

Functional Anatomy of the Association between Motor Units and Muscle Receptors

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SYNOPSIS. Muscle spindles and tendon organs occur in most somatic muscles of the mammal and are particularly concentrated in muscles subserving fine movements, including postural muscles and small muscles of the distal extremities. In those mixed muscles in which the different fiber and motor unit types are "compartmentalized," the spindles, and perhaps tendon organs also, are virtually limited to those compartments predominated by "oxidative" muscle fibers. These morphological observations based on a broad array of muscles in many species, complement electrophysiological studies which have emphasized that (1) the "oxidative" motor units have low reflex thresholds and (2) segmental proprioceptive reflexes may be primarily concerned with the control of finely graded contractions. Consideration of the functional anatomy of the association between motor units and muscle receptors suggests the need for detailed structural-functional analyses of those muscles with specializations in architecture, fiber-type composition and distribution, and in the number and distribution of their muscle spindles and tendon organs. An electrophysiological analysis of the relationship between the spinal cord and such muscles might also reveal certain strategies and mechanisms underlying segmental motor control which are either absent or obscured in the analysis of that select number of "homogenously-mixed" muscles conventionally used in the study of the mammalian segmental motor control system.

INTRODUCTION

Nearly all of the data on the properties and central actions of mammalian muscle receptors have been derived from experiments employing a limited number of "standard" cat hind limb muscles. While these models have yielded a great deal of information, several emerging viewpoints on the segmental motor system can best be developed through the analysis of different types of muscles, where structure and function may reveal control strategies which are either absent or have been obscured in previous studies of conventionally-used muscles. In this report, we will briefly summarize present views on the segmental reflex effects of muscle spindles and tendon organs and

point out how consideration of the functional anatomy of the association between motor units¹ and muscle receptors contributes to our understanding of the mammalian segmental motor control system.

SEGMENTAL PROPRIOCEPTIVE REFLEXES

Since the function of muscles is to contract and ultimately to move, resist or be pulled by loads, it is not surprising that nature would endow them with length and force receptors; and indeed, muscle spindles and tendon organs are distributed throughout most mammalian muscles (Fig. 1). The discharge patterns of muscle spindle primary (1a) and secondary (group II) afferent endings indicate that these receptors are exquisitely sensitive to small changes in length, while the tendon or-

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¹The term "motor unit" is used whenever the neuronal component of the unit is included in the reference (*e.g.*, isolation, activation, recruitment, etc.). The term "muscle unit" is used to refer only to the muscle fiber component of a unit (*e.g.*, contraction, tension, contraction time, etc.).

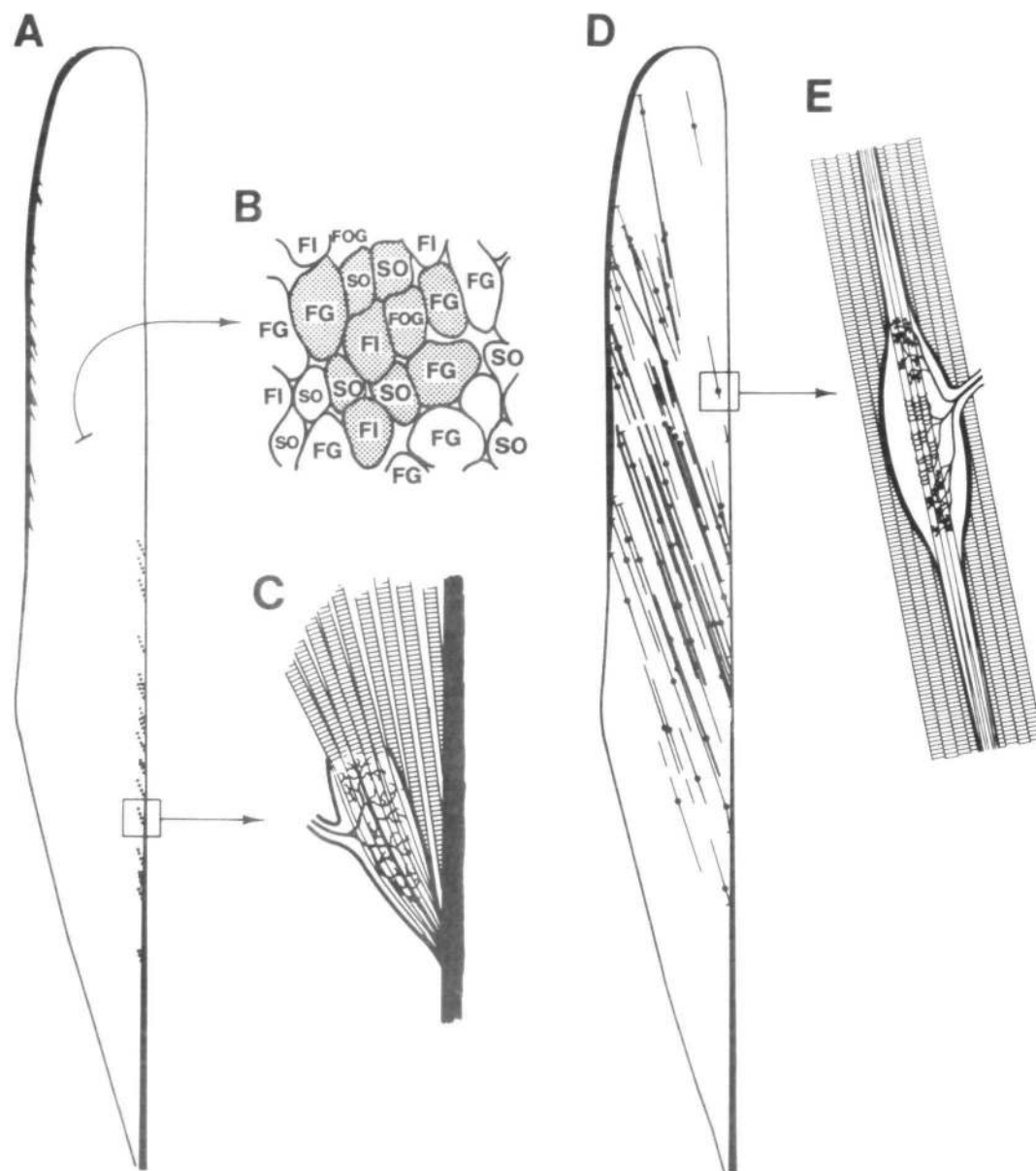


FIG. 1. Number and distribution of muscle spindles and Golgi tendon organs in a mixed mammalian muscle. *A* and *D* are modified from Swett and Eldred (1960) and are schematic lateral views of the left medial gastrocnemius of a 1 kg kitten. *A* shows tendon organs beneath the superficial aponeurosis of origin (continuous lines) and those lining the deep distal aponeurosis (dotted lines). There are 44 tendon organs in all; 25 proximal and 19 distal. Not included are tendon organs within the tendon proper which usually comprise about 7% of the total number (Barker, 1974). *D* shows the location of 70 spindles (defined as a discrete bundle of intrafusal fibers possessing a well-defined nuclear region), including those that might share a capsule or be connected in tandem with another spindle. Note that: (1) areas at each end of the muscle are unoccupied so

that perhaps 40% of the muscle is without spindles; and, (2) superficial spindles are prominent in medial gastrocnemius such that the areas of tendon organ distribution along the aponeurosis correspond with areas where spindles attach (see also Fig. 5). *B* shows a typical cross section of adult cat medial gastrocnemius (courtesy of V. R. Edgerton) with muscle fibers labeled as SO, FOG, FG, and FI (intermediate between FG and FOG for NADH-D stain). The cross-hatched fibers represent those inserting onto a typical tendon organ capsule as shown schematically in *C* and illustrate how the different fiber types are intermingled. *E* shows the relation of a spindle capsule to adjacent skeletomotor fibers. Spindle orientation is generally parallel to the course of the skeletomotor fibers and they lie either in clefts between fascicles or within the fascicles themselves (Barker, 1974).

gans, innervated by Ib afferents, are comparably sensitive to small changes in force (for review on spindles, see Matthews, 1972; and Homma, 1976; and for tendon organs, see Reinking *et al.*, 1975; Fukami and Wilkinson, 1977; Binder *et al.*, 1977; and Houk *et al.*, 1978). The fact that the amount of force generated by a muscle, or any of its component motor units, varies with both muscle length and prior activation history (Burke *et al.*, 1976), attests to the need for both length and force feedback signals (*cf.*, Binder and Stuart, 1978). It follows then that any model of segmental proprioceptive control of muscle behavior should feature input from both spindles and tendon organs as has been emphasized by Houk and his colleagues (Houk, 1972, 1974, 1976, 1978; Crago *et al.*, 1976; Nichols and Houk, 1976). Their model is based on the mechanical variables and the neural signals that are known to change during a stretch reflex. The mechanical responses result from the dependence of muscular force on muscle length (and velocity) changes, whereas reflex actions result from the balanced interplay exerted on motoneurons between excitation attributable to length-related spindle input and inhibition resulting from force-related tendon organ input.

Houk and his colleagues have suggested that proprioceptive reflexes regulate muscle stiffness and in so doing improve the linearity of length-dependent muscle mechanics. This viewpoint implies to us both that mammalian skeletal muscle has been "improperly" designed to the extent that it requires moment-to-moment reflex corrective-assistance to perform movements against even constant loads, and that the mammalian nervous system "prefers" to deal with strictly linear input-output systems. Thus, while we are attracted to Houk's model with respect to its emphasis on autogenetic motoneuronal input from both spindles and tendon organs, we feel that additional studies are required for a full delineation of the functional significance of this dual input. In our view, for example, the muscle spindles and tendon organs might provide complementary input to the motoneurons. The input is used in fine control modulation of their discharge patterns, providing compensation for minor perturbations within the muscle (Binder and Stuart, 1978). This viewpoint, too, of course, requires extensive experimental testing.

While the Houk model (for schematic, see Fig. 25-3 in Houk, 1974, and for its most recent elaboration, see Houk, 1978) emphasizes the monosynaptic ex-

citatory pathway between spindle Ia afferents and their homonymous motoneurons, it is presumably sufficiently flexible to include all other spindle pathways, including at the segmental level a weaker and less prevalent monosynaptic excitatory spindle group II pathway (Stauffer *et al.*, 1976), spindle Ia and group II excitation by way of spinal interneurons, and a presynaptic inhibitory control of the monosynaptic pathways also largely by way of interneurons. There may even be alternative pathways whereby force and length feedback can exert effects of opposite sign on the motoneurons as dictated by the operation of other internuncial circuits. In all such additional cases, the role of the CNS-control signals become more complex, but the concept of an interplay between force and length feedback is preserved.

Furthermore, it is presumably recognized in the Houk model that there are no "private" interneurons in muscle receptor afferent pathways to motoneurons. All such interneurons studied to date receive excitatory and inhibitory inputs from a variety of peripheral and central sources (see, for example, Lundberg *et al.*, 1977). Until proven otherwise, it is nonetheless attractive to speculate that for certain discretely controlled movements, the purely autogenetic effects predominate, while in other instances (*e.g.*, stepping) "interneuronal sharing" plays a major role in the coordination of muscle activity across different joints.

In any model which incorporates both muscle receptor types into the moment-to-moment reflex control of muscle, it is important to remember that the extent to which such reflex effects have significance depends on the relationship between the nature of the movement being executed and on the efficacy of reflex transmission through the spinal cord. For example, in many movements encountering external perturbations, the speed and power of the contractions and perturbations are sufficiently great that segmental reflex effects are either too late or too feeble (Binder and Stuart, 1978) to accomplish an appropriate compensation. In such instances, the organism may rely on the viscoelastic properties of the moving parts themselves. In recent years, several studies have emphasized the advantage to a motor control system of having stiffness built into the active musculature, such that it can be, more or less, "on its own" at certain phases of more demanding movements (Rack, 1970; Grillner, 1972).

In light of growing evidence that segmental proprioceptive reflexes are incapable of providing effective load compensa-

tion for large perturbations (Matthews, 1972; Freedman *et al.*, 1976; Bizzi and Polit, 1978; Bizzi *et al.*, 1978), it has been proposed that this system might be designed to deal with the smaller disturbances that arise due to internal factors within the neuromuscular system itself (Evarts, 1978). These small internal disturbances (arising in muscle and/or the nervous system) generate positional errors even in the presence of fixed external loads. The smallest and most natural internal disturbance that occurs in muscle is the contraction of a single motor unit during the graded development of muscle force. Elsewhere, we have reviewed recent evidence that the normal function of spindles and tendon organs is not restricted to detection of changes in whole muscle length (spindles) and force (tendon organs). Rather, we have proposed that particularly during vernier² contractions, both the Ia and group II afferents of muscle spindles and the Ib afferents of tendon organs can monitor the activity level (reflected in muscle fiber length and force changes) of a discrete number of muscle units within the parent muscle, with this monitoring modulated both by fusimotor input to the spindles and by the overall length-tension status of the parent muscle (Binder and Stuart, 1978).

To accommodate these changing views on the functional design of this system, we believe it is profitable to restructure the Houk model somewhat, as shown in Figure 2. Our major modification consists of delineating the territory of a single muscle unit, innervated by a single alpha (α) or beta (β) motoneuron, within the parent muscle, which permits an intramuscular localization of proprioceptive reflexes. We propose that the excitability of the overall

motoneuronal pool is modulated by ensemble (collective) force and length afferent feedback, while within this pool, individual motoneurons receive a weighted ensemble input, resulting from a disproportionate contribution from afferents whose receptors lie within the territory of the muscle unit innervated by that motoneuron (see Binder and Stuart, 1978).

Most movements studied to date feature a co-activation of alpha and gamma motoneurons to the active musculature, and our model includes this fusimotor drive. It produces a "tonic" spindle discharge that provides supportive excitation to the active motoneurons, and at the same time makes the spindles sufficiently sensitive to detect minor perturbations or irregularities in muscle performance resulting in modulation of afferent input to the relevant motoneurons, a mechanism we believe to be of functional importance only in the elaboration of vernier contractions.

In summary, we are suggesting that any model of segmental motor control must take into account the transducing properties and spinal connections of both spindles and tendon organs. Their ensemble input characterizes whole muscle length and force and is presumably of value for the modulation of efferent outflow in all forms of movement. Segmental proprioceptive reflexes themselves seem to be more efficacious when motoneurons are at or near their threshold (Matthews, 1972; Binder and Stuart, 1978), a situation that is prone to occur during the elaboration of vernier movements. In this instance, only a small percentage of the muscle's motor units are in operation at any one time, and the spindles and tendon organs are sufficiently sensitive and ideally suited to monitor their activity at this level.

When the motor nucleus-muscle-muscle receptor complex is viewed in this light, then the properties and anatomical arrangement of motor units are inexorably tied to the properties and distribution of spindles and tendon organs. Furthermore, the interactions that can occur between motor units and these muscle receptors (both centrally and peripherally) become a

² A "vernier" movement is defined as one produced by the finely controlled and graded contractions of the contributing muscles, each utilizing but a small percentage of their maximum force output (5-10%). Such movements and contractions (also termed vernier) are not restricted to skilled voluntary ones engaging primarily the forelimbs. Rather, it is envisioned that most muscles of the body can contribute to vernier movements and that they can occur during postural, locomotor, and other forms of "subconsciously" or "automatically" controlled movements.

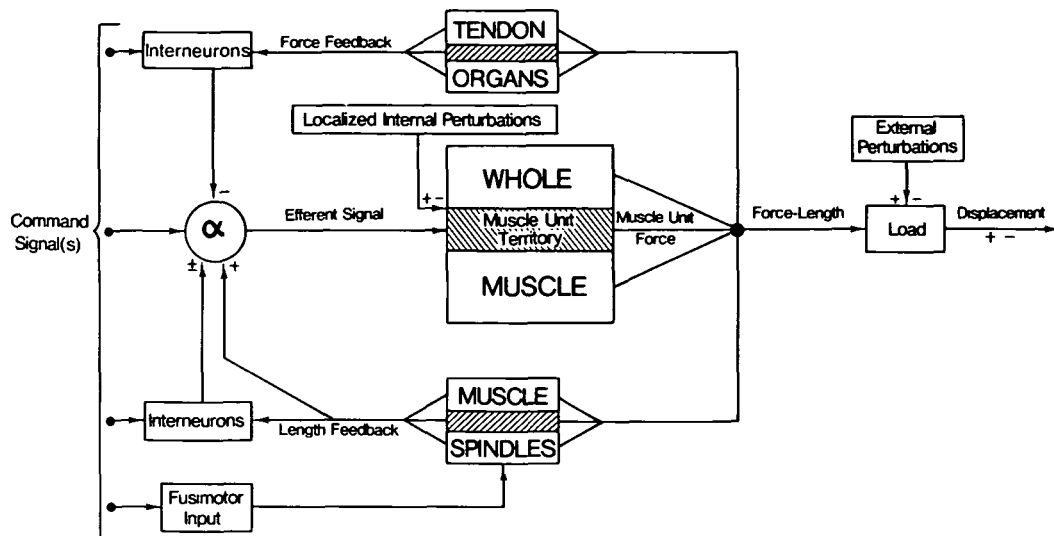


FIG. 2. Block diagram of segmental control of muscle activity. The model is similar to that proposed by Houk (1974), but accommodates the possibility of intramuscular reflex localization by providing the α -motoneurons with a "weighted ensemble input" from both spindles and tendon organs. The cross-hatched portion of the muscle block represents the territory of a single muscle unit. Its activity contributes to changes in whole muscle force and length. The cross-hatched portions of the tendon organ and muscle spindle blocks represent those receptors whose discharge patterns are strongly affected by the muscle unit's contraction. The same receptors are responsive to other units whose territories converge and overlap with the muscle unit shown here. The ensemble input to a motoneuron is then a weighted

sample, reflecting a disproportionate contribution from those receptors located within its muscle unit's territory. Factors affecting fine control of movements include localized internal disturbances resulting from fatigue and the asynchronous activation of single motor units, and external perturbations generated by changes in body position, irregularities in the environment, etc. Muscle spindle feedback originates from both primary and secondary afferent endings, both of which contribute to monosynaptic excitation (subject to presynaptic inhibition) as well as additional excitatory and inhibitory effects which are mediated through a variety of interneurons. The tendon organ pathway is limited to autogenetic inhibition (polysynaptic), although alternative circuitry might be operating under various conditions.

key element in understanding the design and function of the proprioceptive components of the segmental motor control system.

The large number of muscle receptors found in most mammalian muscle may simply be another example of the CNS's tendency to obtain "diminishing returns" from its extensive neuronal machinery. In this case, a sizeable investment is required to obtain a truly fine control of vernier contractions. This principle is readily apparent when one considers the surprisingly subtle deficits in motor performance of animal preparations with deafferented limbs, or with partial or complete destruction of central structures such as the dorsal columns of the spinal cord, the cerebellum and the pyramidal tract(s).

THE PROPERTIES AND RECRUITMENT OF MOTOR UNITS

The properties of motor units have al-

ready been reviewed at this symposium (Burke, 1978). Due largely to recent work from the laboratories of Henneman and Burke, we know a great deal concerning the neural and mechanical properties of different types of motor units and their recruitment order in the graded development of muscle force (Henneman and Olson, 1965; Henneman *et al.*, 1974; Henneman and Harris, 1976; for review of motor unit types, see Burke, 1975; and for recruitment order, Burke, 1977). For the present purposes, the main features of this work are listed below.

1. Motor units are composed of histologically and histochemically similar muscle fibers that are conveniently lumped into the following categories: SO (slow twitch-oxidative) fibers in type S (slow

twitch, non-fatigable) units; FOG (fast twitch-oxidative-glycolytic) fibers in type FR (fast twitch-relatively fatigue resistant) units; and FG (fast twitch-glycolytic) fibers in type FF (fast twitch-highly fatigable) units. It is also necessary to recognize a spectrum of muscle fibers (FI) between the FOG and FG types, that are incorporated into FI units, whose fatigabilities range between those of FR and FF units.

2. The muscle fibers of a single unit (all of which extend in most muscles from aponeurosis of origin to aponeurosis of insertion) are scattered in checkerboard array throughout a limited territory of the muscle (approximately 15-30% of the cross-sectional area). In mixed mammalian muscles, the different motor unit types can be mixed relatively homogeneously, but in many cases there is a predominance of one or two unit types in different portions of a muscle (see below).

3. During the *normal* graded development of muscle force, there is a progressive recruitment of S, FR, FI and finally, FF units. Thus, the "oxidative" motor units (S and FR) have lower functional thresholds and are more likely to be involved in vernier movements and contractions than the more "glycolytic" motor units (FI and FF). This orderly recruitment occurs even in the reflexes of the decerebrate and low spinal preparations. While its underlying mechanism involves many factors (Burke, 1977), this property of orderly recruitment is obviously a key aspect of segmental motor control in that it enables the CNS to delegate a major fine control responsibility to the spinal cord itself.

If spindles and tendon organs serve largely as monitors of motor unit activity for the reflex control of vernier contractions, then their number, distribution, behavior and reflex effects should be consistent with the type, distribution and orderly recruitment of motor units within each mammalian muscle. The remainder of this report is concerned with the extent to which the anatomical features of motor unit-muscle receptor interrelations may provide critical information on this issue.

SOME ANATOMICAL COMPARISONS ACROSS MUSCLES

In studies extending across many mammalian species, spindles and tendon organs have been observed in each striated somatic muscle that operates on a joint(s), develops relatively substantial force and is subject to unpredictable loads. This limits spindle-free muscles to a few innervated largely by cranial nerves (Barker, 1974). In some cases, such as the extraocular muscles, those in one species may possess spindles, while those in another lack them. Tendon organ-free muscles have not been searched for so extensively, but tendon organs may be absent in small muscles that have few spindles (*e.g.*, rat tail muscles, Barker, 1974), or in muscles that develop unusually small forces (*e.g.*, cat tenuissimus, Palmer and Stilwell, 1958; and deep lumbrical muscles, Barker, 1974).

These relatively unusual situations are illustrations of a potential contribution from vertebrate morphology, in that information on differences in the way various species control and use spindle-free and/or tendon organ-free muscles might provide insight into the functional role of these receptors. However, for the present purposes, interest is focused not so much on comparing muscles that have and do not have these receptors, but rather on why some muscles are receptor-rich and some receptor-poor and what implications these differences have for segmental motor control.

With few exceptions then, striated muscles contain a number of spindles and tendon organs scattered throughout them. In general, and as can be seen for the cat in Table 1, there are more spindles in anti-gravity postural muscles and in muscles controlling the fine movements of the head and the distal extremities than in the muscles used for relatively coarse movements. As reviewed by Cooper (1966), Boyd and Davey (1968), Matthews (1972), Barker (1974), Richmond and Abrahams (1975b) and Lund *et al.*, (1978), spindle counts are now available for over 30 muscles in the cat and for a smaller number of muscles in such widely scattered mammalian species as monkey, horse, dog, rabbit, rat, and at least seven ungulates (for full bibliographies, see Eldred *et al.*, 1967; Barker, 1974; and Eldred *et al.*, 1977). For the human, Voss (1971) has compiled an ex-

tensive list of spindle counts which includes 230 muscles.

Tendon organ counts, which are technically more difficult to obtain, are far less numerous. In the cat, for example, they are available for only 11 muscles (Table 1), and their distribution has been studied in only four of these (Swett and Eldred, 1960; Lund *et al.*, 1978; see also, Bridgman, 1968). Taking a variety of indirect anatomical factors into account (Boyd and Davey, 1968; Marchand *et al.*, 1971; Barker, 1974; Richmond and Abrahams, 1975b), it is probably safe to conclude that they will usually be more numerous in muscles that are also rich in spindles, but this point should be verified further.

To compare the density of receptors across muscles, a number of different indices have been used including spindles/gram adult muscle weight (*cf.*, Barker, 1974), spindles/motor unit (Swett and Eldred, 1960), motor units/spindle (Boyd and Davey, 1968) and spindles/100 motor units (Matthews, 1972), all of which demonstrate a wide range in values (*e.g.*, 4 spindles/g to 173 spindles/g in Table 1). However, to assess what functional significance this dramatic range might bear, we must obtain a great deal more information about individual muscles. Important characteristics include gross architecture, histochemical composition and distribution of fibers, number of muscle units per muscle weight, mechanical properties and innervation ratios of muscle units, number and spatial distribution of receptors, and homonymous segmental projections of the receptor afferents, as well as the muscles' and their individual motor units' contribution to, and "activity level" in, a variety of movements. As yet such complete characterizations have been obtained only for cat medial gastrocnemius and soleus, although partial descriptions exist for a wide variety of muscles in cat and other mammals. Even in the case of cat medial gastrocnemius and soleus, the available information has not been fully collated and synthesized, but must be extracted from a number of different sources (see, however, Burke, 1978).

If the hypothesis that muscle receptors are largely concerned with the fine control

of movements is valid, then one might expect that they be more numerous in muscles containing a high percentage of "oxidative" muscle fibers, since these fibers are innervated by motoneurons with lower reflex thresholds than those innervating "glycolytic" fibers (Burke, 1975, 1977). The histogram in Figure 3 shows the distribution of an "oxidative" index (sum of % SO and % FOG fibers) for the 31 cat hind limb muscles studied by Ariano *et al.* (1973) along with each muscle's spindle density (if known). Most upper and lower leg muscles contain all three fiber types, each comprising at least ten percent of the total fiber count. Soleus and vastus intermedius stand out as atypical being composed almost exclusively of SO fibers. These muscles are particularly active during the maintenance of posture, and at least in cat and rat, soleus is known to be relatively rich in both spindles and tendon organs. Tensor fascia latae and caudofemoralis (at least in the cat) are also atypical being composed almost exclusively of FG fibers (85% and 91%, respectively). EMG studies of treadmill locomotion of the dog have shown that tensor fascia latae is minimally active even in galloping (Tokuriki, 1973), while in the cat it is perhaps silent in standing and walking, and minimally active in unrestrained trotting and galloping (Rasmussen *et al.*, 1978). The hypothesis stated above would predict that this muscle should be receptor-poor but no counts are available to date.

Although it would be of interest to know if the three muscles with the highest "oxidative" indices (soleus, vastus intermedius, cruralis) have higher receptor densities than the two with the lowest indices (tensor fascia latae, caudofemoralis), the values in Figure 3 illustrate that receptor density is not correlated with the "oxidative" index alone and presumably muscle usage must be taken into account. For example, soleus is entirely "oxidative" with a relatively high spindle density (23 spindles/g) which is consistent with its postural role. In contrast, flexor digitorum longus (45 spindles/g) and flexor hallucis longus (23 spindles/g) are also relatively rich in spindles, yet their "oxidative" indi-

TABLE 1. Values of spindle and tendon organ indices in certain cat muscles shown in relation to muscle fiber-type composition, and arranged in order of decreasing spindle indices.^a

Muscle	FIBER TYPE ^b (%)				"Oxidative" Mean index ^c weight of motor (%) (g) units			SPINDLES			TENDON ORGANS		
	SO	FOG	FC					Mean no.(N)	No./g	No./motor unit	Mean No.(N)	No./g	No./motor unit
3rd Lumbrical (forelimb) ^d					0.04			7 (4)	173				
5th Interosseus (forelimb) ^e					0.21			25 (20pr)	119				
5th Interosseus (hindlimb) ^{g,h}					0.33			29 (4)	88		25 (4)	76	
Complexus ^{o,p}	39	29	32		2.52	68		222 (2)	88				
Biventer cervicis ^{o,p}	49	23	28		1.71	72		140 (3)	82				
Extensor digitorum brevis ^{k,l,m}					0.8		115	56 (1)	70	0.49	35 (1)	44	0.30
Rectus capitis major ^{o,p}	25	29	46		0.68	54		42 (4)	62				
Splenius ^{o,p}	26	20	54		2.92	46		170 (3)	58				
Tenuissimus ^{l,m,n,u}	20	24	56		0.3	44	20	15 (?)	50	0.75	0.1	0.3	0.00-0.05
Flexor digitorum longus ^{h,j,l,m}	7	32	61		1.06	39	155	48 (20pr)	45	0.31	17 (1)	16	0.11
Flexor carpi radialis ^e	35	28	37		1.27	63		53 (4)	42				
Tibialis posterior ^{l,j,m}	21	19	60		0.78	40	60	31 (20pr)	39	0.52		24	
4th Intercoastal (ext. and int.) ^{h,w}					1.4			49 (1)	35				
2nd External intercostal ^d					0.7			18 (3)	27				
Flexor hallucis longus ^{j,m}	14	23	63		3.25	37	255	75 (20pr)	23	0.29			
Popliteus ^{l,m,u}	4	30	66		1.5	34	120	34 (?)	23	0.28			
Soleus ^{j,j,m}	100	0	0		2.49	100	155	56 (20pr)	23	0.36	45 (1)	18	0.29
Semitendinosus ^{h,j,l,m}	17	18	65		6.41	35	255	114 (20pr)	18	0.45	86 (3)	13	0.34
Extensor digitorum communis ^d					1.3			22 (2)	18				
Flexor digitorum superficialis ^d					2.2			35 (2)	17				
Occipitocapularis ^{o,p}	56	18	26		0.66	74		11 (3)	17				
Tibialis anterior ^{e,l,m}	19	20	61		4.57	39	200	71 (20pr)	15	0.36			
Extensor carpi radialis longus ^d					1.3			18 (4)	14				
Rectus femoris ^{e,m}	22	17	61		8.36	39		104 (20pr)	12		78 (9)	9	
Temporalis ^{n,s,v}	10	8	82		6.6	18		74 (1)	11		20 (1)	3	
Masseter ^{l,n,s,v}	2	26	72		3.2	28		34 (1)	11		6 (1)	2	
Biceps brachii ^{d,a}	20	21	59		6.4	41		53 (4)	9				
Medial gastrocnemius ^{l,j,m}	25	14	61		7.34	39	280	62 (20pr)	9	0.22	44 (1)	6	0.16
Extensor digitorum longus ^{l,m,u}	14	31	55		3.4	45	130	21 (?)	6	0.16			
Sartorius ^{d,m}	30	24	46		11.4	54		66 (2)	6				
Lateral gastrocnemius ^{l,m}	18	16	66		7.61	34		35 (20pr)	5				
Rectus abdominus ^d					20.5			87 (2)	4				

ces are only at the median level. These two muscles no doubt subserve some postural role, but they are also particularly engaged in the fine control of the digits, with flexor digitorum longus concerned with even finer control than flexor hallucis longus (Goslow *et al.*, 1972). Similarly, the diaphragm which is involved in relatively coarse movements has a high "oxidative" index, at least in the rat (80% computed from data in Gauthier, 1970), but has a relatively small number of spindles and tendon organs as indicated electrophysiologically in the cat (Corda *et al.*, 1964).

A particularly detailed muscle-muscle receptor analysis has been done by Richmond and Abrahams (1975*a, b*) for five neck muscles of the adult cat. As shown in Table 2, these include two slow-twitch muscles (occipitoscapularis and biventer cervicis) in which the "oxidative" indices are relatively high (74% and 72%, respectively), while the spindle densities are vastly different (17/g and 82/g, respectively). Occipitoscapularis is not involved in control of the head but rather with elevation of the scapula. Its spindle count, while generous, is closer to that of the muscles of the cat hind limb. In contrast, biventer cervicis not only plays a postural role in the maintenance of head position, but it is also

involved in the control of head movements, which are known to be unusually finely tuned (see, for example, Lindsay *et al.*, 1976). The spindle density of biventer cervicis (82 spindles/g) is one of the highest shown yet for the cat. Note further in Table 2, that excluding the occipitoscapularis muscle, the remaining four muscles are all involved in both postural and fine control; in this instance, the correlation between spindle density and the "oxidative" index holds reasonably well.

At this stage, it would appear that a high "oxidative" index occurs together with a high spindle density when a muscle is involved in vernier contractions including those associated with postural adjustments. Conversely, a high percentage of FG fibers and a low spindle density are to be expected in muscles whose use is restricted to relatively coarse and powerful movements. Exceptions to these generalizations require detailed but as yet largely unavailable information on the quality of the movements in which the muscle participates.

In addition to comparisons of receptor and muscle fiber-type content across muscles, we must also consider the distribution of these receptors and muscle fiber types within each muscle. In our opinion, this issue may be of critical importance in delineating certain control mechanisms in the

^a Spindle and tendon organ indices expressed as number of receptors per gram adult muscle weight and per motor unit.

^b For fiber-type nomenclature see Peter, Barnard, Edgerton, Gillespie and Stempel (1972).

^c Defined as the sum of the % SO and % FOG fibers.

^d Oshima (1938) from Hosokawa (1961).

^e Barker and Chin (1960).

^f Swett and Eldred (1960).

^g Ip (1961).

^h Barker (1962).

ⁱ Boyd (1962).

^j Chin, Cope and Pang (1962).

^k Eldred, Bridgman, Swett and Eldred (1962).

^l Boyd and Davey (1968).

^m Ariano, Armstrong and Edgerton (1973).

ⁿ Taylor, Cody and Bosley (1973).

^o Richmond and Abrahams (1975*a*).

^p Richmond and Abrahams (1975*b*).

^q Collatos, Edgerton, Smith and Botterman (1977).

^r Gonyea and Ericson (1977).

^s Lund, Richmond, Touloumis, Patry and Lamarre (1978).

^t Barker, personal communication; see also Palmer and Stilwell (1958).

^u Eldred, personal communication.

^v present work.

^w mean weight estimated.

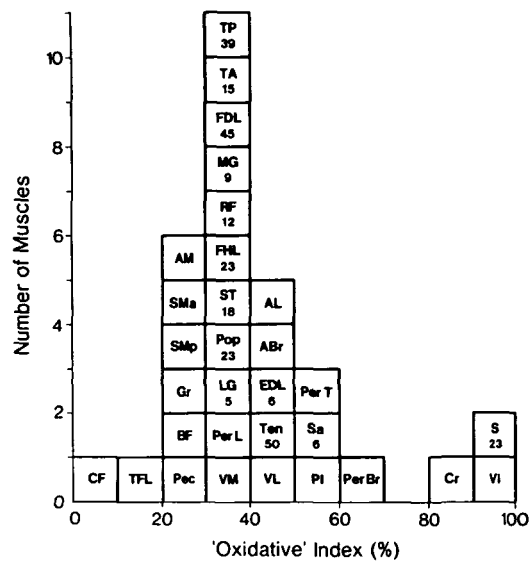


FIG. 3. Distribution of "oxidative" indices for 31 cat hindlimb muscles based on data from Ariano *et al.* (1973). Numbers in muscle block represent spindles/g of muscle tissue as based on data assembled in Table 1. Muscle abbreviations from left to right include: CF, caudofemoralis; TFL, tensor fascia latae; Pec, pectineus; BF, biceps femoris; Gr, gracilis; SMp, semimembranosus posterior; SMA, semimembranosus anterior; AM, adductor magnus; VM, vastus medialis; Per L, peroneus longus; LG, lateral gastrocnemius; Pop, popliteus; ST, semitendinosus; FHL, flexor hallucis longus; RF, rectus femoris; MG, medial gastrocnemius; FDL, flexor digitorum longus; TA, tibialis anterior; TP, tibialis posterior; VL, vastus lateralis; Ten, tenuissimus; EDL, extensor digitorum longus; ABr, adductor brevis; AL, adductor longus; PI, plantaris; Per T, peroneus tertius; Sa, sartorius; Per Br, Peroneus brevis; Cr, cruralis (often considered to be a part of VI); VI, vastus intermedius; and S, Soleus.

segmental motor system, and will be elaborated in the remainder of this discussion.

SOME FEATURES OF INTRAMUSCULAR DESIGN

In muscles where the distribution of muscle fiber and motor unit types is relatively homogenous, and the spindles and tendon organs are scattered relatively evenly throughout the muscle, each receptor should respond to the contraction of the different types of motor units around it. In adult cat medial gastrocnemius, physiological experiments have been performed in our laboratory to show that this may indeed be so for the tendon organs (Reinking *et al.*, 1975). In that study, probability theory was used to conclude that each tendon organ usually clasps a single fiber from each of 10 to 11 single muscle units and that the receptor should be particularly responsive to the action of each of these truly "in-series" units. It was further argued that if the 44 tendon organs in medial gastrocnemius (Swett and Eldred, 1960) are each connected to an average of 10.5 muscle fibers (Barker, 1974), then the maximum possible number of muscle units that could be connected to these tendon organs is 462 (10.5×44). This number is considerably greater than 280 motor units reported by Boyd and Davey (1968) for medial gastrocnemius. We reasoned (pp. 509-510) that the most uniformly representative arrangement would involve 98 muscle units contributing a single fiber to a

TABLE 2. Relation between fiber-type percentages, "oxidative" index, spindle counts and spindle index in cat dorsal neck muscles.

Muscle ^a	Fiber type ^b (%)			"Oxidative" index (%)	Spindle counts ^c		
	FG	FOG	SO		Muscle wt. (g)	No. of spindles	Spindle index ^d
Occipitocapularis	26	18	56	74	0.66	11	17
Biventer cervicis	28	23	49	72	1.71	140	82
Complexus	32	29	39	68	2.52	222	88
Rectus capitis major	46	29	25	54	0.68	42	62
Splenius	54	20	26	46	2.92	170	58

^a All values mean of 3 different muscles except spindle counts for complexes (N = 2).

^b From Richmond and Abrahams (1975a).

^c From Richmond and Abrahams (1975b).

^d Spindles per gram of adult muscle weight.

single tendon organ and 182 contributing a fiber to each of two tendon organs.

In retrospect, however, there are three problems not addressed in the Reinking *et al.* (1975) analysis. The first involves the fact that the territory of the average muscle unit in medial gastrocnemius is approximately one-fifth the total cross-sectional area of the muscle (Burke and Tsairis, 1973). If there were a relatively even spacing of tendon organs along the borders of this muscle, then each muscle unit should have within its territory 8-9 tendon organs (*i.e.*, 44/5), which suggests that motor units insert muscle fibers into a select number of tendon organs within their territories, and exert "in-parallel" effects on others.

The second problem arises from the assumption in the original Reinking *et al.* (1975) analysis that in the adult medial gastrocnemius there was a relatively even spacing of tendon organs along the borders of the aponeurosis of origin and insertion. In the kitten, however, Swett and Eldred (1960) have emphasized that "perhaps 40% of the muscular part of the gastrocnemius is without spindles." Careful inspection of their Figure 2 (included in the present Fig. 1) suggests that this may also be the case for the tendon organs. Furthermore, there is a potential change in the distribution of these muscle receptors throughout the muscle as immature animals grow to adulthood (Yellin, 1969). This could result in an even more uneven spindle and tendon organ distribution than shown for kitten medial gastrocnemius.

Finally, the third problem arises from the fact that the distribution of muscle fiber and motor unit types is not truly homogenous in most adult mammalian muscles. At one extreme are muscles such as cat soleus which contains only one fiber type and some "remarkably extensive" motor unit territories (Burke *et al.*, 1974), as if to suggest truly homogenous blending, while at the other extreme are muscles such as occipitoscapularis, composed of all four fiber types (SO, FOG, FI and FG) evenly distributed throughout (Richmond and Abrahams, 1975a). Presumably, most muscles lie between these extremes, con-

taining 2 to 4 of the fiber types, with their distributions ranging from nearly exclusive "compartmentalization" to completely homogenous blending. One relatively common fiber-type distribution consists of a large core of evenly mixed different fiber types, surrounded by peripheral fascicles comprised predominately of FG fibers. This arrangement has been reported for guinea pig medial gastrocnemius and vastus lateralis (Maier *et al.*, 1976), and cat biventer cervicis, splenius, rectus capitis major and complexus (Richmond and Abrahams, 1975a). Similarly, in cat medial gastrocnemius FF motor units (FG muscle fibers) predominate in the dorsal margin of the muscle (Burke *et al.*, 1977). There are also muscles in which the SO fibers tend to be separated from the FG fibers to an even greater extent, but with the FOG fibers either distributed relatively evenly throughout the muscle (Gonyea and Ericson, 1977) or showing a diminishing representation when progressing away from the region of highest SO fiber concentration (Maier, personal communication). These arrangements result in the muscles containing an "oxidative" region often limited to an axial or deeper territory, although in human extraocular muscles, the slow-twitch fibers predominate in the outer regions rather than the interior of the muscles (Bach-y-Rita, 1971). Such "compartmentalized" muscles include rat medial gastrocnemius (Yellin, 1969); rat sternomastoideus, cleidomastoideus and clavotrapezius (Grimm, 1972); rat medial pterygoid, temporalis and masseter (Maier, personal communication); and cat flexor carpi radialis (Gonyea and Ericson, 1977).

A common and striking feature of intramuscular design is the association usually found between the muscle spindles and "oxidative" muscle fibers. Thus, in cat (Swett and Eldred, 1960) and guinea pig (Maier *et al.*, 1976) soleus composed entirely of SO fibers, spindles are found quite broadly throughout the muscle. However, in guinea pig medial gastrocnemius and vastus lateralis (Maier *et al.*, 1976), and cat complexus, splenius and rectus capitis major (Richmond and Abrahams, 1975b)

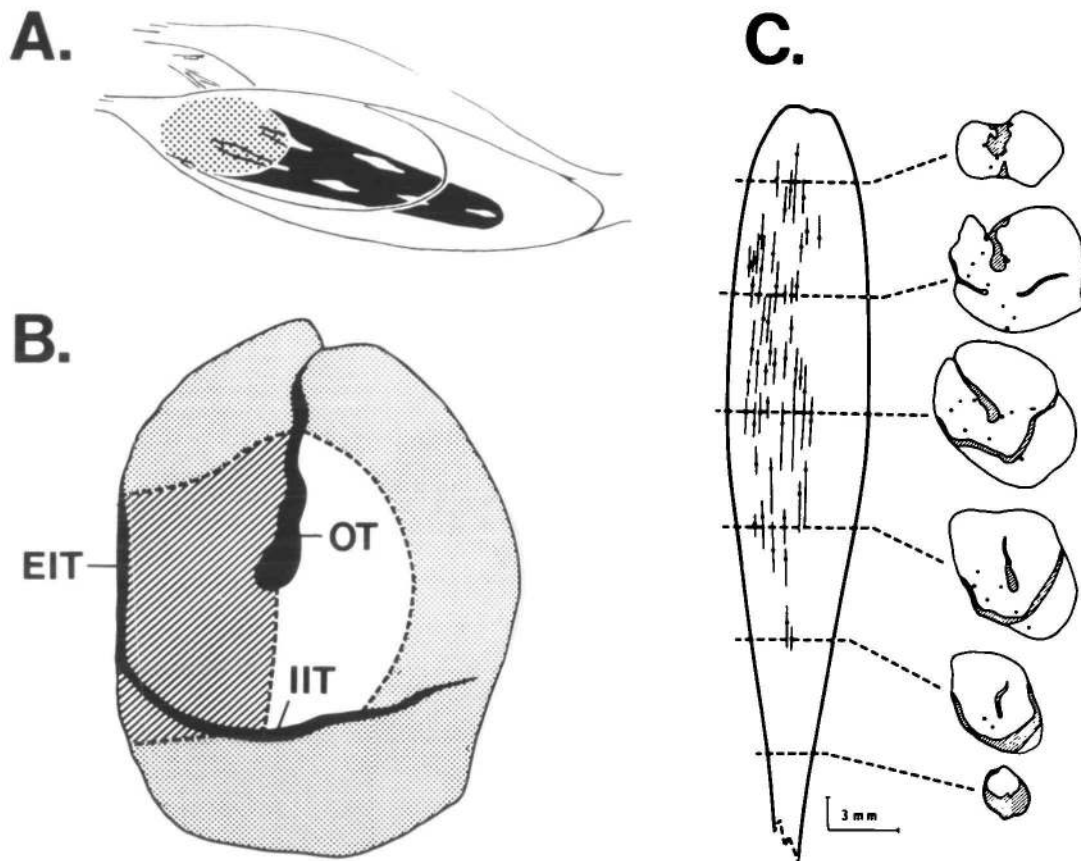


FIG. 4. Intimate relation between spindles and "oxidative" (SO and FOG) fibers in select muscles. *A* is taken from Yellin (1969) and is a diagrammatic (mediodorsal view) of the right gastrocnemius muscle of the rat, illustrating the general distribution of spindles with respect to muscle fiber types. The muscle origins are at the left, the insertion on the right. In the medial head of the muscle (foreground), the spindles are found within a core of deep, "oxidative" (presumably SO and FOG) fascicles. The superficial and juxtaseptal "glycolytic" (FG) fascicles lack spindles. Normally, the transition between regions is gradual. The precise number and disposition of the spindles are not depicted. *B* is taken from Gonyea and Ericson (1977) which depicts a cross-section through the greatest girth of a representative cat flexor carpi

radialis showing: dotted area, the location of the predominantly "fast-twitch" (47% FG, 29% FOG, 24% SO) region; cross-hatched area, the "slow-twitch" (25% FG, 25% FOG, 50% SO) region; and, open area, the "intermediate" (31% FG, 32% FOG, 37% SO) region. Abbreviations: OT, tendon of origin; EIT, external insertion tendon; IIT, internal insertion tendon. As illustrated in *C*, also taken from Gonyea and Ericson (1977), the spindles are contained primarily within the "slow-twitch" region of the muscle. In the longitudinal projection of the muscle, the lines represent the length of the spindle and the dot, the location of the equatorial region of the spindle. The transverse sections indicate the locations of spindles (dots) within the muscle and were made at levels shown by horizontal lines.

spindles are absent from peripheral fascicles comprised predominately of FG fibers. Moreover, in all the "compartmentalized" muscles mentioned above, the same studies showed that the spindles were limited to the more "oxidative" portion of the muscle, including even the human extraocular muscles (Cooper and Daniels, 1949). This phenomenon is illustrated in Figure 4 for

rat medial gastrocnemius (Yellin, 1969) and for cat flexor carpi radialis (Gonyea and Ericson, 1977). In both these instances, the spindles are concentrated in the more "oxidative" portions and are optimally located along the line of muscle pull for the sensing of small changes in overall muscle length. We do not mean to imply that FF units are completely absent

from the "oxidative" portion of a "compartmentalized" muscle or that they cannot influence receptor discharge in this region. Rather, this anatomical arrangement suggests that the activity of the "oxidative" fibers may be preferentially monitored by these receptors.

It has been reported that spindles are found where the major nerve trunks in a muscle begin to branch into finer fibers (Barker, 1974). A trophic effect of afferent fibers on spindle development has also been emphasized (Barker, 1974). Presumably the close anatomical association of spindles and type S and FR motor units involves a combination of as yet undetermined genetic, developmental and trophic factors. These may help to explain the exceptions to the generalizations cited above (e.g., cat occipitoscapularis and biventer cervicis, Richmond and Abrahams, 1975a, b).

Another interesting feature of the association of spindles with SO and FOG fibers is the recent evidence, based on glycogen-depletion techniques, demonstrating that skeletofusimotor (β) axons are distributed to SO and "bag₁" intrafusal fibers (Barker *et al.*, 1977). In addition, Harker *et al.* (1977) have shown a class of fast-conducting β -axons (>85 m/s) that innervate fast-twitch fibers and almost exclusively nuclear chain fibers. However, due to the methods employed in this study, these authors were unable to determine which type of motor unit (FF and/or FR) was associated with glycogen depletion in nuclear chain fibers. Of the three histochemically distinct types of intrafusal fiber, nuclear chain fibers are most similar to the FOG fiber type (Maier *et al.*, 1974), suggesting that fast-conducting β -axons innervate both types of fiber. For both fast- and slow-conducting β -axons, it would be of interest to know the relationship between the location of the spindle(s) supplied by a β -axon and its muscle unit territory. This type of analysis has been done to a limited degree for the cat peroneus brevis tenuissimus (Barker *et al.*, 1977) and soleus (Burke and Tsairis, 1977), but it is difficult to interpret these results because of the difficulty in depleting SO fibers of their glycogen (see also Burke *et al.*, 1973; Burke *et al.*, 1974).

Reports noting "compartmentalization" of "oxidative" fibers and muscle spindles have not ascertained whether or not the tendon organs are also confined to the same portion of the muscle. Such "compartmentalization" is implicit and emphasized in the work of Swett and Eldred (1960) on cat medial gastrocnemius and

soleus, and of Richmond and Abrahams (1975b) on cat neck muscles. Figure 5 is from a paper from the Eldred laboratory (Marchand *et al.*, 1971) and shows the patterns of association of tendon organs with spindles encountered in two cat extensor digitorum brevis muscles. In many instances, the spindles and tendon organs are found in anatomical contiguity (the "dyad arrangement"). Indeed the number of tendon organs forming dyads with spindles has been counted as 50% in cat extensor digitorum brevis (Marchand *et al.*, 1971), 20% in medial gastrocnemius and 27% in soleus (Swett and Eldred, 1960). In fact, such intimate anatomical associations between spindles and tendon organs may be higher than these percentages indicate. Of all the tendon organs in one of the extensor digitorum brevis muscles examined by Marchand *et al.* (1971), "82% were in either obvious dyad relationships or in close longitudinal alignment with spindles." Similarly, high percentages of dyads have recently been observed in the neck muscles studied by Richmond and Abrahams (1975b). These authors have emphasized that the association of spindles and tendon organs is not by chance, but rather suggest that dyads should be recognized "as a common muscle receptor entity which must serve a functional role."

With such high percentages of dyads in muscles with relatively homogenous muscle fiber-type distributions, we would anticipate that in the "compartmentalized" situation, the tendon organs should indeed be also confined to the same portion of the muscle as the spindles. Lund *et al.* (1978) have recently presented evidence of striking "compartmentalization" of both spindles and tendon organs to a very limited portion of the masseter and temporalis (Fig. 6) muscles of both the kitten and adult cat. The receptors were located in deep portions of both muscles (near the origin of the masseter and near the insertion of the temporalis). In both muscles, there is indirect evidence that the receptor-rich portion of the muscle is also rich in "oxidative" muscle fibers (Hiimae, 1971; Kawamura *et al.*, 1967). Obviously, it would be of great interest to

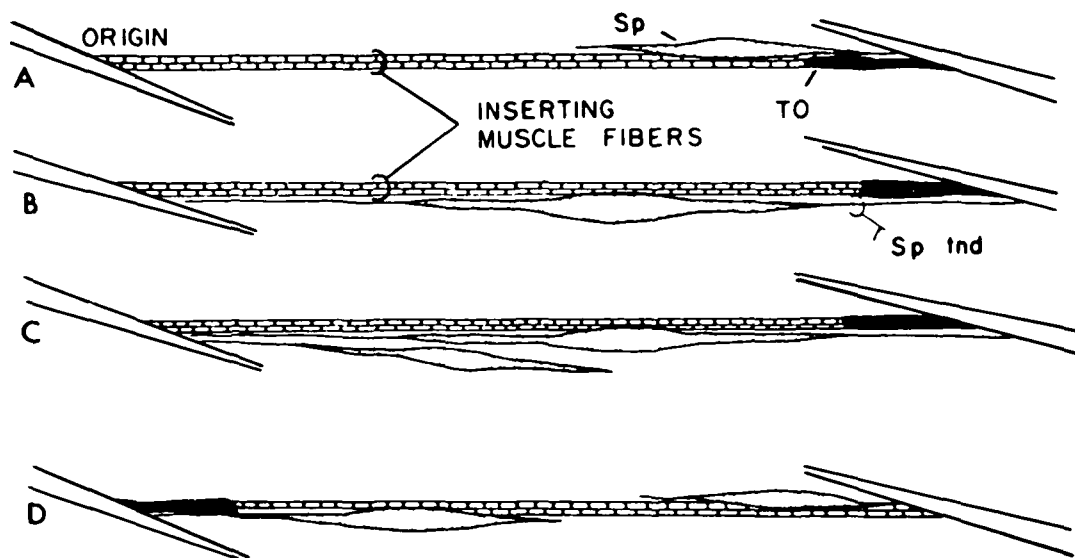


FIG. 5. Patterns of association of tendon organs (TO) with spindles (Sp) encountered in cat extensor digitorum brevis muscle (from Marchand *et al.*, 1971). Skeletomotor fibers inserting onto a particular tendon organ are represented as striated bands extending from the aponeurosis of origin (left) or insertion (right). Spindles that were in contact with the skeletomotor fibers inserting onto a TO are shown as overlapping it. Other spindles, like the smaller one in C, were separated by one or several intruding skeletomotor motor fibers from those fibers inserting onto the TO. Outlines are exaggerated in the trans-

verse dimension, but relationships lengthwise along the muscle fascicles are in true proportion. A simple dyad arrangement is seen in A, with the spindle in this case occupying the acute angle at the tendon organ attachment. In B, the tendon of a large centrally located spindle runs along the deep surface of the TO peduncle. The other end of this spindle almost reached the opposite aponeurosis. C and D show instances in which two spindles were intimately related to the tendon organ and its inserting skeletomotor fibers.

know if tendon organs in cat flexor carpi radialis are also limited to the "oxidative" portion of the muscle in which the spindles are located.

SUMMARY

It is not known whether the proprioceptive reflex control system operates differently in "compartmentalized" muscles than it does in muscles where there is a relatively more homogenous distribution of motor unit types and receptors. We would predict, however, that in both instances segmental proprioceptive reflexes are primarily concerned with modulating the activity of type S and FR units which are used in vernier contractions. This does not mean that there is no functional significance to the substantial (particularly tendon organ) receptor input during more powerful contractions in which FF units also participate. The ensemble input must

be considerably augmented once FF units are recruited to a contraction such that the weighted (localized) effects lose their efficacy at the segmental level. This ensemble input has wide-spread segmental and suprasegmental distribution with the possibility that its segmental reflex effects represent the "first line of defense against an opposing load before the intervention of longer latency adaptative mechanisms" (Bizzi *et al.*, 1978; see also Allum, 1975). Furthermore, an ensemble proprioceptive input is not exclusively used for load compensating mechanisms. It appears to play a prominent role in a variety of suprasegmental mechanisms including position sense (Gandevia and McCloskey, 1976) the sense of effort (McCloskey *et al.*, 1974) and the adaptative modifications of central programs (Nashner, 1976; Bizzi and Polit, 1978).

If spindles, tendon organs and "oxida-

LEFT TEMPORALIS OF KITTEN

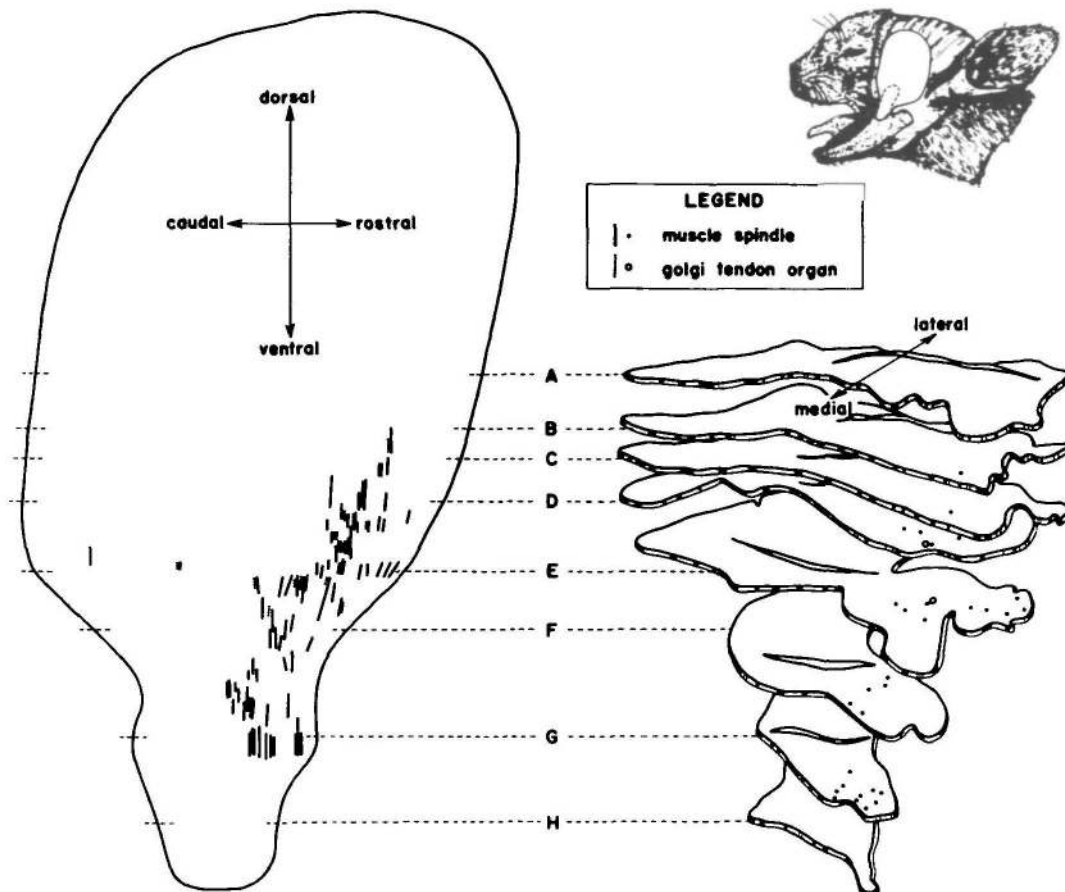


FIG. 6. Example of the close association between muscle spindles and tendon organs within a restricted portion of a mixed mammalian muscle. Scaled lateral

view of left temporalis of the kitten. A similar relationship between spindles and tendon organs exists for the masseter. From Lund *et al.* (1978).

tive" muscle fibers are at times "compartmentalized" together into a limited portion of the muscle then motor control neurobiologists would have to take this into account in any model of segmental proprioceptive reflex control. It was emphasized earlier that in certain phases of many demanding movements, the muscle may be more or less "on its own" in compensating for external perturbations. In contrast, segmental proprioceptive reflex control appears to be most efficacious when the motoneurons are at or near their threshold in the elaboration of vernier contractions. If tendon organs, like spindles, can be shown to be limited to a portion of the muscle involving fibers

more concerned with vernier contractions than the execution of forceful contractions, then functional anatomy will have made a major contribution to our evolving concepts on the role of spindles and tendon organs in motor control.

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