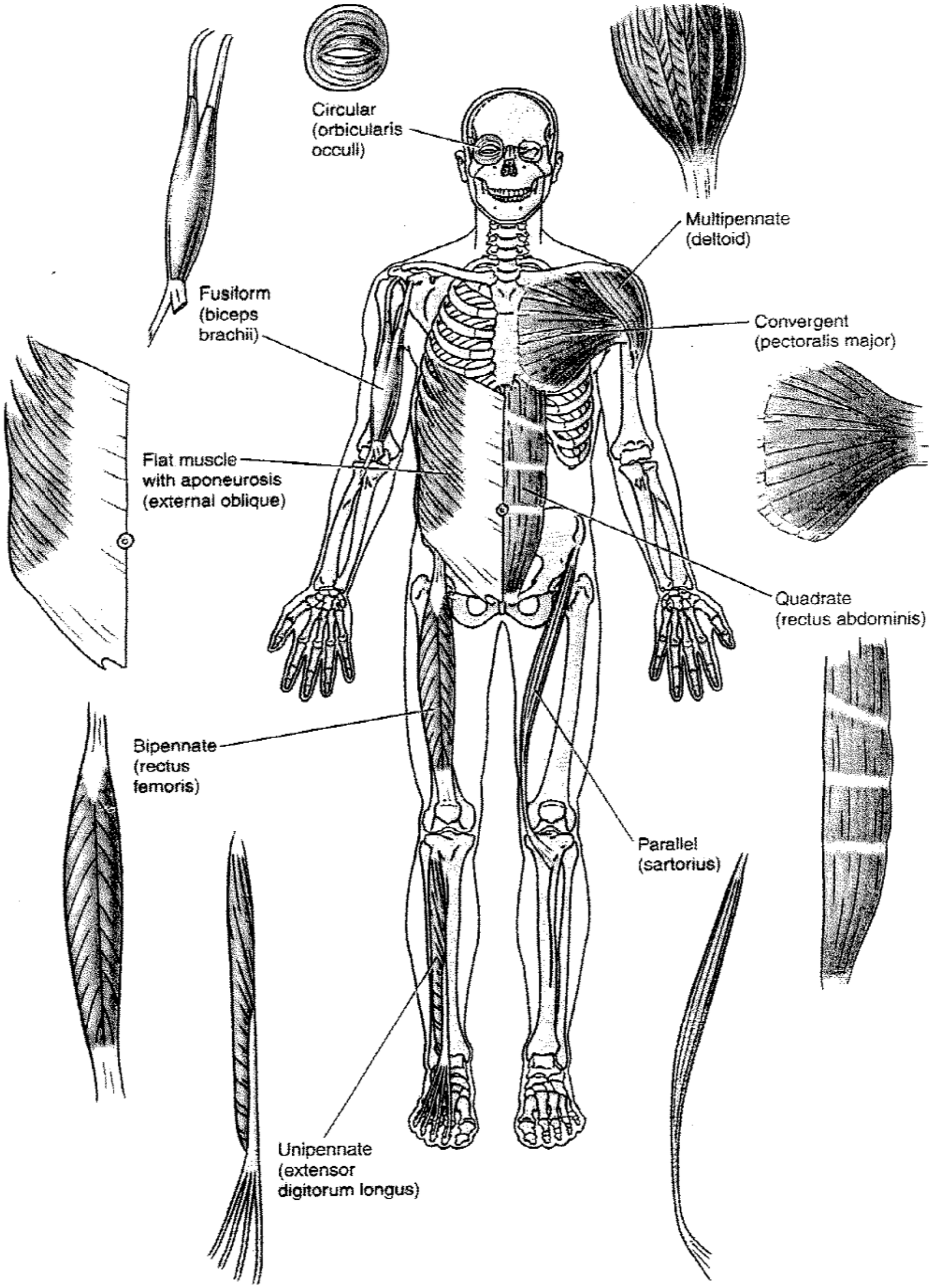
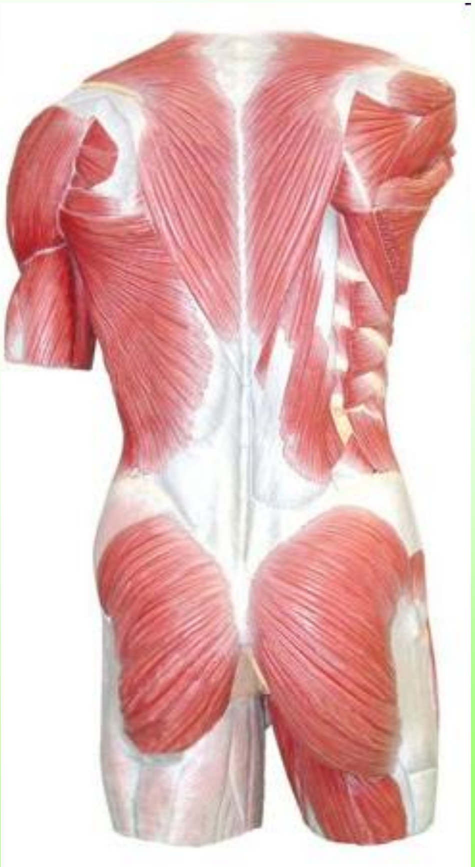
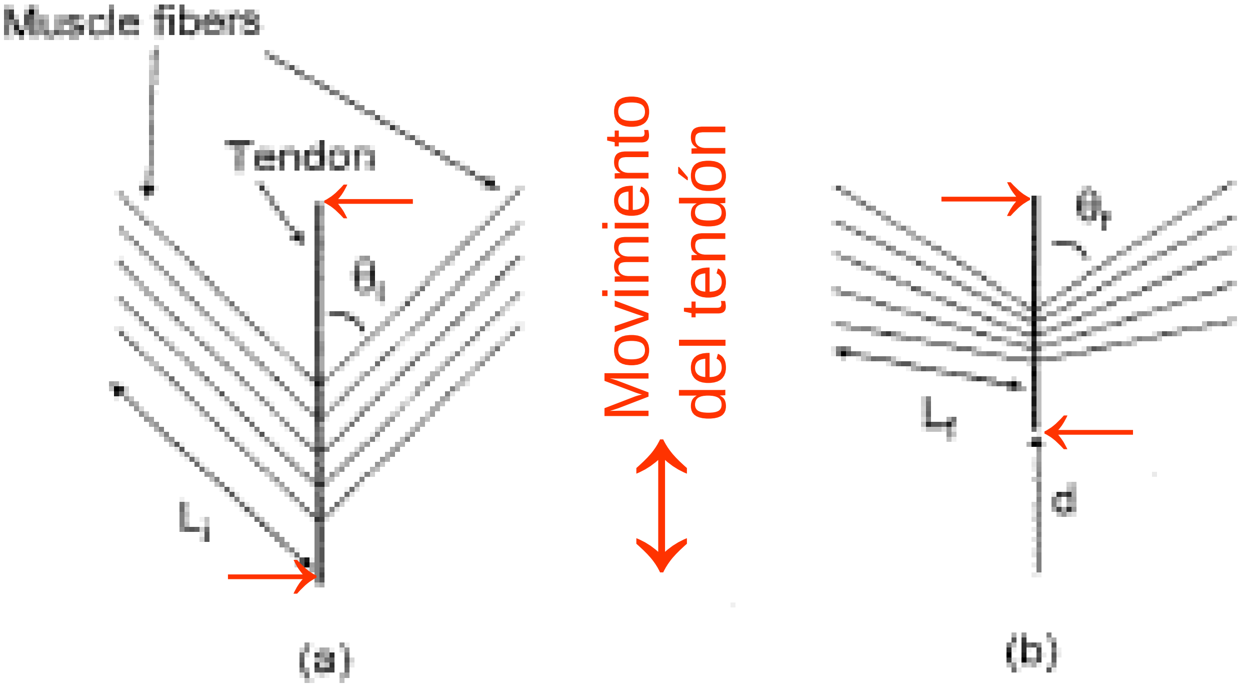


Fig. 5.4. Examples of muscle fiber arrangements in the body. (From [275]. Used with permission)



ACCION DE LAS FIBRAS MUSCULARES DEL TIPO PLUMA



Movimiento del tendón

Fig. 5.5. Muscle fibers in pinnate muscles (a) before and (b) after fiber contraction with accompanying tendon movement

%PCA: AREA DE LA SECCION FISIOLOGICA DE LOS MUSCULOS I

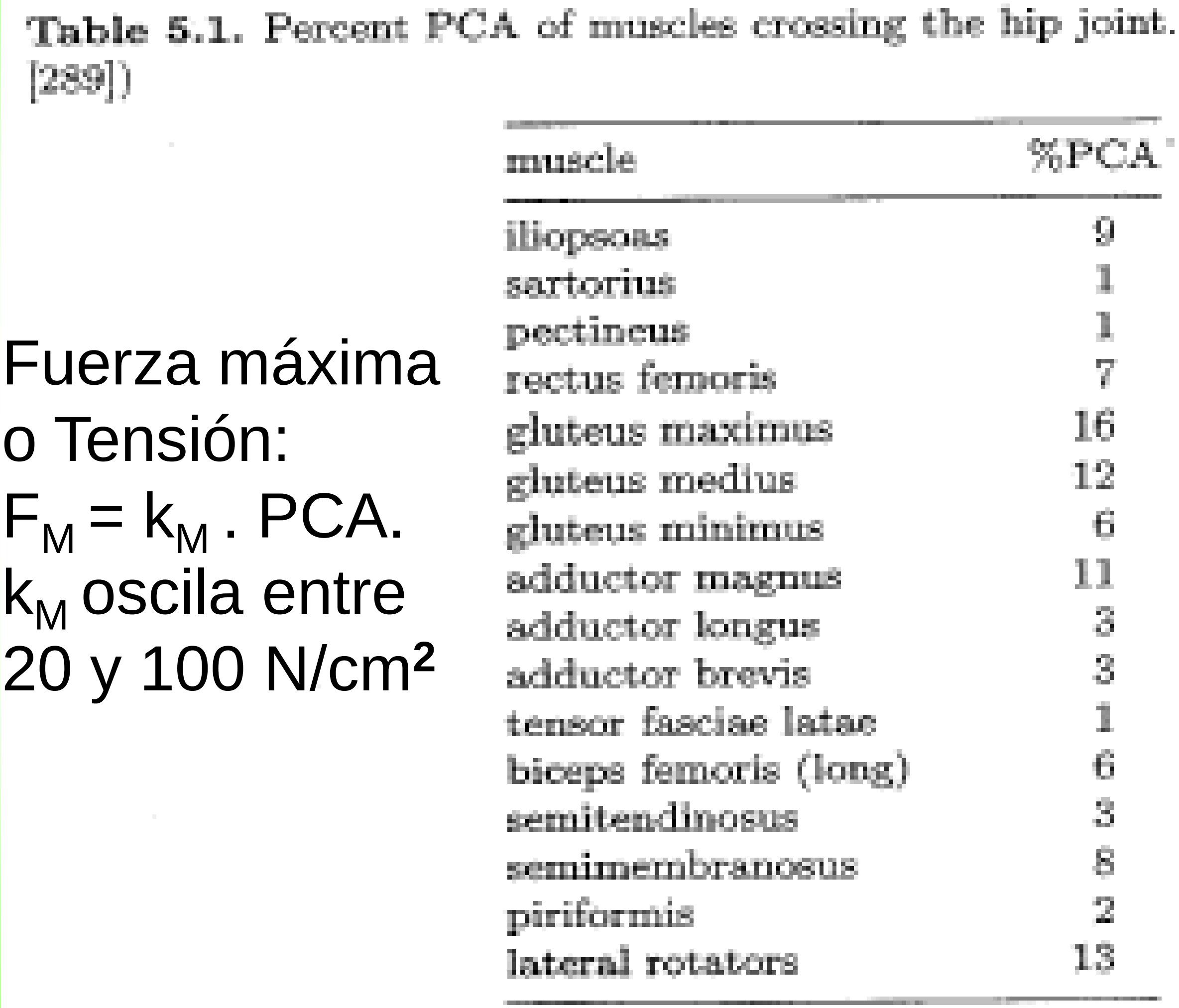


Table 5.1. Percent PCA of muscles crossing the hip joint. (From [292], data from [289])

muscle	%PCA
iliopsoas	9
sartorius	1
pectineus	1
rectus femoris	7
gluteus maximus	16
gluteus medius	12
gluteus minimus	6
adductor magnus	11
adductor longus	3
adductor brevis	3
tensor fasciae latae	1
biceps femoris (long)	6
semitendinosus	3
semimembranosus	8
piriformis	2
lateral rotators	13

Fuerza máxima o Tensión:
$F_M = k_M . PCA.$
k_M oscila entre 20 y 100 N/cm^2

Los músculos de mayor PCA ejercen mayor fuerza. Ellos realizan **trabajo dinámico** con **contracciones no isométricas**. No obstante los músculos de menor PCA contribuyen a la estabilidad y realizan **trabajo estático** con **contracciones isométricas**.

PCA: Physiological cross-sectional area.

%PCA: AREA DE LA SECCION FISIOLOGICA DE LOS MUSCULOS II

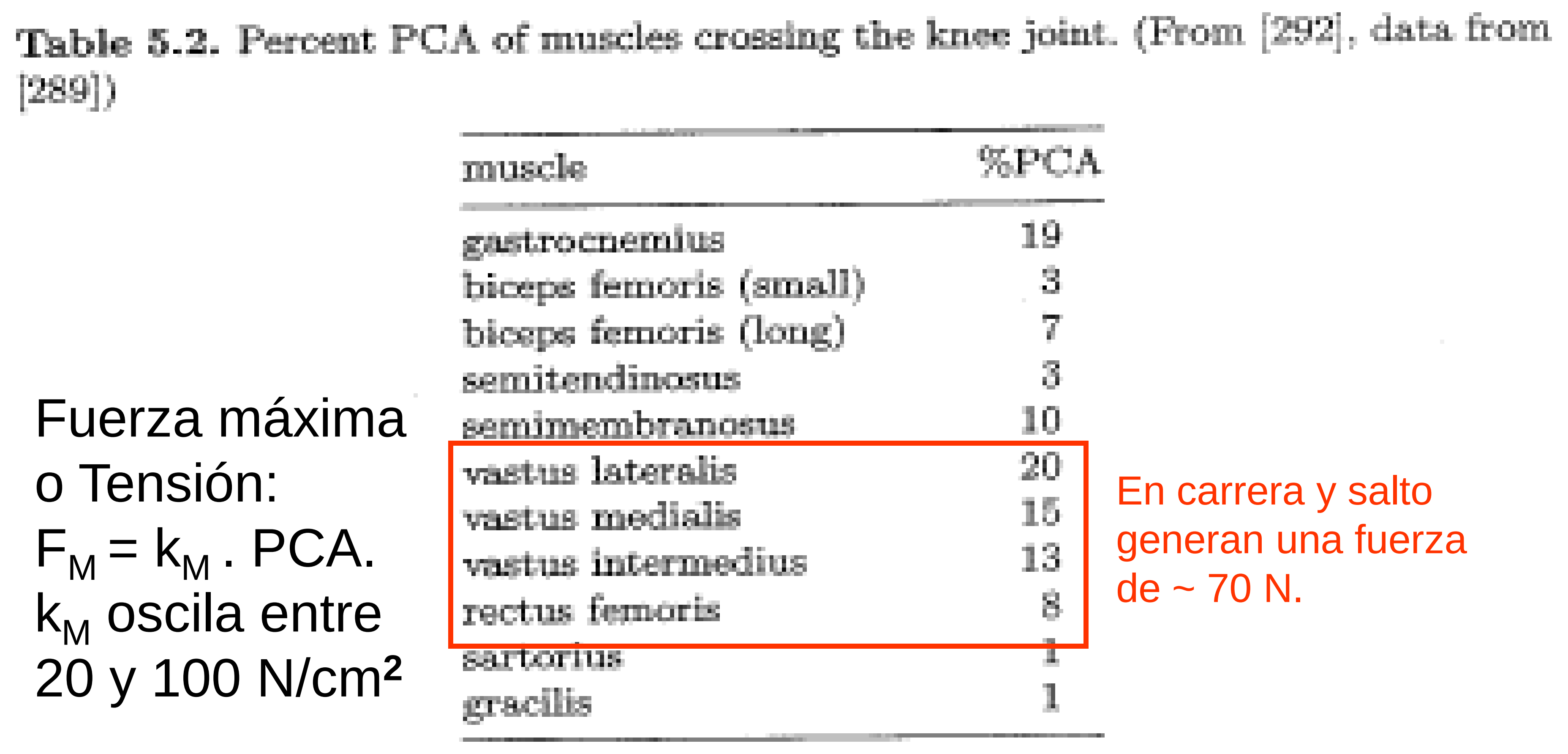


Table 5.2. Percent PCA of muscles crossing the knee joint. (From [292], data from [289])

muscle	%PCA
gastrocnemius	19
biceps femoris (small)	3
biceps femoris (long)	7
semitendinosus	3
semimembranosus	10
vastus lateralis	20
vastus medialis	15
vastus intermedius	13
rectus femoris	8
sartorius	1
gracilis	1

Fuerza máxima o Tensión:

$F_M = k_M \cdot PCA.$

k_M oscila entre 20 y 100 N/cm²

En carrera y salto generan una fuerza de ~ 70 N.

%PCA: AREA DE LA SECCION FISIOLOGICA DE LOS MUSCULOS III

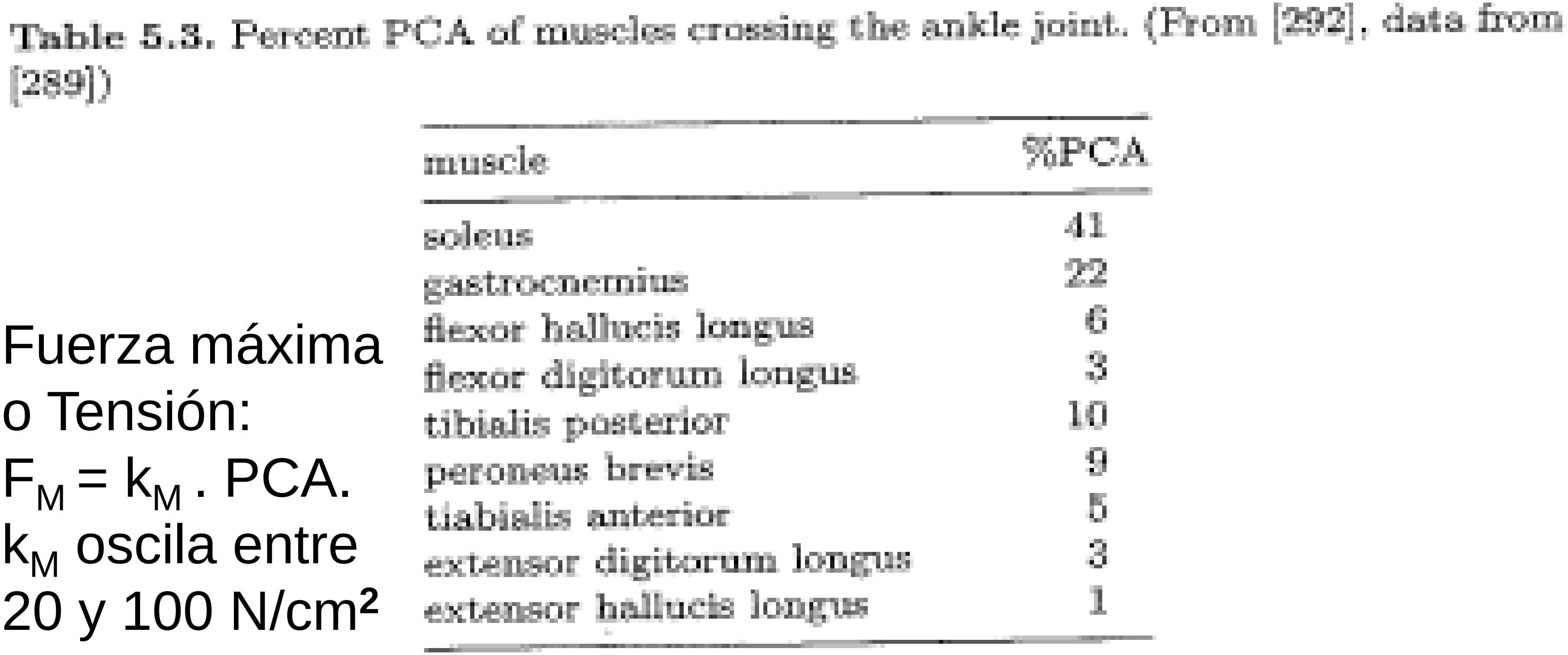


Table 5.3. Percent PCA of muscles crossing the ankle joint. (From [292], data from [289])

muscle	%PCA
soleus	41
gastrocnemius	22
flexor hallucis longus	6
flexor digitorum longus	3
tibialis posterior	10
peroneus brevis	9
tiabialis anterior	5
extensor digitorum longus	3
extensor hallucis longus	1

Fuerza máxima o Tensión:

$F_M = k_M . PCA.$

k_M oscila entre 20 y 100 N/cm^2

PROPIEDADES DE LOS MUSCULOS

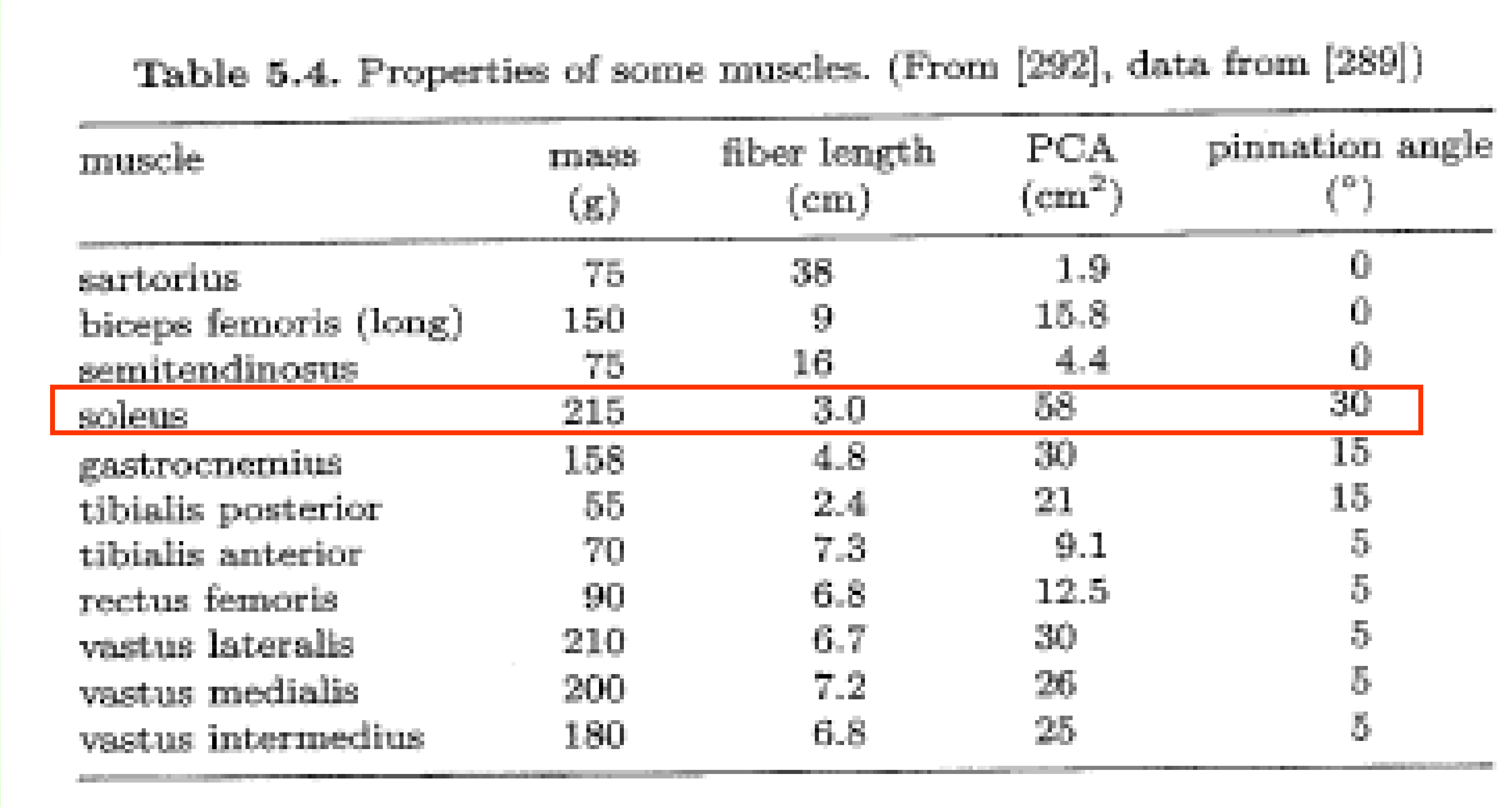


Table 5.4. Properties of some muscles. (From [292], data from [289])

muscle	mass (g)	fiber length (cm)	PCA (cm^2)	pinnation angle (°)
sartorius	75	38	1.9	0
biceps femoris (long)	150	9	15.8	0
semitendinosus	75	16	4.4	0
soleus	215	3.0	58	30
gastrocnemius	158	4.8	30	15
tibialis posterior	55	2.4	21	15
tibialis anterior	70	7.3	9.1	5
rectus femoris	90	6.8	12.5	5
vastus lateralis	210	6.7	30	5
vastus medialis	200	7.2	26	5
vastus intermedius	180	6.8	25	5

Músculo Liso

Mientras que el modelo de deslizamiento de filamentos describe apropiadamente el mecanismo básico de contracción muscular y se puede aplicar a todos los tipos musculares, existen diferencias significativas entre el músculo esquelético y el músculo liso. Una apreciación de estas diferencias se basa en la observación que aunque el músculo liso no precisa de troponina, su actividad contráctil es regulada por niveles citoplasmáticos de calcio.

Este concepto se explicó cuando se descubrió una proteína que se une al Ca2+/calmodulina (CaCM) conocida como caldesmon, estaba involucrada en regular el movimiento de la tropomiosina sobre la superficie del músculo liso; así descubriendo y ocultando los sitios de unión de la miosina localizados en los filamentos delgados. Posteriormente se observó que la elevación de los niveles de calcio en el citosol elevaban los niveles de CaCM la cual se unía al caldesmon y así removiéndola de su localización en los filamentos delgados

Actividad Muscular

- Isométrica: longitud constante
- No-isométricas:

1. Concéntrica (trabajo positivo)
2. Excéntrica (trabajo negativo)
3. Isokinética (velocidad cte)
4. Isotónica (tensión constante)
5. Isoinercial (resistencia constante)

MATERIALES DE LOS MUSCULOS I

Obedecen la Ley de Hooke

$$\sigma = Y.\varepsilon$$

$$\frac{d\sigma}{d\varepsilon} = Y$$

No obedecen la Ley de Hooke: Músculos en estado pasivo

$$\frac{d\sigma}{d\varepsilon} = \alpha.\left(\sigma + \beta\right),$$

$$\alpha = cte.$$

$$\beta = cte.$$

MATERIALES DE LOS MUSCULOS II

$$\frac{d\sigma}{(\sigma+\beta)} = \alpha.d\varepsilon,$$

Integrando:

$$\ln(\sigma+\beta) = \alpha.\varepsilon + \gamma,$$

$$\gamma = cte.$$

Exponenciando:

$$\sigma+\beta = \exp(\alpha.\varepsilon).\exp(\gamma),$$

$$\sigma = \mu.\exp(\alpha.\varepsilon) - \beta,$$

$$\mu = \exp(\gamma).$$

MATERIALES DE LOS MUSCULOS III

Para:

$$\sigma\left(\varepsilon = 0\right) = 0,$$

$$\beta = \mu,$$

Luego:

$$\sigma = \mu\left[\exp\left(\alpha.\varepsilon\right) - 1\right].$$

$$\sigma = \mu'.\exp\left(\alpha\frac{L}{L_0}\right) - \mu,$$

$$\frac{L}{L_0} = \lambda = \varepsilon + 1,$$

$$\mu' \neq \mu.$$

MATERIALES DE LOS MUSCULOS IV

Si la carga es:

$$\sigma = \mu'.\exp\left(\alpha \frac{L}{L_0}\right) - \mu,$$

La fuerza muscular es:

$$F_M = \sigma.PCA$$

$$F_M = \mu'.PCA.\exp\left(\alpha \frac{L}{L_0}\right)\Bigg|_{L_i}^{L_f} - \mu.PCA.$$

FUERZA vs. LONGITUD DEL MUSCULO O DEL SARCOMERO

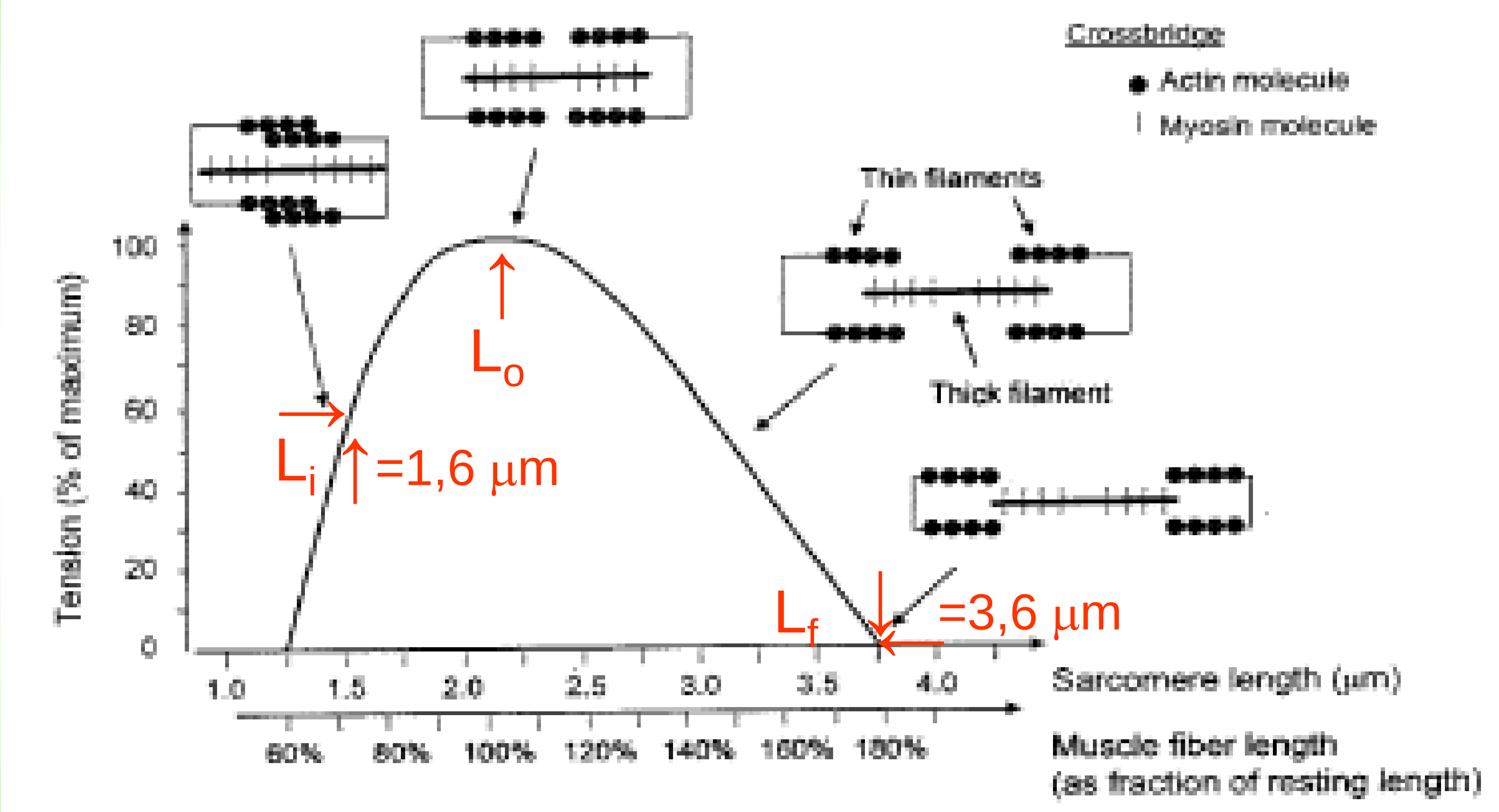


Fig. 5.23. Force vs. sarcomere or muscle length, with schematics of the variation of the overlap of the thick (myosin) and thin (actin) filaments for different sarcomere lengths. The sarcomere and total muscle lengths scale the same way. The crossbridge between an actin and myosin molecule is also shown. (Based on [254], [271], [280], and [284])

TENSION TOTAL vs. LONGITUD DE MUSCULOS TIPOS PLUMA Y PARALELO

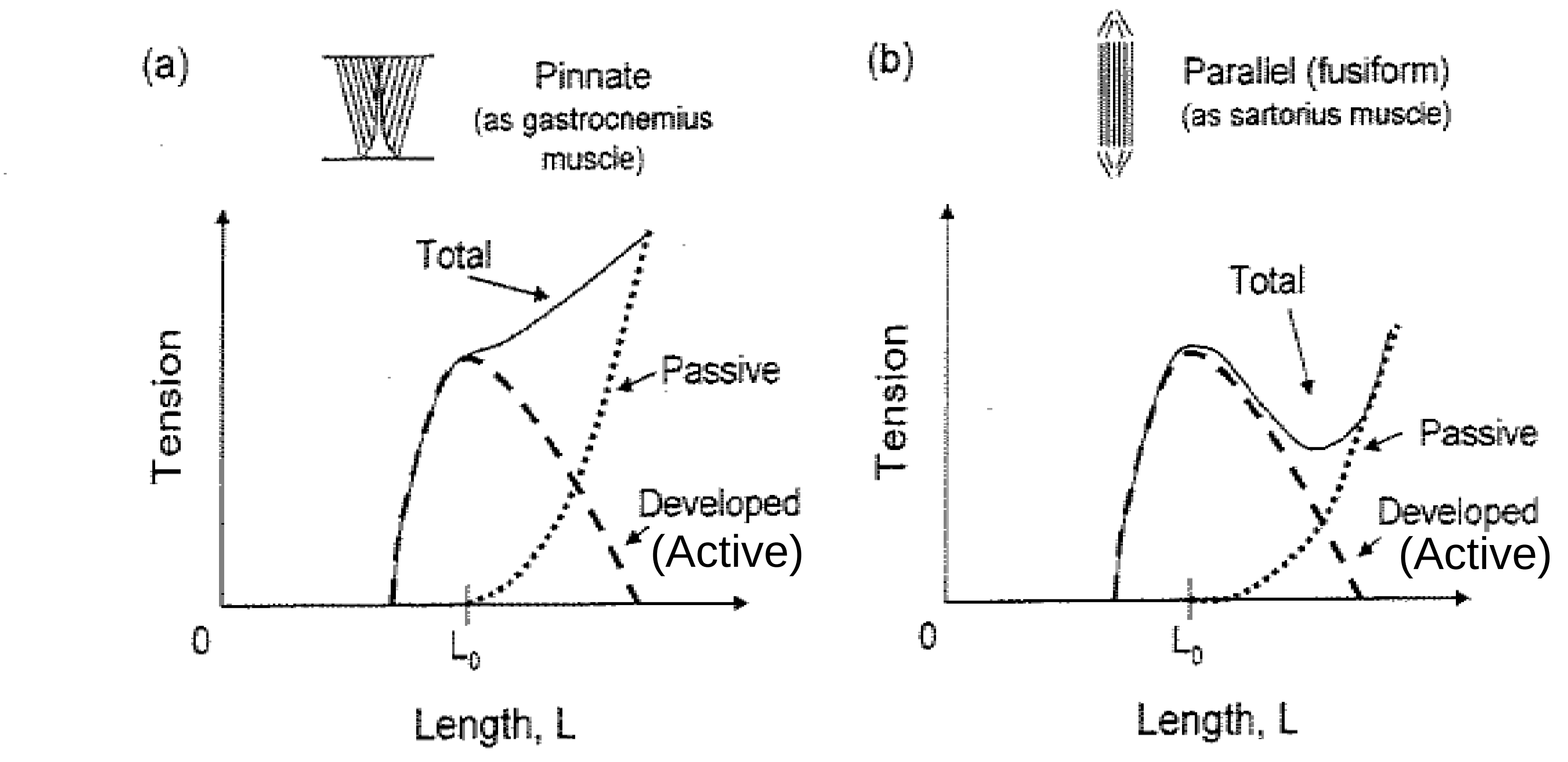


Fig. 5.25. Schematic of passive, developed (active), and total tension vs. length for pinnate and parallel muscles. (Based on [240] and [271]. Also see [237])

MODELO COMPLETO DE MUSCULO EN ESTADO ACTIVO

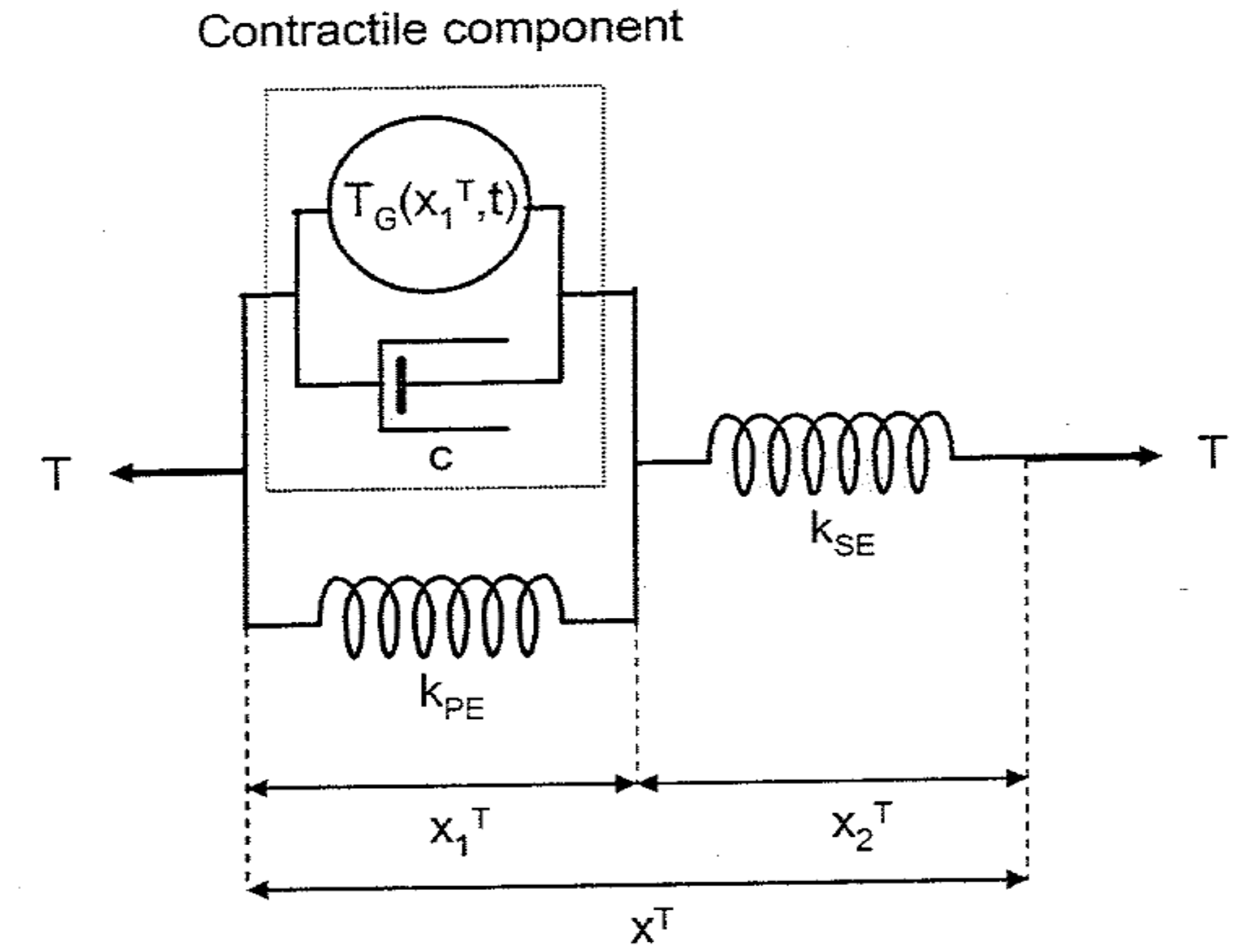


Fig. 5.13. Complete active state muscle model. (Based on [271])

DOS VARIANTES

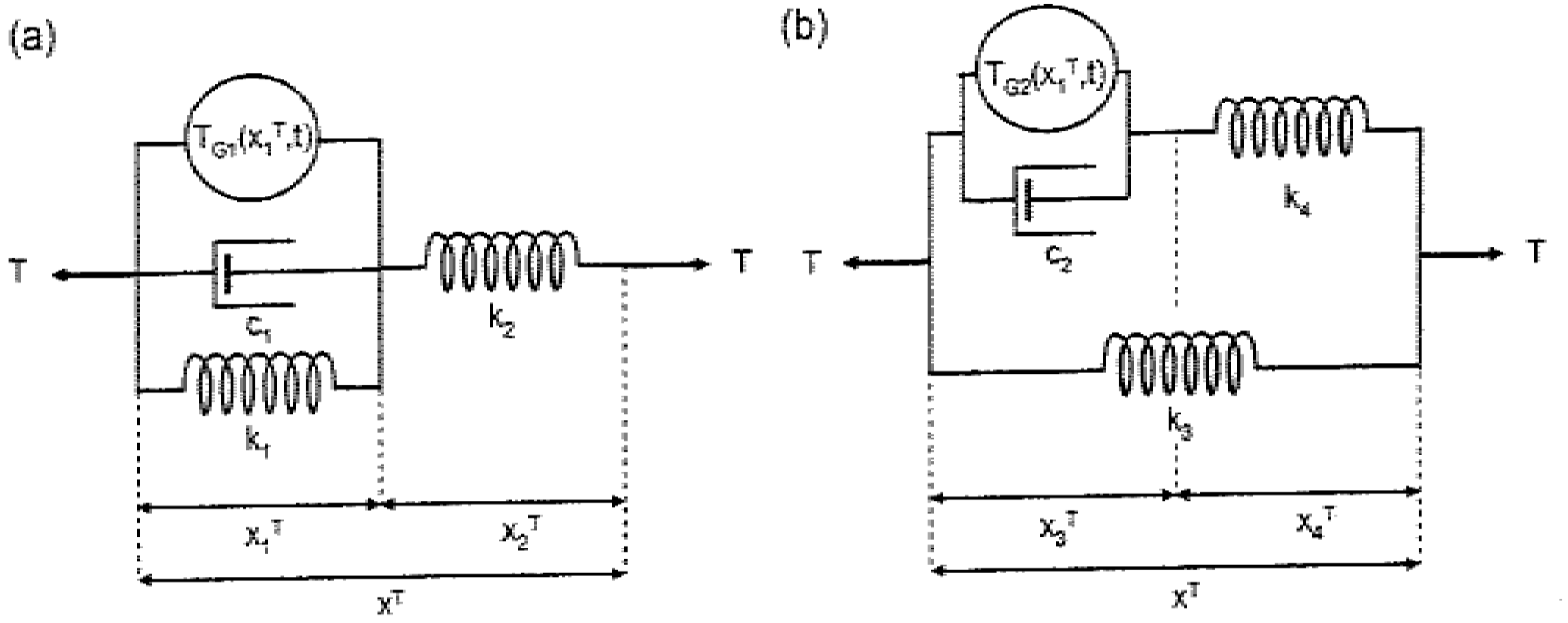


Fig. 5.14. Equivalent active state muscle models. The model in part **(a)** is the same as that in Fig. 5.13. (Based on [271])

UNA SIMPLIFICACION I

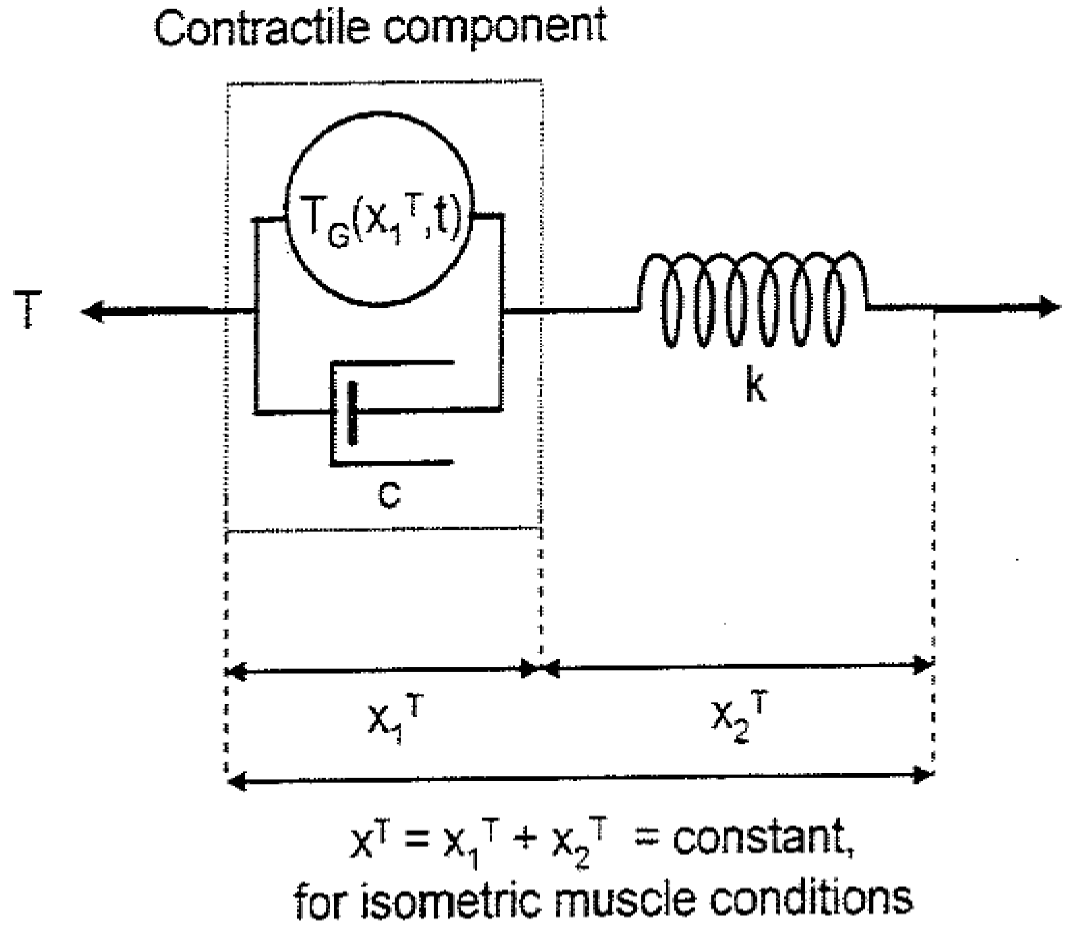
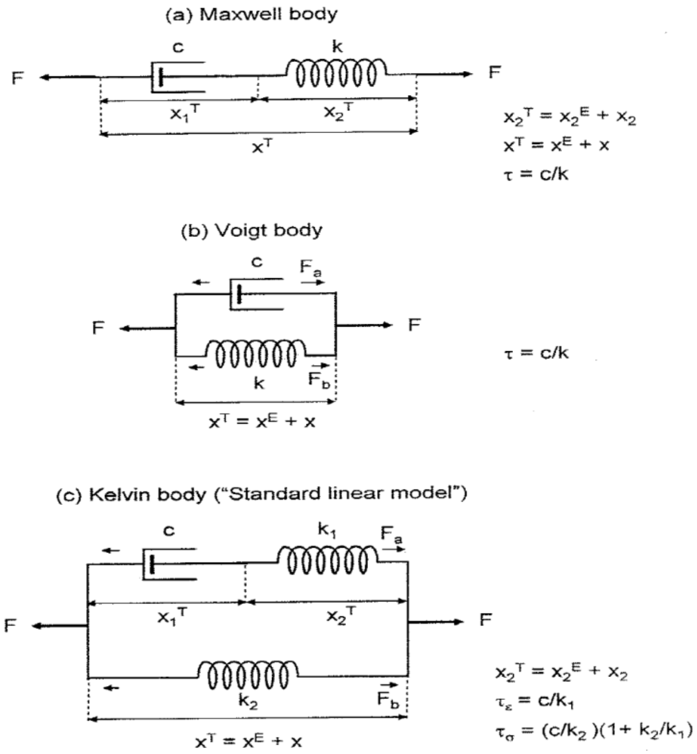
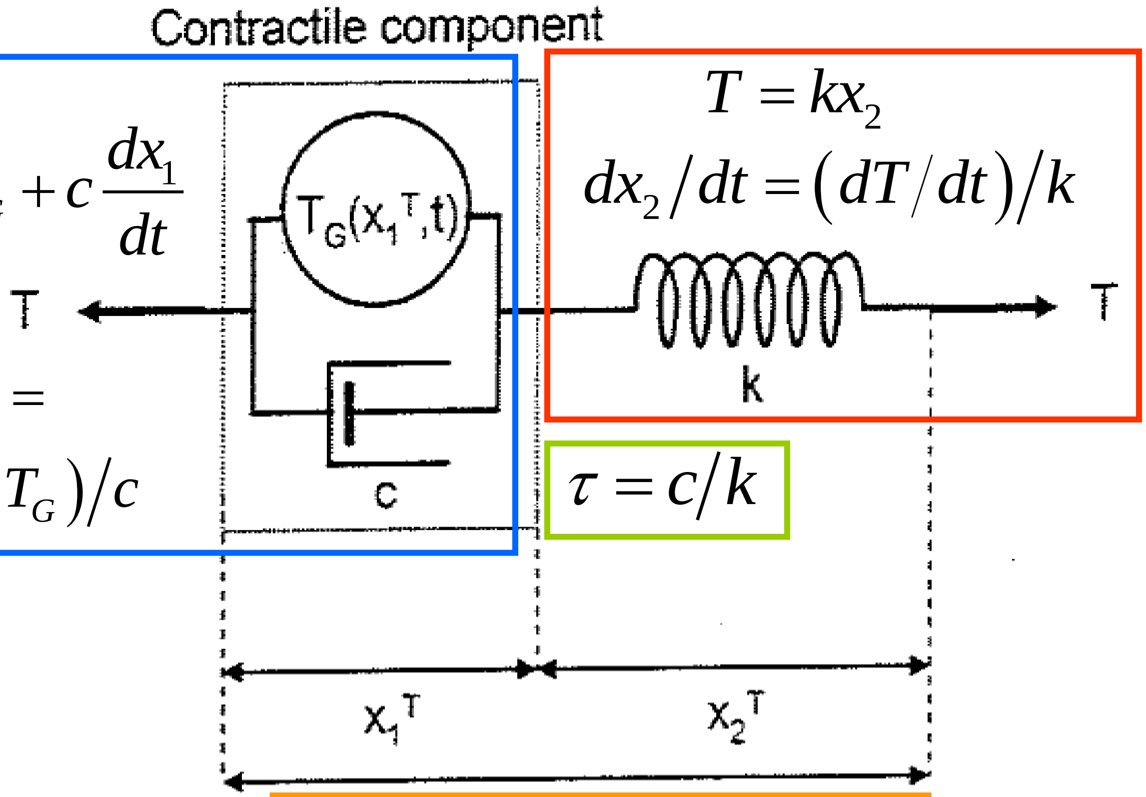


Fig. 5.15. Simpler active state muscle model. (Based on [271])



UNA SIMPLIFICACION II



$$T = T_G + c\frac{dx_1}{dt}$$

$$dx_1/dt = $$
$$= (T - T_G)/c$$

$$T = kx_2$$
$$dx_2/dt = (dT/dt)/k$$

$$\tau = c/k$$

$x^T = x_1^T + x_2^T$ = constant, for isometric muscle conditions

$$\frac{dx}{dt} = \frac{dx_1}{dt} + \frac{dx_2}{dt} = 0$$

$$\frac{(T - T_G)}{c} + \frac{1}{k}\frac{dT}{dt} = 0$$

$$\frac{dT(t)}{dt} + \frac{T(t)}{\tau} = \frac{T_G(t)}{\tau}$$

Fig. 5.15. Simpler active state muscle model. (Based on [271])

RESPUESTAS DEL MODELO SIMPLIFICADO I

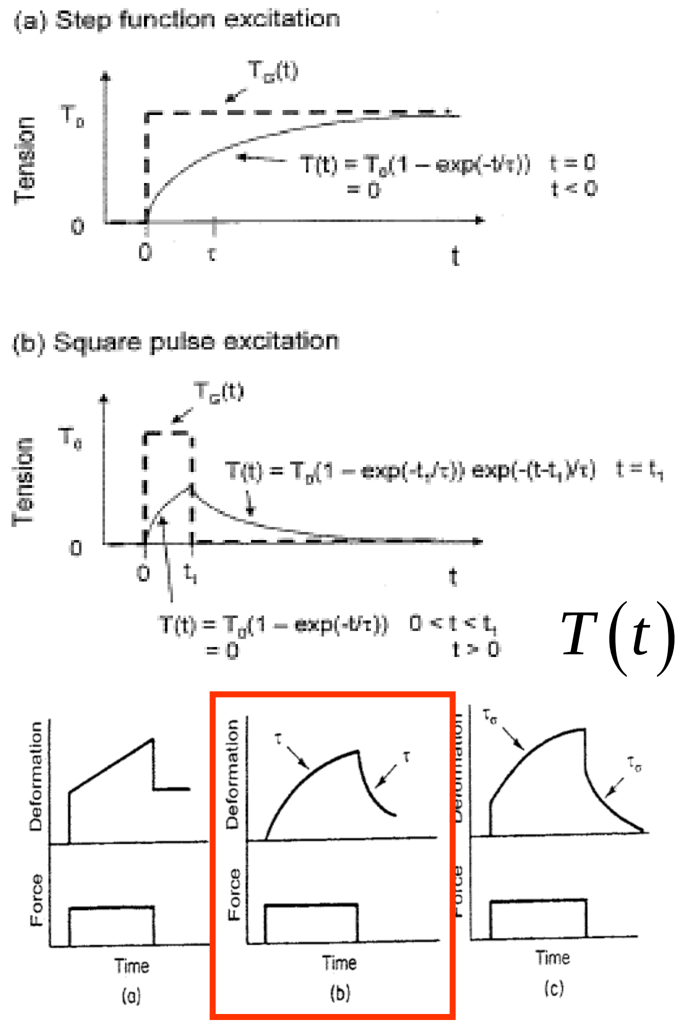


Fig. 4.58. Creep functions for the (a) Maxwell, (b) Voigt, and (c) Kelvin/linear standard models of viscoelasticity, with force loading and subsequent unloading. Characteristic relaxation times are shown. (From [198])

$$\frac{dT(t)}{dt} + \frac{T(t)}{\tau} = \frac{T_G(t)}{\tau}$$

Solución para el aumento de la tensión desde t = 0:

$$T(t) = T_0\left(1 - \exp\left(-t/\tau\right)\right) \quad \text{S1}$$

Solución para el decaimiento de la tensión desde t = t_1 :

$$T(t) = T_0\left(1 - \exp\left(-t_1/\tau\right)\right)\exp\left(-\left(t - t_1\right)/\tau\right)$$

S2

Comportamiento del tipo Voigt

RESPUESTAS DEL MODELO SIMPLIFICADO II

La aplicación del segundo pulso en t = t_1+t_2 encontrará al sistema con una tensión dada por la ecuación S2 al reemplazar t por t_1+t_2 según:

$$T\left(t_1+t_2\right)=T_0\left(1-\exp\left(-t_1/\tau\right)\right)\exp\left(-t_2/\tau\right) \qquad \text{S3}$$

de modo que al anularse el segundo pulso en t = $2t_1+t_2$ la tensión habrá alcanzado el valor de:

$$T\left(t\right)=T_0\left\{1+\left[\exp\left(-t_2/\tau\right)-\exp\left(-\left(t_1+t_2\right)/\tau\right)-1\right]\times\right.$$

$$\left.\times\exp\left(-\left(t-\left(t_1+t_2\right)\right)/\tau\right)\right\}=$$

$$T_0\left\{1-\exp\left(-t/\tau\right)+\exp\left(-\left(t+t_1\right)/\tau\right)-\exp\left(-\left(t-\left(t_1+t_2\right)\right)/\tau\right)\right\} \qquad \text{S4}$$

en la que deberá reemplazarse t por t = $2t_1+t_2$:

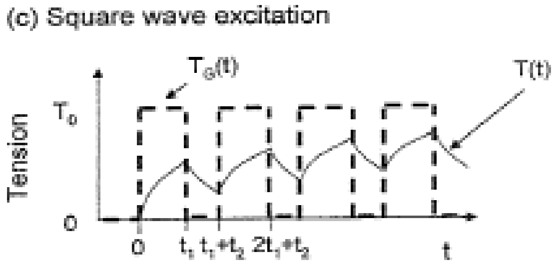
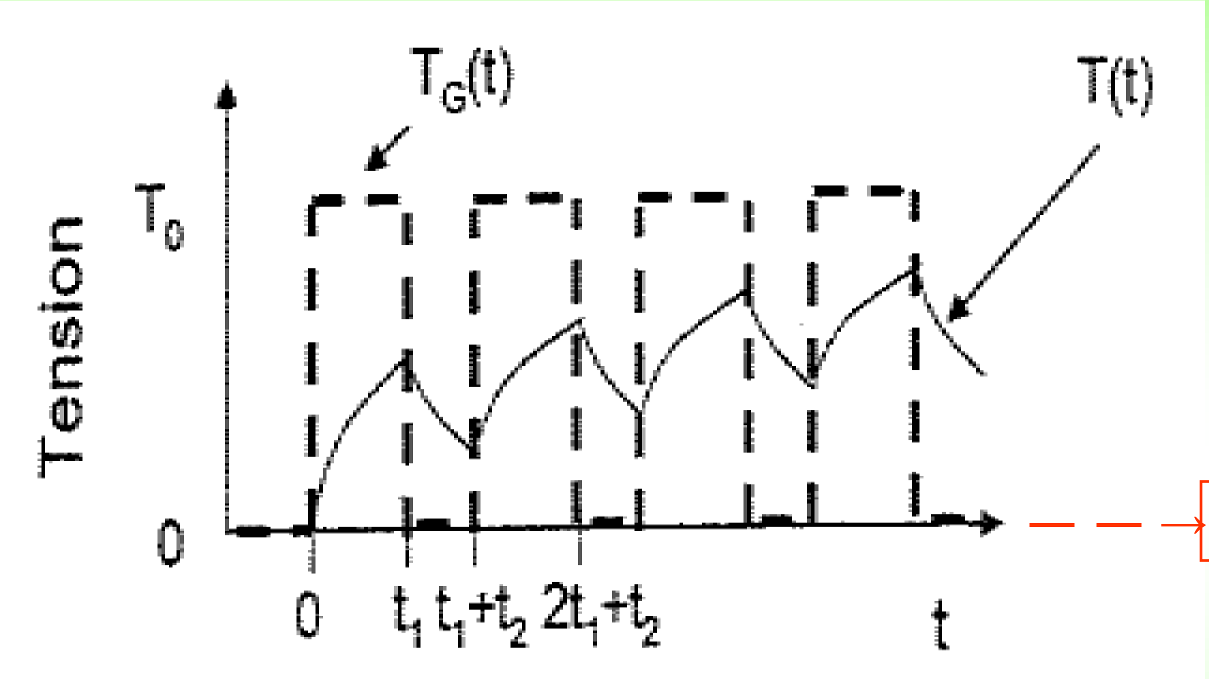


Fig. 5.16. Solutions of the active state muscle model in Fig. 5.15 for the tension with excitation by (a) a step function, (b) a square pulse, and (c) a square wave. The text derives the solution after two sequential square pulses at time $2t_1+t_2$ in (c). (Based on [271])

RESPUESTAS DEL MODELO SIMPLIFICADO III



$\rightarrow$ $Nt_1+Nt_2 = N(t_1+t_2)$

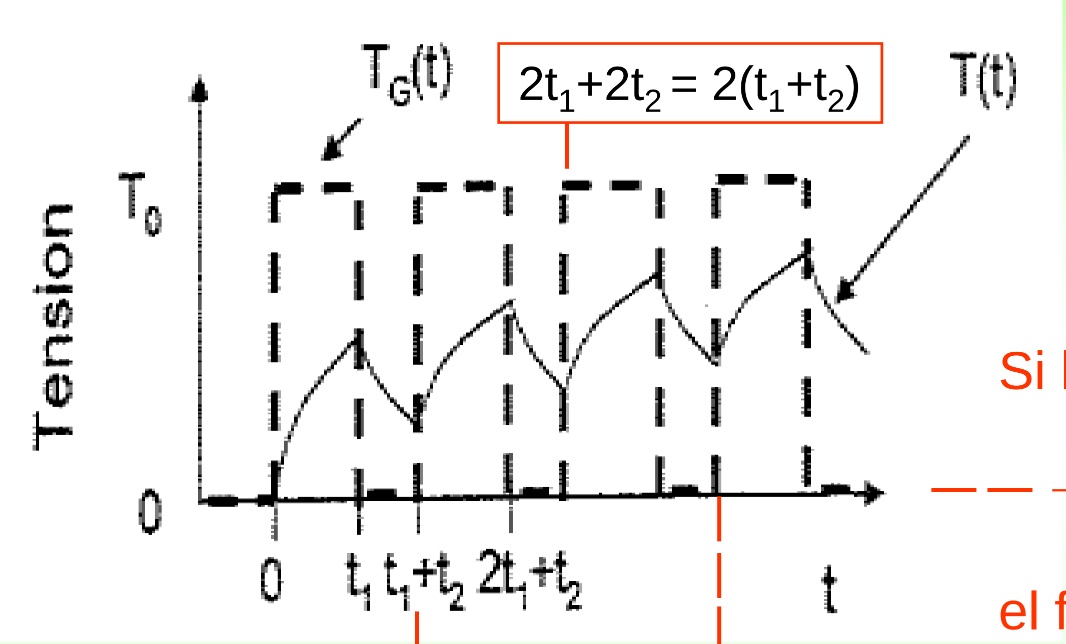
$$T(2t_1+t_2)=T_0\left\{1-\exp\left(-(2t_1+t_2)/\tau\right)+\exp\left(-(t_1+t_2)/\tau\right)-\exp\left(-t_1/\tau\right)\right\}=$$

$$T_0\left[1-\exp\left(-t_1/\tau\right)\right]\left[1+\exp\left(-(t_1+t_2)/\tau\right)\right]$$

S5

La expresión S5 indica la tensión en el sistema al finalizar el segundo pulso, la que es igual a la que tenía el sistema al finalizar el primer pulso en t_1, según la expresión S1, por el factor: $\left[1+\exp\left(-(t_1+t_2)/\tau\right)\right]$

RESPUESTAS DEL MODELO SIMPLIFICADO IV



$2t_1+2t_2 = 2(t_1+t_2)$

$t_1+t_2 = (t_1+t_2)$

$3t_1+3t_2 = 3(t_1+t_2)$

Si la cantidad de pulsos es N:

$Nt_1+Nt_2 = N(t_1+t_2)$

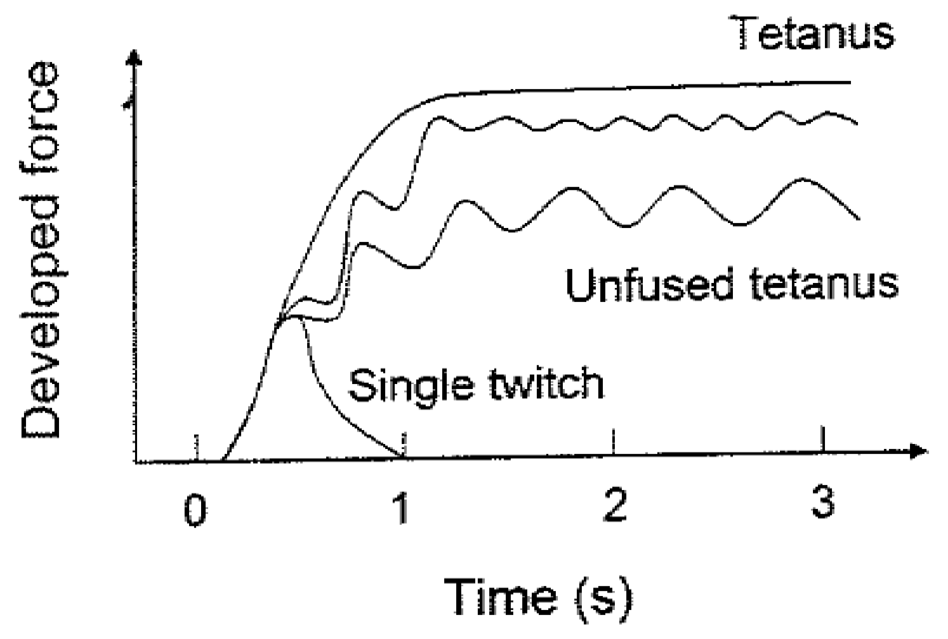
el factor resulta ser:

$$1+\exp\left(-\left(t_1+t_2\right)/\tau\right)+\exp\left(-2\left(t_1+t_2\right)/\tau\right)+\ldots+\exp\left(-N\left(t_1+t_2\right)/\tau\right)=$$

$$\sum_{n=0}^{n=N}\exp\left(-n\left(t_1+t_2\right)/\tau\right)=\left(1+\exp\left(-N\left(t_1+t_2\right)/\tau\right)\right)\Big/\left(1+\exp\left(-\left(t_1+t_2\right)/\tau\right)\right)$$

S6

RESPUESTAS DEL MODELO SIMPLIFICADO V



Como en la S6 :

$$0 < \left(\exp\left(-\left(t_1 + t_2\right)/\tau\right)\right) < 1$$

si $N \rightarrow \infty$ la S6 queda:

$$1/\left[1 - \exp\left(-\left(t_1 + t_2\right)/\tau\right)\right]$$

y por lo tanto la tensión en la tetanización resulta ser:

$$T_{Tet.} = T_0 \frac{1 - \exp\left(-t_1/\tau\right)}{1 - \exp\left(-\left(t_1 + t_2\right)/\tau\right)}$$

MODELO DE UNA RED DE N SARCOMEROS

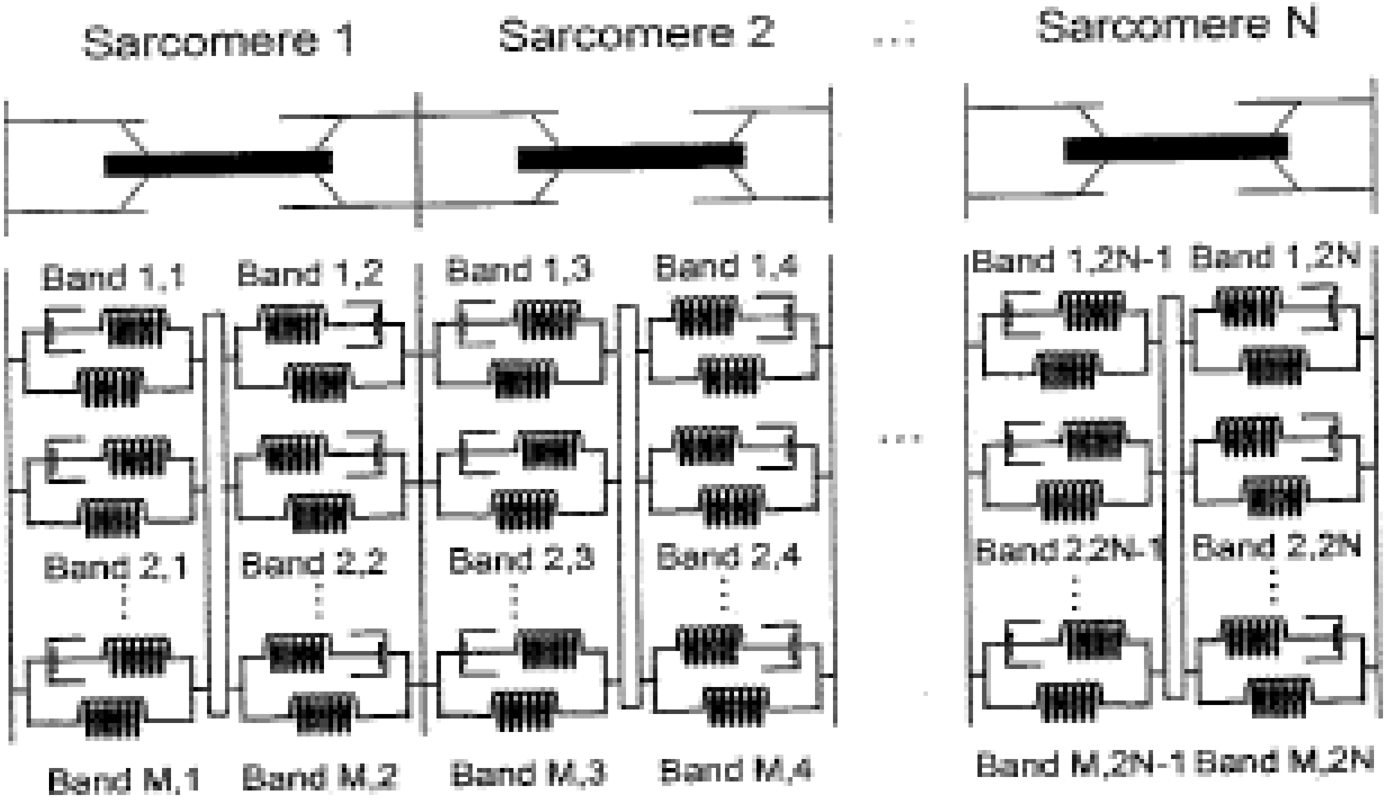


Fig. 5.17. Schematic diagram of a muscle fiber that consists of the simpler models. This more complete muscle model is built from a distributed network of N sarcomeres. (Based on [246] and [278])

- Cada músculo tiene 10^4 – 10^6 fibras musculares
- Cada fibra tiene unas 2.000 miofibrillas.
- Cada miofibrilla tiene unos 1500 filamentos gruesos.
- Cada filamento grueso tiene unas 200 moléculas de miosina (puentes cruzados).
- Todos los puentes cruzados están en paralelo. Las fuerzas se suman.
- Todas las miofibrillas en una fibra muscular están paralelas. Las fuerzas se suman.
- Todas las fibras musculares están paralelas. Las fuerzas se suman.

- Cada molécula de miosina produce una fuerza promedio de 3pN (dependiendo de su longitud)
- Luego, el esfuerzo total provisto por un músculo estándar es:

$$4\times10^{4}\times2000\times1500\times200\times3\,pN=30\,{}^{N}\!\big/_{cm^{2}}$$

Fibra por cm^2

Miofibrillas por fibra

Filamentos gruesos por miofibrilla

Moléculas de miosina por filamento grueso

Fuerza por molécula de miosina

FUERZA vs. DESPLAZAMIENTO DE LA INTERACCION DE UNA MOLECULA DE MIOSINA CON UNA DE ACTINA

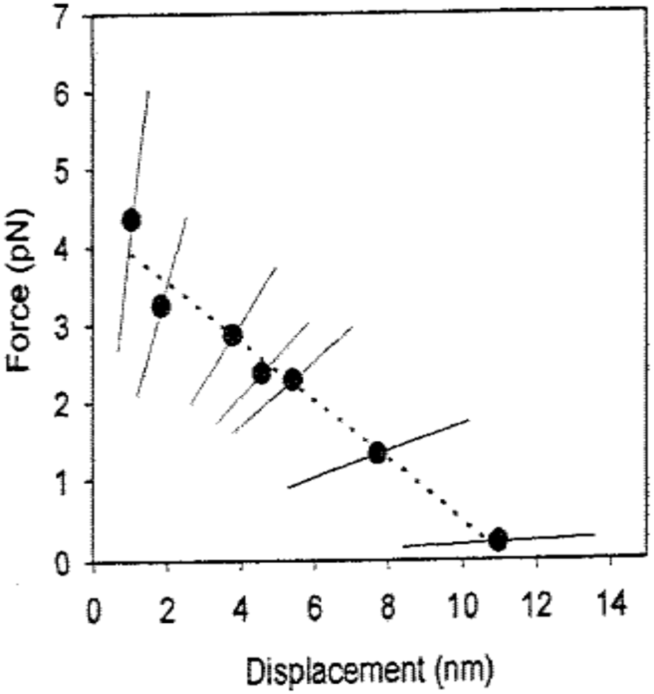
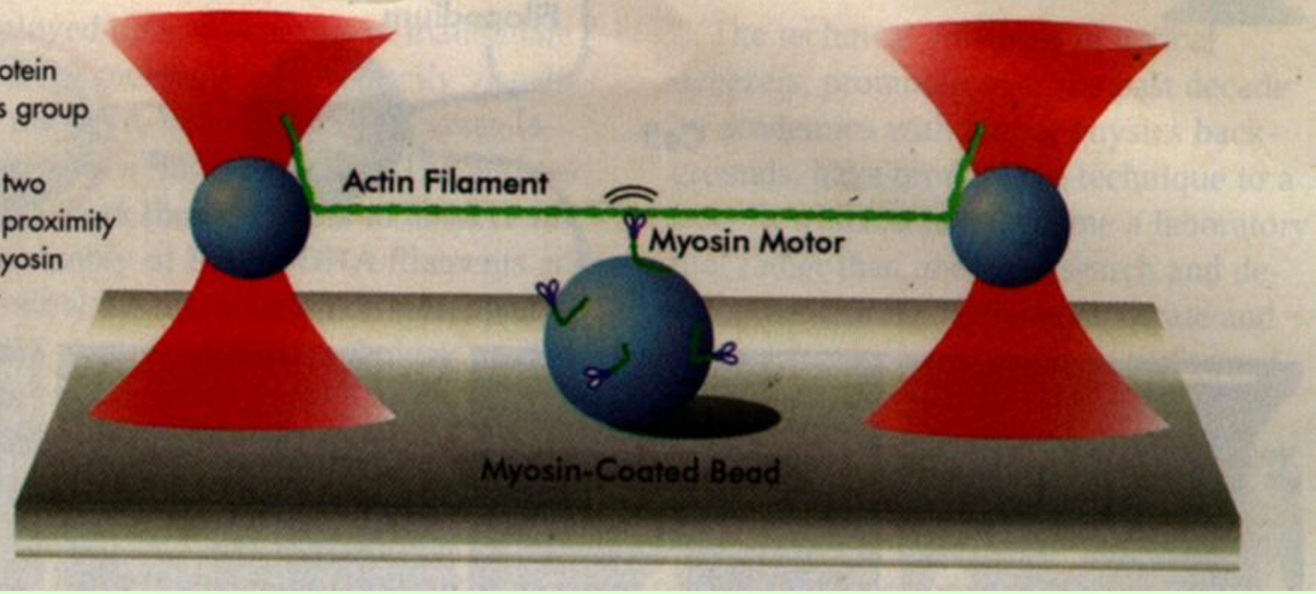


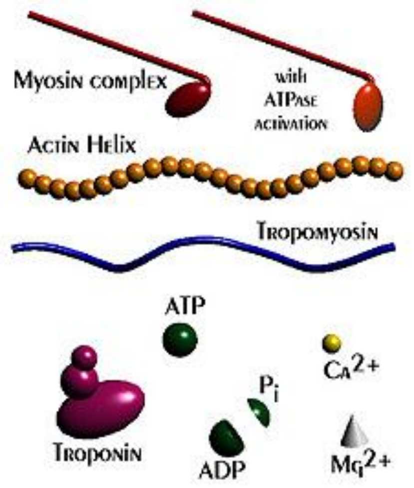
Fig. 5.36. Force vs. displacement curve of a single myosin molecule interacting with an actin molecule during a powerstroke, as measured by "optical tweezers." (From [247]. Used with permission of the Biophysical Society)

Characterization of single actin-myosin interactions. J.T. Finer, A.D. Mehta, J.A. Spudich. Biophys. J. **68**, 291s-297s, 1995.

OBSERVACION DE UN NANOMOTOR DE MIOSINA POR “OPTICAL TWEEZERS”

Figure 2. This diagram represents a motor protein motility assay as performed by Justin Molloy's group at the Medical Research Council in London. A single actin filament is suspended between two optically trapped beads and brought into the proximity of a surface-immobilized bead coated with myosin motor proteins. Motor pulling activity is transduced to the trapped beads, which can be accurately measured.





FUERZA vs. LONGITUD DEL MUSCULO O DEL SARCOMERO

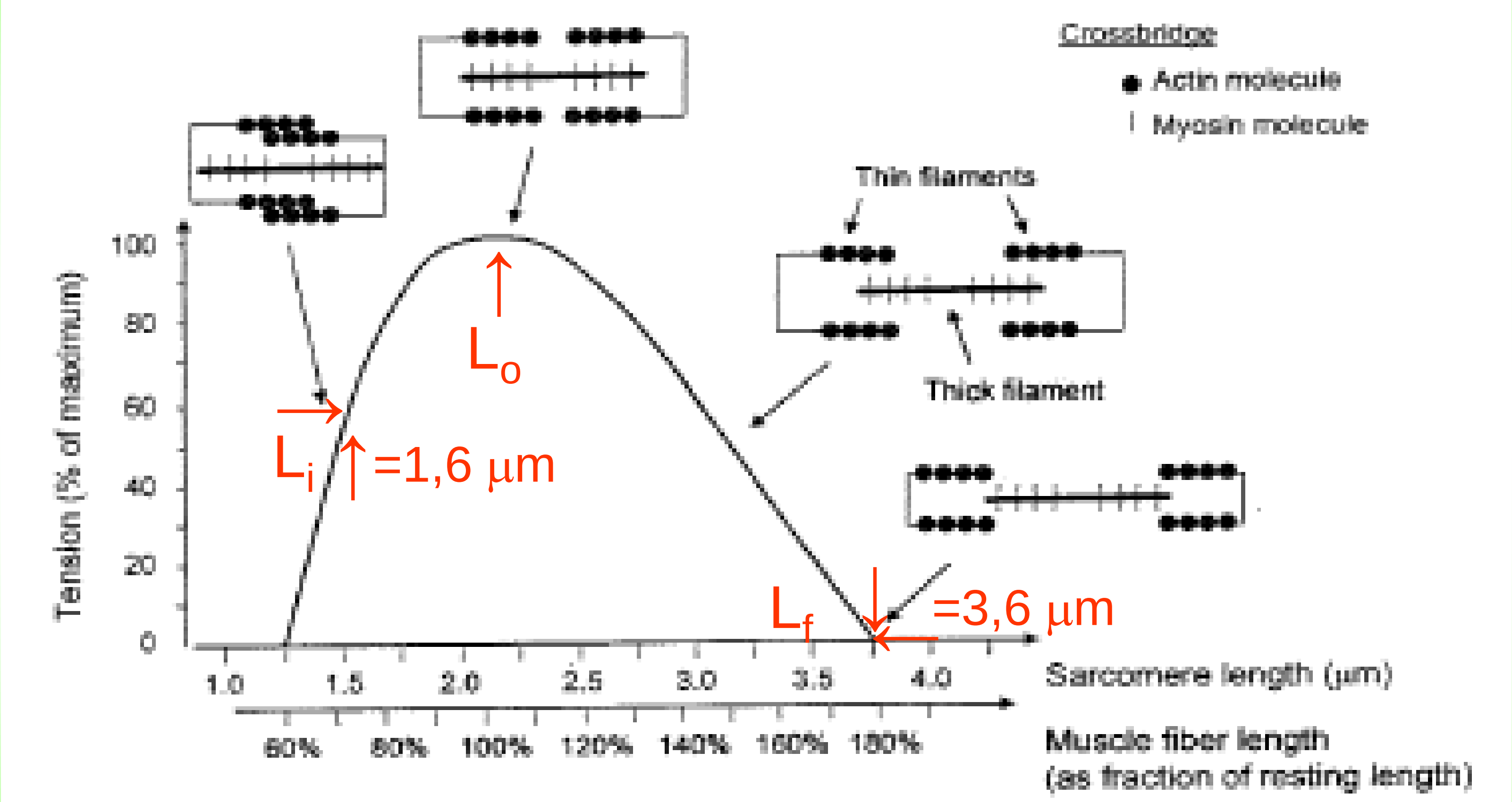


Fig. 5.23. Force vs. sarcomere or muscle length, with schematics of the variation of the overlap of the thick (myosin) and thin (actin) filaments for different sarcomere lengths. The sarcomere and total muscle lengths scale the same way. The crossbridge between an actin and myosin molecule is also shown. (Based on [254], [271], [280], and [284])

TENSION TOTAL vs. LONGITUD DE MUSCULOS TIPOS PLUMA Y PARALELO

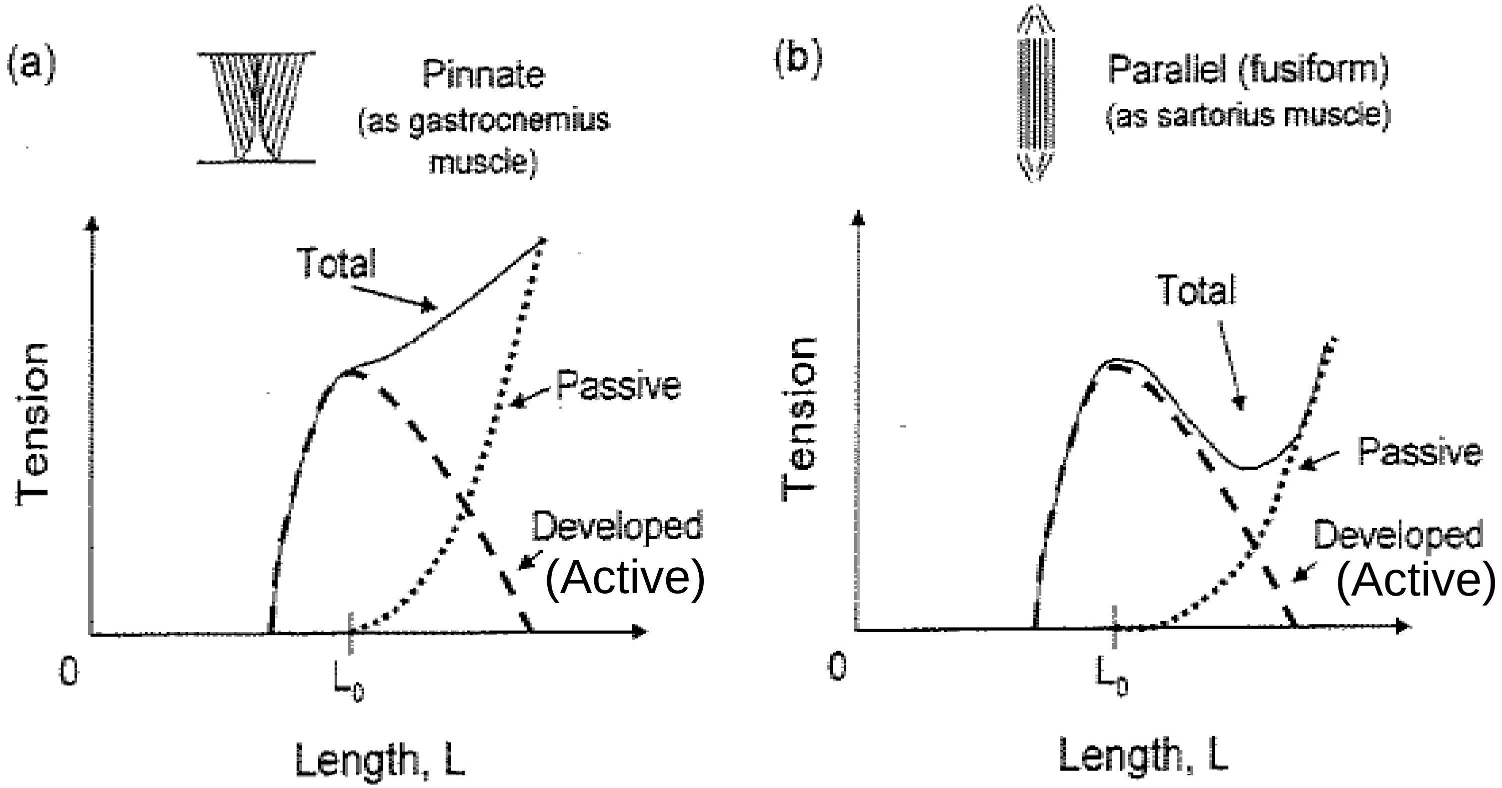


Fig. 5.25. Schematic of passive, developed (active), and total tension vs. length for pinnate and parallel muscles. (Based on [240] and [271]. Also see [237])

DIFICULTAD PARA CERRAR EL PUÑO I

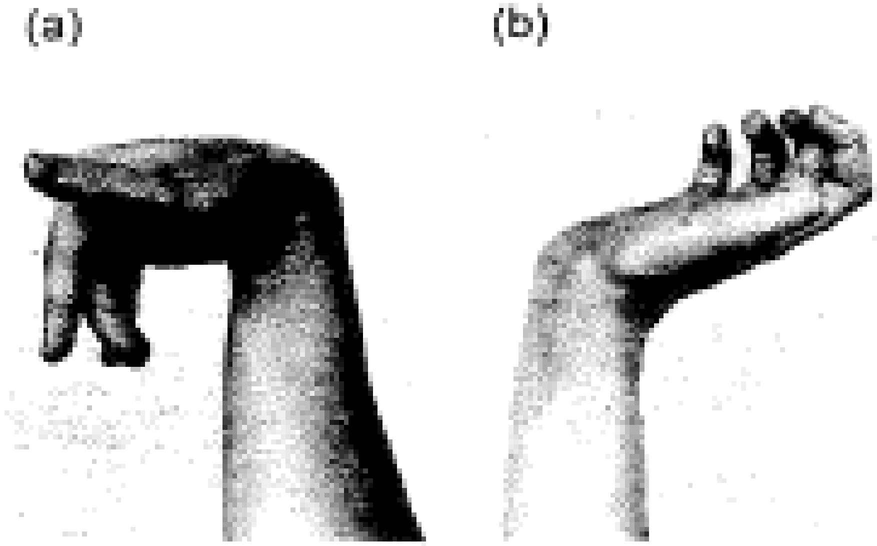
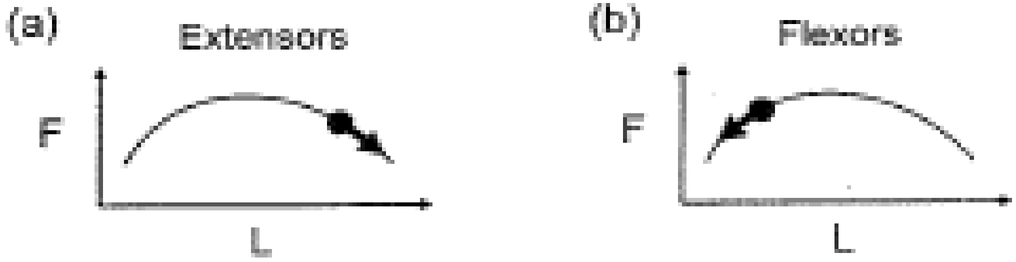


Fig. 5.28. It is difficult to clench your fist with a strongly flexed wrist (a) and straighten your fingers with a strongly hyperextended wrist (b). (From [239]. Copyright 1992 Columbia University. Reprinted with the permission of the press)

DIFICULTAD PARA CERRAR EL PUÑO II



Clenching a flexed wrist

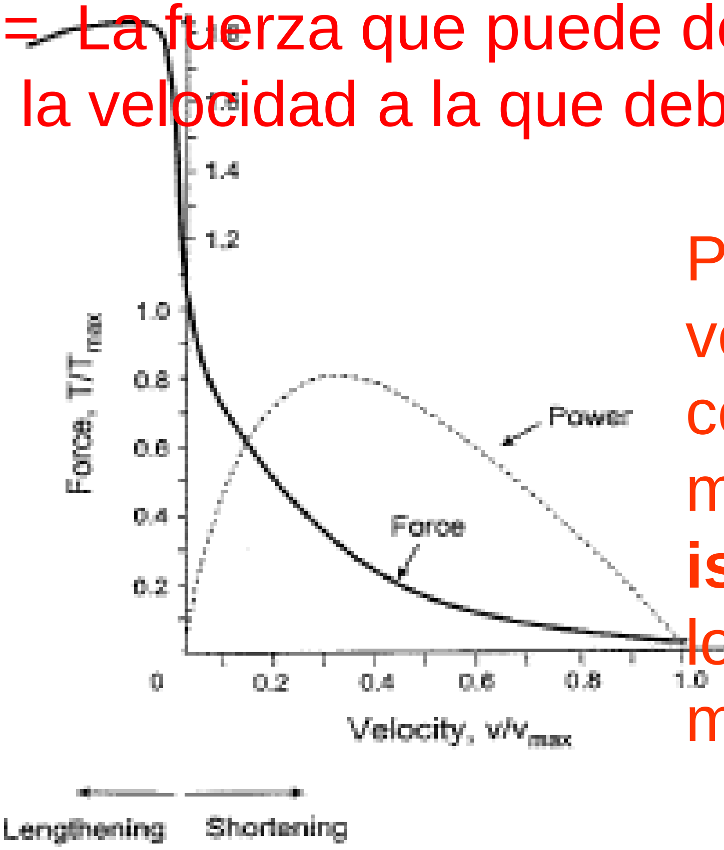
Straightening fingers in a hyperextended wrist

Fig. 5.29. Schematic of forces on extensors and flexors for clenching a flexed wrist and straightening fingers in a hyperextended wrist as shown by the closed circles. The arrows show the continued slackening or stretching described in the text

CURVA FUERZA vs. VELOCIDAD DE HILL

La velocidad a la que se contrae un músculo depende de lo tensionado que esté = La fuerza que puede desarrolla un músculo depende de la velocidad a la que debe contraerse.

La velocidad de contracción del músculo se mide con uno de sus extremos fijos y el otro cargado por una pequeña masa, **isotónicamente**.



Pero cuando la velocidad v = 0 las contracciones del músculo se hacen **isométricas**, su longitud no se modifica.

Fig. 5.30. Hill force–velocity curve. Both muscle shortening and lengthening are shown. Power = Force × velocity, is also shown, with arbitrary vertical units. (Based on [271])

Archibald V. Hill, Premio Nobel de Fisiología o Medicina (1922) por la demostración de la producción de calor por los músculos.

CURVA FUERZA vs. VELOCIDAD DE HILL II

Región hiperbólica

$$\left[T(v)+a\right](v+b)=\left(T_{Máx}+a\right)b$$

$$\left[T(v)+a\right]=\frac{\left(T_{Máx}+a\right)b}{(v+b)}$$

$$T(v)=\frac{T_{Máx}b+ab}{(v+b)}-a$$

$$T(v)=\frac{bT_{Máx}-av}{v+b}$$

$$P(v)=T(v)\times v=v\frac{bT_{Máx}-av}{v+b}$$

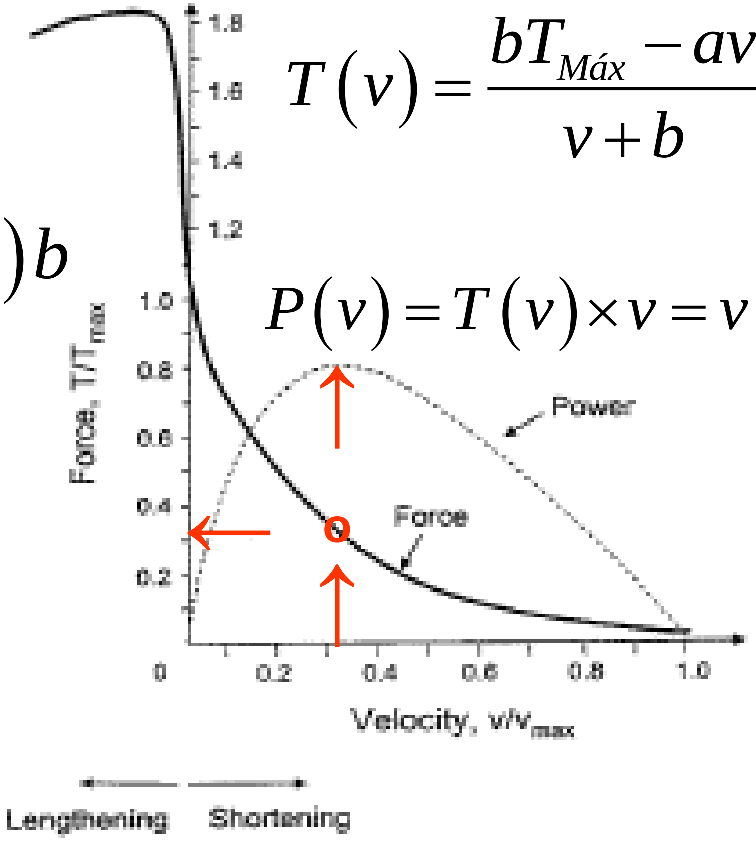


Fig. 5.30. Hill force–velocity curve. Both muscle shortening and lengthening are shown. Power = Force × velocity, is also shown, with arbitrary vertical units. (Based on [271])

CURVA FUERZA vs. VELOCIDAD DE HILL III

$$v \geq 0,3 v_{Máx}$$

$$T \geq 0,3 T_{Máx}$$

$$P\left(v \geq 0,3 v_{Máx}\right) \approx 0,1 v_{Máx} \times T_{Máx}$$

Región hiperbólica

$$\left[T\left(v\right)+a\right]\left(v+b\right)=\left(T_{Máx}+a\right)b$$

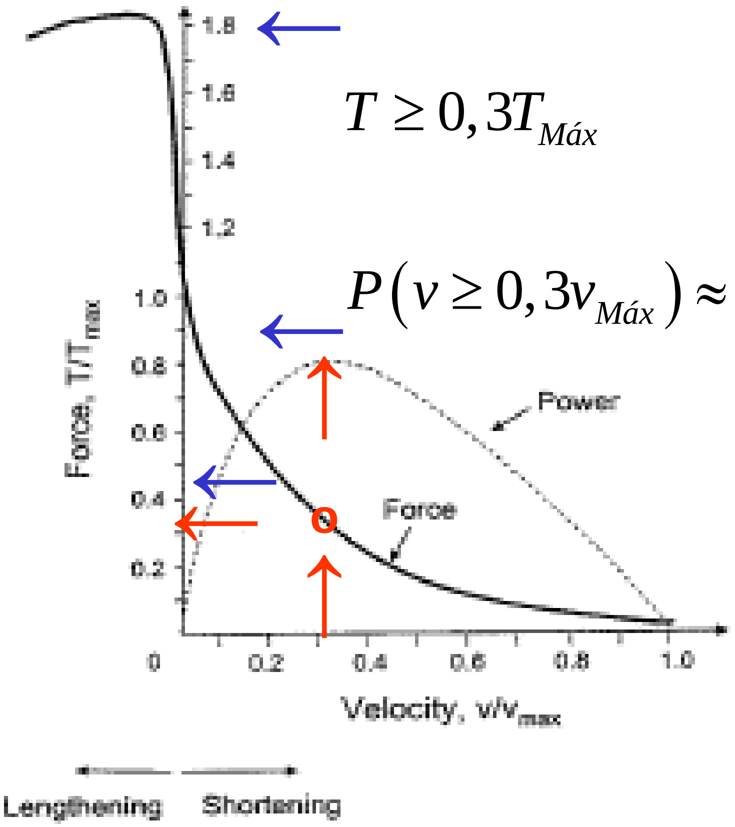


Fig. 5.30. Hill force–velocity curve. Both muscle shortening and lengthening are shown. Power = Force × velocity, is also shown, with arbitrary vertical units. (Based on [271])

PARAMETROS DE HILL

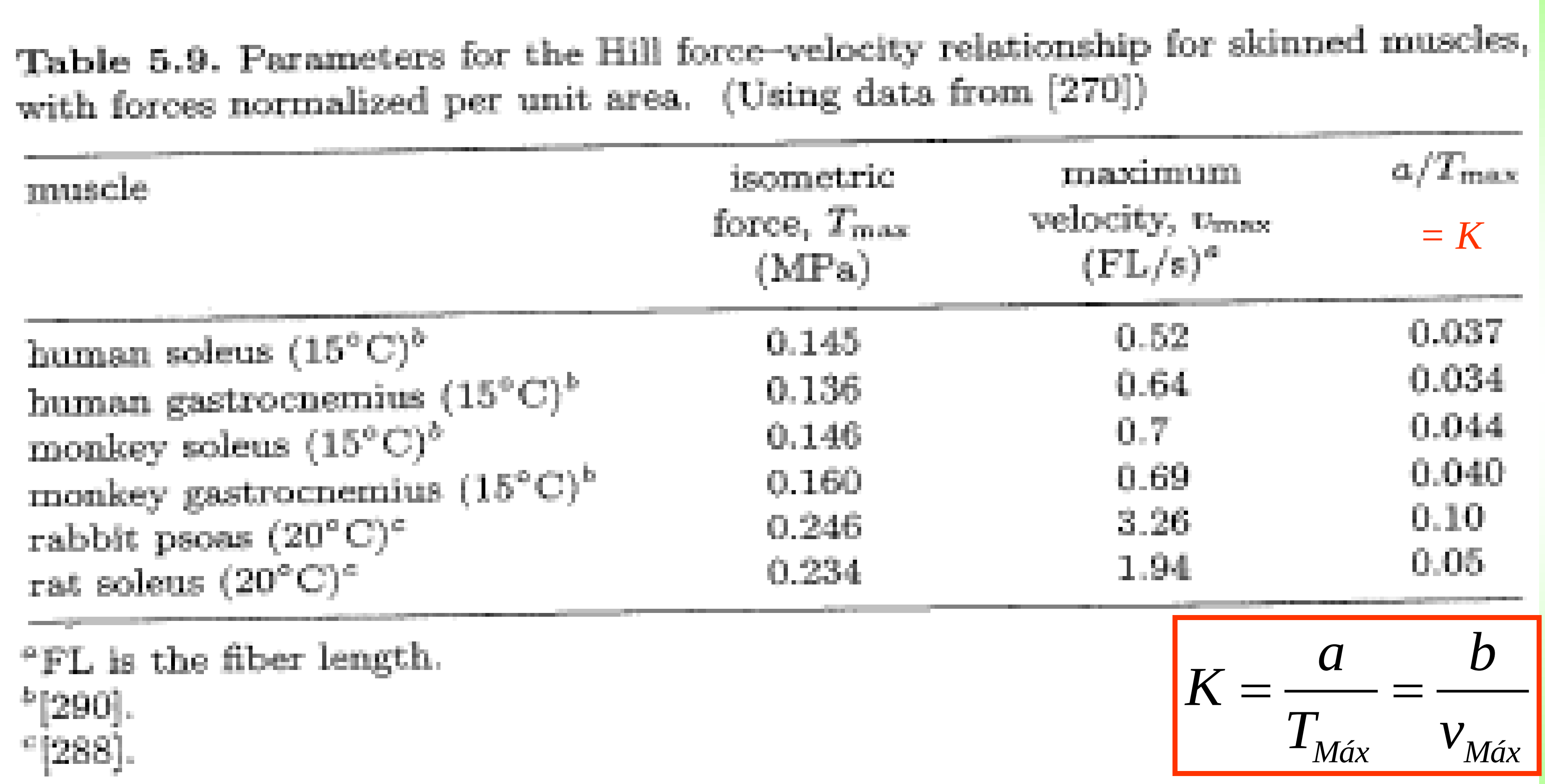


Table 5.9. Parameters for the Hill force–velocity relationship for skinned muscles, with forces normalized per unit area. (Using data from [270])

muscle	isometric force, T_{max} (MPa)	maximum velocity, v_{max} (FL/s)[a]	a/T_{max} $= K$
human soleus (15°C)[b]	0.145	0.52	0.037
human gastrocnemius (15°C)[b]	0.136	0.64	0.034
monkey soleus (15°C)[b]	0.146	0.7	0.044
monkey gastrocnemius (15°C)[b]	0.160	0.69	0.040
rabbit psoas (20°C)[c]	0.246	3.26	0.10
rat soleus (20°C)[c]	0.234	1.94	0.05

[a] FL is the fiber length.
[b] [290].
[c] [288].

$$K = \frac{a}{T_{Máx}} = \frac{b}{v_{Máx}}$$

DIAGRAMA 3D DE UN MUSCULO ACTIVO

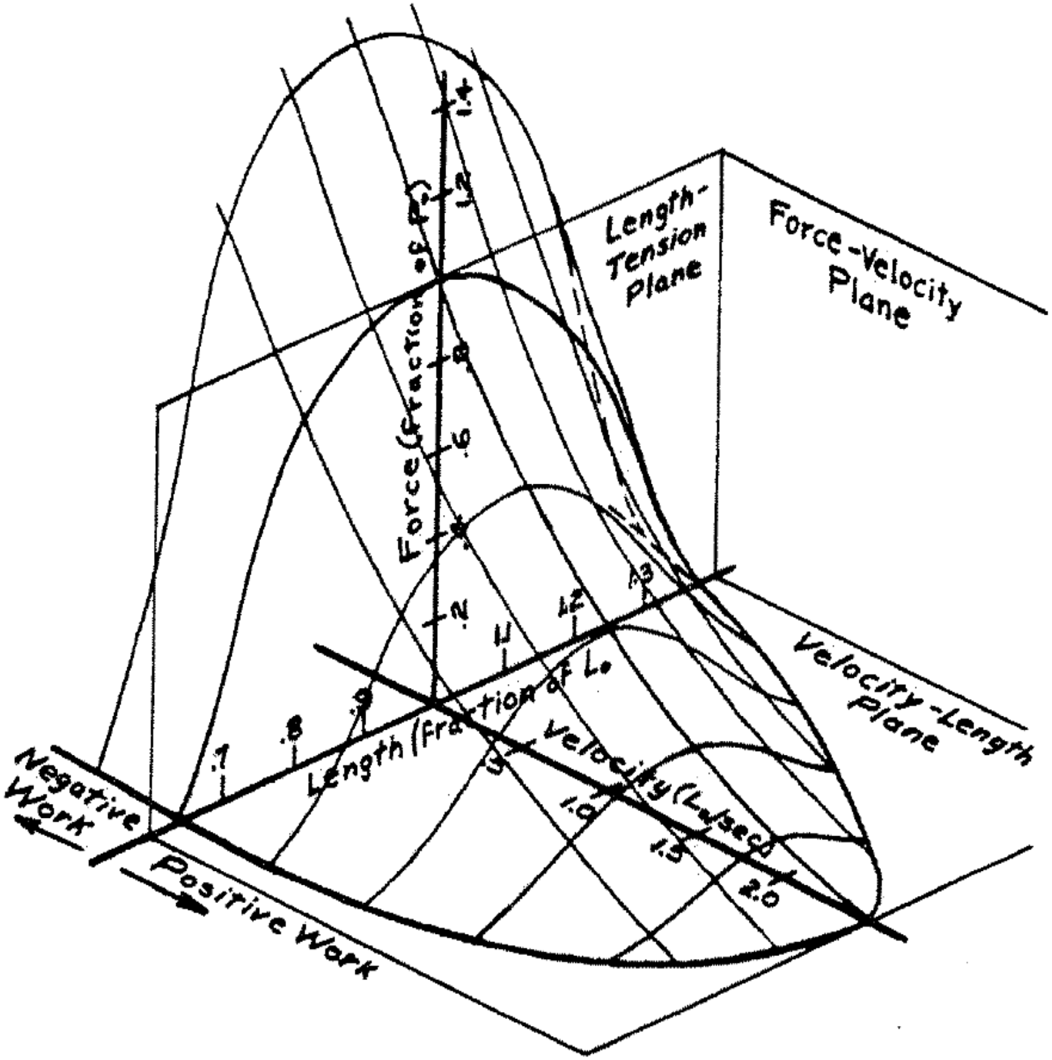


Fig. 5.33. Three-dimensional plot showing the tension of the active part of a muscle vs. velocity and length. This is for maximum muscle activation and excludes the passive muscle response. (From [292]. Reprinted with permission of Wiley)

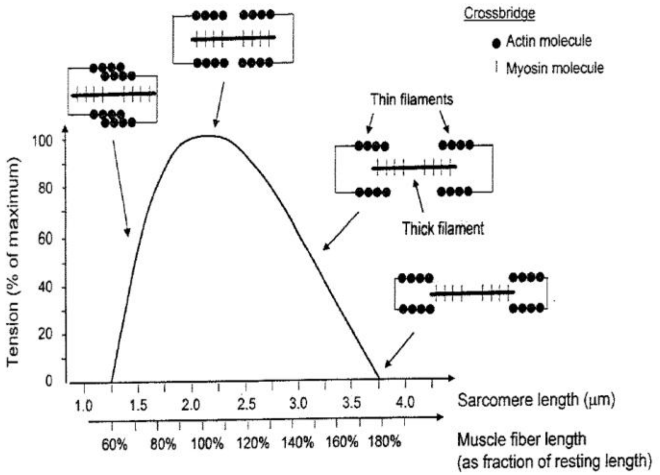


Fig. 5.23. Force vs. sarcomere or muscle length, with schematics of the variation of the overlap of the thick (myosin) and thin (actin) filaments for different sarcomere lengths. The sarcomere and total muscle lengths scale the same way. The crossbridge between an actin and myosin molecule is also shown. (Based on [254], [271], [280], and [284])

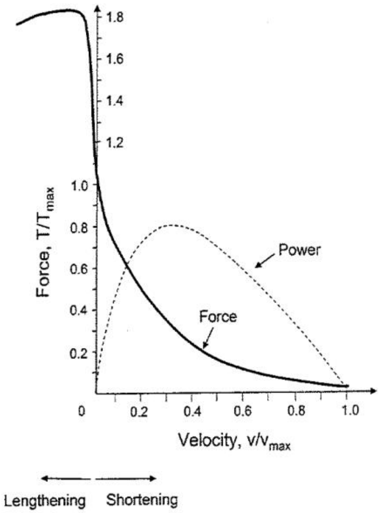


Fig. 5.30. Hill force–velocity curve. Both muscle shortening and lengthening are shown. Power = Force × velocity, is also shown, with arbitrary vertical units. (Based on [271])