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Review Article

Smooth Muscle and Their Contractile Activity

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Abstract

Muscle tissue provides the body's motor activity, carrying out both voluntary movements and involuntary functions of internal organs. While striated muscle has been well studied, smooth muscle, which forms the walls of internal organs and blood vessels, is of particular interest due to its unique contractile activity. This tissue is responsible for fundamental processes—peristalsis, regulation of vascular tone, labor—demonstrating high plasticity, the ability for prolonged tonic contractions, and low energy expenditure in maintaining tone.

Keywords: smooth muscle; phasic contraction; myofibril; sarcoplasm; myosin; tropomyosin; ATPase activity; smooth muscle cell

Introduction

Muscle tissue provides the body's motor activity, carrying out both voluntary movements and involuntary functions of internal organs. While striated muscle has been well studied, smooth muscle, which forms the walls of internal organs and blood vessels, is of particular interest due to its unique contractile activity. This tissue is responsible for fundamental processes—peristalsis, regulation of vascular tone, labor—demonstrating high plasticity, the ability for prolonged tonic contractions, and low energy expenditure in maintaining tone [1].

The central question remains the molecular mechanism underlying the two types of contraction—fast phasic and slow tonic. There are two main viewpoints: one explains the differences by quantitative features of the contractile apparatus, the other suggests the existence of qualitatively different molecular substrates. An important argument in favor of the second hypothesis is data on the low content of classical actomyosin in smooth muscles specialized for tonic function.

This review systematizes current knowledge about the structural and functional organization of smooth muscle. It considers its embryological origin, morphological features, and unique physiological properties. The main focus is on the biochemical aspect: a comparative analysis of the protein composition of different muscle types and the identification of molecular determinants of tonic function. Analysis of experimental data shows a clear correlation between the functional profile of muscle tissue and the ratio of myofibrillar protein fractions—the actomyosin complex and the "T-fraction" (proteins soluble at low ionic strength). It is shown that a gradual decrease in the actomyosin/T-fraction ratio in the progression from skeletal to smooth muscle corresponds to an enhancement of its tonic capacity.

The totality of the presented data points to a complex multicomponent molecular mechanism of smooth muscle contractile activity. Its further study is of fundamental importance for physiology and may open new perspectives in understanding pathologies associated with impaired muscle tone.

Main Part

In humans and vertebrates, the term smooth muscle refers to the muscular layers of internal organs (such as intestines, stomach, uterus, bladder, urogenital organs, and others) and blood vessels. This type of muscle tissue also includes contractile elements incorporated into the connective tissue of the skin and various organs. Vertebrate smooth muscle differs significantly from striated muscles in a number of characteristics and properties [1].

First of all, it must be noted that these two muscle types have different embryonic origins. Smooth muscle elements in vertebrates develop from mesenchyme. The embryonic basis for almost all highly differentiated somatic (skeletal) musculature in vertebrates is the myotomes, i.e., the part of the dorsal segments that remains after the segregation of all mesenchymal primordia. Thus, vertebrate smooth muscle cells are similar to fibroblasts, which also originate from undifferentiated mesenchyme. Therefore, the formation of new smooth muscle cells is possible even in the adult organism from poorly differentiated connective tissue elements. Such new formation of smooth muscle fibers is observed, for example, in the uterine muscle during pregnancy, during the transformation of capillaries into larger vessels due to changes in blood flow conditions, etc. This property, known as plasticity, is one of the key features of this tissue and distinguishes it from the strictly determined skeletal musculature [2].

At the same time, it is necessary to emphasize with certainty that the locomotor smooth muscle fibers of invertebrates, capable of rapid contractions and often combined based on the absence of transverse striations into a single smooth muscle tissue with the mesenchymal musculature of vertebrates, represent, in essence, a modification of somatic-type musculature. In terms of a number of properties—the ability for tetanic contraction, sensitivity to induction current, obedience to the "all or nothing" law, as well as high myosin and actomyosin content—these muscles are maximally close to striated muscle. This circumstance is especially important to consider when studying various muscle types from a biochemical point of view, as it indicates that the term "smooth muscle" unites functionally heterogeneous structures.

The morphological unit of smooth muscle of mesenchymal origin is a single-nucleated spindle-shaped cell, most often 60 to 100 μm long (often up to 200, less often up to 500 μm) and 4–5 μm in diameter. Smooth muscle cells, like striated muscle fibers, consist of sarcoplasm and myofibrils. However, the latter lack transverse striations and throughout consist of a substance exhibiting noticeable positive uniaxial birefringence. According to the latest data, myofibrils should be considered the contractile element of the smooth muscle cell, just as in the striated fiber. It is essential that smooth muscle cells lack an external membrane—the sarcolemma. However, according to some researchers, smooth muscle cells are still covered by a very thin membrane—the myolemma—formed by an intertwining of thin collagen fibrils and intercellular substance [3]. Such organization provides not only structural integrity but also effective mechanical and chemical integration of cells into a single functional syncytium.

Just as in the striated fiber, the sarcoplasm of the smooth muscle cell is a sufficiently complex system in which a number of microstructures can be identified. Significant is the presence in the sarcoplasm of minute particles—microsomes—possessing ATPase activity that differs in a number of properties, for example, resistance to high pressure, from myosin ATPase. The activity of this ATPase is especially high in the smooth muscle of the myometrium. With conventional methods of isolating myosin and actomyosin from smooth muscles, microsomes also pass into the extract, leading to an increase in the ATPase activity of KCl extracts not due to myosin ATPase. Therefore, to determine the true ATPase activity of myosin in these cases, it is necessary to separate microsomes from myosin by ultracentrifugation. This underscores the importance of methodological nuances in the biochemical analysis of smooth muscle tissue [4].

Smooth muscles also differ from skeletal musculature in the nature of their contractile activity. The excitability of smooth muscles is significantly lower than that of striated muscle; the conduction of excitation in typical smooth muscles proceeds very slowly; their latent period of contraction is much longer; their chronaxie is very high; plasticity, i.e., the ability to change length without changing tension, is expressed in smooth muscles to a much greater degree than in skeletal muscles, etc. Most importantly, a single contraction of smooth muscle and, especially, its relaxation following contraction, is extremely prolonged in time. This enables the possibility of prolonged maintenance of tone without signs of fatigue.

An interesting feature of some smooth muscles is also their ability to "freeze" or harden, or more precisely, to resist forces attempting to stretch the muscle at a given degree of contraction, without producing continuous energy expenditure. Such maintenance of the muscle in a state of tonic shortening (the locking function of the muscle) is usually not associated with significant change or increase in bioelectrical activity. Clearly expressed action currents from the closing muscle of mollusks are recorded only during rapid closing contractions or when the muscle transitions from one state of tonic shortening to another. During the maintenance of established tone or during very slow relaxation, bioelectrical activity is almost indistinguishable from the resting state. This indicates a fundamentally different, compared to phasic contraction, energetic and electrophysiological basis for tonic function [5].

The locking function of smooth muscle can apparently be viewed as an absence of relaxation or as delayed relaxation. Prolonged multi-hour tonic contraction likely represents nothing more than the superposition of individual contractions, increasingly stretched out in time due to viscous aftereffect. Interestingly, the tonic tension of smooth muscle is associated with an extremely insignificant expenditure of chemical energy, hundreds of times less than that of tetanic tension of corresponding force. Such high energy efficiency is a key adaptive advantage of smooth muscles performing continuous functions in the organism.

The debate about the existence of two substrates of muscle activity—the contraction substrate and the substrate of fatigue-resistant tone, transitioning in some cases into a locking action—was for a long time conducted almost exclusively by morphologists and physiologists. This debate revolved around the question of the existence of functionally and anatomically distinct substrates for tetanic contraction and tonic activity. Some authors believed that tonic activity and phasic muscle contraction are based on two different contractile mechanisms or even two different protein substrates; while others viewed the features of tonic and tetanic muscle activity solely as quantitative, not qualitative differences.

At present, it seems possible to present an accurate picture of the relationship between tetanic and tonic muscle activity. Here and below, the fatigue-resistant plastic tone of smooth muscle is implied. As already mentioned, tonic contraction can indeed be viewed as the summation of extremely slow contraction waves. However, at the same time, it is beyond doubt that the very ability of the muscle for viscous aftereffect, leading to extremely slow relaxation of the contracted muscle, transitioning in some cases into a locking function, is determined by the presence in muscle fibers of a special protein (or protein system) not identical to actomyosin. The very type of muscle organ, its adaptation either to rapid phasic movements or, conversely, to carrying out slowly progressing tonic contraction and prolonged stay in a state of fatigue-resistant tonic shortening, is undoubtedly determined by the fractional composition of myofibrillar proteins. This, of course, does not at all contradict the fact that the same muscle, if it contains both protein substrates, can, depending on stimulation conditions, respond either with a relatively fast twitch or with a slow "tonic" shortening. This kind of view has become possible to substantiate as a result of studying muscles of various types using the latest methods of investigating contractile muscle proteins [6].

Since it is now known that the contraction of the most diverse organs and organelles of movement is caused by a change in the physical state of the proteins of the actomyosin complex or proteins similar in their properties to actomyosin as a result of interaction with ATP, the question of the actomyosin content in muscles of various types was of great interest. Conducted research has established, on the one hand, a pronounced parallelism between the content of actomyosin complex proteins in muscle tissue and the muscle's ability for rapid and strong contractions, and on the other hand, the absence of any correlation between the muscle's ability to develop and maintain tonic resistance to stretching and the content of actomyosin in smooth muscles. Rather the opposite, the lower the content of actomyosin complex proteins in a muscle organ, the more reason to expect it to have a pronounced ability for tonic (locking) function and vice versa. These data indicate that phasic and tonic

(locking) activity are based on changes in the physical state of different protein substrates. The development of tone by smooth locking muscle is accompanied by a change in electrical parameters different from that in phasic activity. Other biophysical data also testify to the existence of different mechanisms for phasic and tonic activity. There is a position according to which one can speak not of different mechanisms of fast and slow contraction, but of different mechanisms of contraction and fatigue-resistant resistance to stretching (viscous aftereffect, locking function). However, since the protein substrates of contraction and "viscous aftereffect" in myofibrils are most closely interconnected, contraction and tonic tension of smooth muscle are difficult to consider as independently proceeding processes; rather, they are two components of a single contractile cycle [2, 6].

The pronounced peculiarity of the fractional composition of smooth tonic muscle proteins compared to striated muscle, in particular, the smaller quantity of actomyosin complex proteins in smooth muscles, has been confirmed and demonstrated by a number of authors. These studies made it possible to link the weaker contractile ability of smooth muscle with its relatively low actomyosin content with full certainty. However, the question of the nature of the protein substrate of tonic tension or viscous aftereffect remained completely unclear. The study of this problem was particularly hindered by the circumstance that the development of muscle tone, unlike the act of contraction, cannot be reproduced in model systems, for example, on muscle fibers washed with 50% glycerol.

Nevertheless, a certain idea about the nature of proteins involved in the realization of tonic or locking function of muscles can still be formed on the basis of a detailed study and comparison of the fractional composition of proteins in muscles of different types, adapted, on the one hand, to rapid phasic movements, and on the other—to the development of fatigue-resistant tone. As was established, the fractional composition of proteins of various types of musculature—skeletal, cardiac, stomach and uterine muscle—has significant differences. To one degree or another, these differences concern all major protein groups—myofibrillar, sarcoplasmic, and stromal proteins [7].

From the point of view of the problem under consideration, data on the fractional composition of myofibrillar proteins, extracted from muscle tissue with saline solutions of high ionic strength after preliminary exhaustive extraction of easily soluble sarcoplasmic proteins, are of the greatest importance. The total content of myofibrillar proteins is highest in skeletal muscle, where the nitrogen of these proteins accounts for about 50% of total nitrogen or 57% of muscle protein nitrogen. In the heart and stomach muscles these values are two times lower, and in the uterine muscle the nitrogen of myofibrillar proteins accounts for only 16.7% of total tissue nitrogen or 18% of protein nitrogen, respectively. Upon dialysis against distilled water or upon strong dilution with water of an extract containing all extractable myofibrillar proteins, they can be separated into two groups: 1) proteins soluble in salt media with high ionic strength but precipitating under these conditions, and 2) proteins soluble at low ionic strength, remaining in the supernatant. The latter group of proteins is called the T-fraction. It has been suggested that tropomyosin may play an important role in the locking function of smooth muscle. The content of this protein in the locking muscle of mollusks indeed reaches 30% of the total amount of muscle proteins.

It is necessary to emphasize that in experiments, muscle tissue homogenates were completely freed from sarcoplasmic proteins, and only after that was the extraction of myofibrillar proteins carried out. Consequently, the T-fraction indeed represents myofibrillar proteins soluble at low ionic strength, apparently bound in the living muscle (in myofibrils) to proteins of the actomyosin group. This peculiar complex breaks down into its components during dialysis or upon strong dilution of the salt solution with distilled water. In terms of percentage content of actomyosin complex (AM) proteins, different muscle types differ greatly from each other. If in skeletal muscle the nitrogen of these proteins (AM) constitutes about 40% of total muscle tissue nitrogen or about 45% of protein nitrogen, then in the heart muscle it accounts for about 17.0 and 18.6% respectively (in stomach musculature 11.3 and 12.1% and in myometrium 4.2 and 4.6%). Consequently, the content of myofibrillar proteins insoluble at low ionic strength, i.e., actomyosin complex (AM) proteins, in the uterine muscle is almost 10 times lower than in skeletal muscle. Considering that smooth muscle actomyosin also includes nucleoproteins, which are extracted from muscle pulp and then precipitate during dialysis together with actomyosin, as well as, apparently, a water-insoluble form of tropomyosin, the true content of myosin and actomyosin in smooth muscle is likely even lower.

The percentage content of T-fraction proteins, calculated on total tissue nitrogen or protein, is approximately the same in all muscle types. However, the percentage content of T-fraction proteins, calculated on extractable myofibrillar nitrogen or protein, i.e., in other words, the ratio between the content of actomyosin complex proteins and myofibrillar proteins soluble in salt media with low ionic strength, is not the same for different muscles and represents a very characteristic value for each muscle type. Thus, for skeletal muscle this AM/T ratio is approximately 3.5/1, for cardiac muscle 1.5:1, for stomach musculature 1:1.5 and for uterine muscle 1:3.

Thus, a clear parallelism is revealed between the ability of a muscle for a particular type of physiological activity and the fractional composition of proteins that are integral components of the most functionally important muscle structures—myofibrils. This parallelism cannot be accidental and compels, when studying the nature of the protein substrate of muscle tone, to pay special attention to myofibrillar proteins soluble at low ionic strength, i.e., the T-fraction [8].

The proteins of this fraction were studied using the electrophoretic method. In agreement with literature data, it was established that the T-fraction of skeletal muscle is not homogeneous. It contains a small amount of some protein with high electrophoretic mobility, probably myoalbumin. The main mass of protein separates into two parts upon electrophoresis, of which one (the smaller) is tropomyosin, and the second appears to be another protein. In addition, the T-fraction contains a significant amount of some myofibrillar proteins extremely prone to spontaneous denaturation, apparently similar in their properties to globulins. The T-fraction of cardiac muscle, stomach musculature, and uterus also represents a heterogeneous system in which electrophoresis can establish the presence of at least two to three main subfractions: a water-soluble myofibrillar protein, tropomyosin, and one fast-moving component [9].

The obtained data are fully consistent with the assumption about the important role of tropomyosin and, possibly, other myofibrillar proteins soluble in salt media with low ionic strength, in imparting to smooth tonic muscle its peculiar properties and features in contractile activity. Indeed, tropomyosin solutions can under certain conditions exist in the form of either well-mobile sols or extremely viscous, low-mobility gels. Tropomyosin isolated from invertebrate muscles is almost insoluble in water at pH 7 or 8 and ionic strength 0.15, but its solubility sharply increases in the presence of 0.005 M ATP. ATP is adsorbed on protein particles but does not undergo cleavage, as tropomyosin does not possess ATPase activity. It can thus be thought that the increase in viscosity of muscle fiber proteins during the development of locking action is associated with the transformation of tropomyosin or some of its

complexes with other proteins into a gel-like state as a result of desorption of ATP and salt ions from the particles of this protein.

Since the realization of tonic (locking) function is not accompanied by a substantial increase in energy metabolism and is obviously associated with a change in the physical state of proteins not identical to actomyosin, it can be expected that myofibrillar proteins of smooth tonic muscle should possess significantly lower ATPase activity than myosin of skeletal muscles. Especially low should be the ATPase activity of those muscle protein fractions whose change in physical state may be directly related to the development of fatigue-resistant tone, i.e., proteins of the T-fraction. It is known that proteins extracted from smooth tonic muscle indeed possess significantly (10–20 times) lower ATPase activity than myosin of skeletal muscles [2, 10]. It was established that proteins of the T-fraction of skeletal muscle are characterized by particularly low, practically zero, ATPase activity. Extremely low is also the ATPase activity of the T-fraction of stomach, heart, and uterine muscles. On the other hand, the cholinesterase activity of T-fraction proteins is quite pronounced. The highest cholinesterase activity is exhibited by T-fraction proteins of the uterus and, to a lesser degree, of the stomach. All these data are also fully consistent with the assumption about the important role of myofibrillar proteins soluble in salt media with low ionic strength (T-fraction) in the realization of tonic, in particular, locking function of muscles [11].

The proposition concerning the non-identity of the protein substrate of tonic (locking) muscle function to actomyosin has recently found confirmation in the works of a number of foreign authors. It is believed that the substrate of tonic tension in the smooth locking muscle of mollusks is water-insoluble tropomyosin, which is identical to paramyosin. It is particularly important that, according to available data, invertebrate smooth muscle contains two fiber types. Some of them are rich in water-insoluble tropomyosin and exhibit a sharply pronounced ability to resist stretching and a weakly pronounced contractile function. In tropomyosin-poor fibers, this difference between the ability for active contraction and resistance to stretching is expressed to a much lesser degree.

In experiments on frog striated muscles, as well as on mollusk locking muscles, the existence of a direct dependence was shown between the nature of contraction of a single muscle fiber upon stimulation by electric current and the degree of contraction of a washed fiber upon its interaction with ATP. Experiments were conducted on single muscle fibers isolated from tonic and non-tonic bundles. A single muscle fiber was stimulated by induction current in a special chamber, and the nature of contraction was recorded. After assessing the nature of contraction, the same fiber was washed in bidistilled water, after which the degree of its contraction in the presence of ATP was determined. With respect to ATP, muscle fibers could be divided into three groups. Fibers of the first group, contracting by more than 40% upon exposure to ATP and obviously containing a large amount of actomyosin, correspond in terms of physiological contraction type to tetanic fibers. The second group of fibers, reacting weaklier with ATP (contraction by 20–40%), corresponds to mixed or transitional fibers [12]. Finally, the third group comprises fibers contracting very weakly in the presence of ATP; these fibers exhibit a tonic type of contraction when stimulated by induction current.

It was established that in so-called tonic bundles of frog striated muscles and mollusk locking muscles, fibers of all three types are present. The content of transitional fibers in them is especially high. However, the percentage of so-called purely tonic fibers, contracting weakly upon interaction with ATP and obviously containing insignificant amounts of actomyosin, in these bundles is significantly higher than in tetanic areas. Tetanic areas of muscles are characterized, on the contrary, by a very large number of fibers giving a well-expressed contractile reaction with ATP, due to high actomyosin content. Thus, confirmation has been found for the position that the type of contractile response of a muscle fiber is determined primarily by the nature of the protein substrates of contraction and fatigue-resistant tone entering into their composition [2, 13, 14].

Conclusion

The present analysis allows formulating key conclusions regarding the structural and functional organization and molecular bases of the contractile activity of smooth muscle.

Smooth muscle, unlike striated muscle, is evolutionarily specialized for performing long-term tonic functions, which is ensured by its unique physiological properties: high plasticity, low conduction velocity, and exceptional energy efficiency in maintaining tone [15].

Accumulated biochemical and physiological data indicate that these properties cannot be explained solely by quantitative variations of the classical contractile apparatus. There is a convincing inverse correlation between the content of actomyosin complex proteins in the tissue and its tonic capacity, which points to the existence of a qualitatively distinct molecular substrate for tonic function.

Key evidence for this position is the revealed pattern in the change of myofibrillar protein composition. It is shown that in the progression of muscles with increasing tonic function, a systematic decrease occurs in the ratio of the actomyosin complex (AM) to proteins soluble at low ionic strength ("T-fraction"). In the smooth muscle of the uterus, possessing pronounced tonic properties, this ratio reaches 1:3. T-fraction proteins (primarily tropomyosin and related structures) are characterized by minimal ATPase activity, corresponding to low energy expenditure during tone, and are likely capable of reversible changes in aggregate state, forming the basis of "viscous aftereffect."

Thus, the contractile activity of smooth muscle is ensured by the synergy of two molecular systems: 1) the substrate of phasic contraction (actomyosin complex) and 2) the substrate of tonic tension (T-fraction proteins). The dominance of the latter in myofibrils determines the unique functional profile of this tissue.

Consequently, the fundamental determinant underlying the unique ability of smooth muscle for prolonged tonic contractions is the specific protein composition of its myofibrils with a predominance of the "T-fraction" over classical actomyosin [16]. An in-depth study of the interaction mechanisms of these components represents a crucial direction for further research, having both fundamental significance for physiology and applied significance—for developing new approaches to correcting pathologies associated with impaired smooth muscle tone [17].

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