Adenosine Triphosphatase Activities of Muscle Sarcolemma*

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PRAKASH V. SULAKEH,t GEORGE I. DRUMMOND, AND DAVID C. NG

From the Department of Pharmacology, School of Medicine, University of British Columbia, Vancouver 8, Canada

SUMMARY

Isolated sarcolemma hydrolyzed ATP in the presence of Mg²⁺ and Ca²⁺. MgATPase was stimulated by low concentrations of Ca²⁺; this activity was stimulated by Ca²⁺ and K⁺. La³⁺ stimulated MgATPase at low concentrations (up to 50 μM) and caused inhibition at higher concentrations (above 0.2 mM). Phosphoprotein was formed when the membranes were incubated with [γ-32P]ATP. Formation of phosphoprotein was strongly dependent on Ca²⁺ and Mg²⁺. The phosphoprotein was acid-stable and hydroxylamine-sensitive. In the presence of Mg²⁺ high concentrations of Ca²⁺ (above 0.3 mM) inhibited ATPase activity by Ca²⁺ and K⁺. La³⁺ stimulated MgATPase at low concentrations of Ca²⁺ and inhibited by high concentrations of phosphate in the presence of Mg²⁺; this activity was stimulated by Ca²⁺ and K⁺. La³⁺ stimulated MgATPase at low concentrations (up to 50 μM) and caused inhibition at higher concentrations (above 0.2 mM). Phosphoprotein was formed when the membranes were incubated with [γ-32P]ATP. Formation of phosphoprotein was strongly dependent on Ca²⁺ and Mg²⁺. The phosphoprotein was acid-stable and hydroxylamine-sensitive. In the presence of Mg²⁺ high concentrations of Ca²⁺ (above 0.3 mM) inhibited ATPase activity but not the level of phosphoprotein formation.

Membrane-bound (Na⁺-K⁺)-ATPase and CaATPase are considered to participate in the active transport of Na⁺ and K⁺, and Ca²⁺, respectively (1-3). Numerous studies have been carried out to investigate the kinetic properties of (Na⁺-K⁺)-ATPase in a variety of tissues and CaATPase from muscle sarcoplasmic reticulum and red cell membranes (1, 4, 5). Recently sarcolemmal preparations from skeletal and cardiac muscle have been reported to possess CaATPase and (Na⁺-K⁺)-ATPase (6-11). We have observed that muscle plasma membranes bind and accumulate Ca²⁺ in the presence of ATP, and hydrolyze ATP in the presence of Mg²⁺ and Ca²⁺ (6). MgATPase was stimulated by low concentrations of Ca²⁺. Such observations suggest the possible mediation of ATPase in the active Ca²⁺ binding system of muscle sarcolemma. CaATPase of muscle sarcoplasmic reticulum and red blood cells is believed to provide energy for the calcium “pump” located in these structures (1-5). A phosphoprotein has been implicated in the Ca²⁺ transport of sarcoplasmic reticulum (12-14). In this paper we describe the properties of muscle sarcolemmal ATPase. The formation and some characteristics of a phosphoprotein isolated from sarcolemma are also presented.

EXPERIMENTAL PROCEDURE

Materials

[γ-32P]ATP (4.5 to 8.4 Ci per mmole) was purchased from New England Nuclear. Nucleotides were purchased from Sigma. All other reagents were analytical grade.

Methods

Sarcolemma and sarcoplasmic reticulum were isolated from rabbit muscle as described previously (12).

Assay of ATPase—MgATPase activity was determined by incubating membrane protein (about 200 μg) in a medium (final volume 1 ml) containing 50 mM Tris-HCl, pH 7.5, 5 mM MgCl₂, 0.5 mM EGTA, and 5 mM ATP at 37°. The reaction was started by the addition of ATP, and after 10 min was terminated by the addition of 1 ml of 12% trichloroacetic acid. Following removal of denatured protein by centrifugation, an aliquot of the supernatant fluid was assayed for inorganic phosphate by the method of Taussky and Shorr (16). MgCaATPase was measured in a similar manner except that EGTA was omitted and 40 μM CaCl₂ was present in the incubation medium. CaATPase was determined using an incubation medium consisting of 50 mM Tris-HCl, pH 7.0, 5 mM CaCl₂, 0.5 mM EDTA and 5 mM ATP. Under all conditions not more than 25% of the substrate was hydrolyzed. ATPase activities of sarcoplasmic reticulum were measured as described above except that 175 μg of protein were used and the incubation time was 5 min at 37°.

Assay of p-Nitrophenylphosphatase—Membranes (200 to 300 μg of protein) were incubated at 37° in a medium (final volume 1.0 ml) containing 50 mM imidazole-HCl, pH 7.5; 5 mM MgCl₂, 0.5 mM EGTA, and 5 mM sodium p-nitrophenylphosphate. The reaction was started by the addition of substrate and stopped at 10 min (sarcolemma) or 5 min (sarcoplasmic reticulum) by the addition of 0.5 ml of 12% trichloroacetic acid. The tubes were centrifuged at 4°, 1.0 ml of the supernatant fluid was removed and mixed with 0.5 ml of 1.2 M Tris. Absorbance was read at 400 nm. Appropriate controls were run without protein and with heat denatured membranes.

Phosphorylation of Membranes with [γ-32P]ATP—Membranes were incubated at 0° or 37° (final volume 0.2 ml) in a medium containing 50 mM imidazole-HCl, pH 7.5; 5 mM MgCl₂; 0.5 mM EGTA; and 1 mM [γ-32P]ATP (specific activity 10,000 to 20,000 cpm per nmole). ATP was added to start the reaction which was stopped at 30 s by the addition of 2 ml of 12% cold trichloroacetic acid. The tubes were centrifuged and the residue was washed twice with 12% trichloroacetic acid (2 ml) by centrifuga-
tion. After the second washing, radioactivity in the supernatant fluid was near background. The residue was dissolved in 0.3 ml of 1 M NaOH by immersing the tubes in a boiling water bath for 10 min. The tubes were then centrifuged, 200 μl were withdrawn, mixed with 20 ml of Bray’s solution (17), and radioactivity was determined by liquid scintillation spectrometry.

Protein was determined by the method of Lowry et al. (18).

RESULTS

Muscle sarcolemma isolated by the procedure used here in addition to (Na+—K+)-ATPase (6) possess ATPase stimulated by Mg2+ and Ca2+. They also have the ability to hydrolyze p-nitrophenylphosphate. These activities are shown in Table I and are compared with similar activities in isolated sarcoplasmic reticulum. Hydrolysis of ATP in the presence of 5 mM Mg2+ was stimulated by low concentrations of Ca2+ (40 μM). The p-nitrophenylphosphatase activity observed in the presence of Mg2+ was stimulated by K+ and low concentrations of Ca2+. ATP inhibited p-nitrophenylphosphate hydrolysis. Ouabain inhibited the stimulation obtained in the presence of 10 mM K+. Similar observations regarding ouabain-K+ antagonism have been reported (19, 20). The p-nitrophenylphosphatase of sarcoplasmic reticulum was qualitatively similar but quantitatively greater than sarcolemma (Table I). It has been reported that p-nitrophenylphosphate can support active Ca2+ binding by sarcoplasmic reticulum (4). Muscle sarcolemma exhibited a more rigid requirement for ATP; binding of Ca2+ was very low in the presence of p-nitrophenylphosphate or acetylphosphate (15). Stimulation of sarcolemmal p-nitrophenylphosphatase (Mg2+ present) by Ca2+ was much lower than that for the sarcoplasmic reticulum enzyme (Table I).

Effect of Ca2+ and Mg2+ on ATPase—The effect of Mg2+ in the presence of several fixed concentrations of Ca2+ is shown in Fig. 1A. Mg2+ stimulated ATPase activity at concentrations between 0.1 and 1 mM. Activity in the presence of this cation was greatly increased by low concentrations of Ca2+. Higher concentrations of Ca2+ were inhibitory. Mn2+ and Co2+ could replace Mg2+ (inset). The effect of Ca2+ on reaction velocity at several fixed concentrations of Mg2+ is shown in Fig. 1B. Low Ca2+ concentrations (10 to 100 μM) stimulated enzyme activity at all Mg2+ concentrations tested. In these experiments 0.1 mM EGTA was present in the assay; thus, free Ca2+ concentration of 2 × 10−4 M activated MgATPase maximally, while concentrations greater than 5 μM were inhibitory. Ca2+ supported the hydrolysis of ATP in the absence of Mg2+ (Fig. 1B) (6). Both CaATPase and MgATPase have been previously reported in muscle sarclemma (6–9).

Substrate Specificity—The effect of ATP concentration on enzyme activity is shown in Fig. 2. The Km values for Mg-ATPase, MgCaATPase, and CaATPase were approximately the same (0.5 to 0.6 mM). Data in the inset shows the dependency of CaATPase on Ca2+ concentration at two fixed ATP concentrations (0.5 and 2 mM). In each case maximal activity was observed at a Ca2+ : ATP ratio of about 1, indicating that CaATP may be the substrate for the enzyme. When assayed in the presence of Mg2+, Ca2+ or Mg2+ plus Ca2+, sarcolemmal ATPase hydrolyzed GTP, UTP, and CTP, at rates 40 to 60% that of ATP (Fig. 3) which were only slightly lower than the relative rates of hydrolysis of these triphosphates by sarcoplasmic reticulum. Sarcolemmal ATPase also hydrolyzed ADP, but at rates only 8 to 20% that of ATP. In contrast, sarcoplasmic reticular ATPase hydrolyzed ADP at a considerable rate in the presence of Mg2+, or Mg2+ plus Ca2+. These observations on the effectiveness of ADP to serve as substrate for sarcoplasmic reticular ATPase are in agreement with those of Carsten and

![Fig. 1. Effect of divalent cations on ATPase activity. A, standard assay conditions were used except Mg2+ was varied as indicated and several fixed concentrations of Ca2+ were present (indicated by the numbers on each curve, mM). I, inset, comparison of effect of Mn2+ and CO2+ with Mg2+ on ATPase. B, Ca2+ concentration was varied in the presence of several fixed Mg2+ concentrations (indicated by the numbers on each curve, mM). EGTA, 0.1 mM was present, except with 0 Mg2+.

| TABLE 1 |

| ATPase and p-nitrophenylphosphatase of skeletal muscle sarcolemma and sarcoplasmic reticulum |

For p-nitrophenylphosphatase assay, when added, Mg2+ was 5 mM; Ca2+, 20 μM; K+, 10 mM; ATP, 1 mM; and ouabain, 1 mM.

<table>
<thead>
<tr>
<th>Additions</th>
<th>Sarrolemma</th>
<th>Sarcoplasmic reticulum</th>
</tr>
</thead>
<tbody>
<tr>
<td>MgATPase</td>
<td>0.23 ± 0.02 (18)</td>
<td>0.55 ± 0.04 (5)</td>
</tr>
<tr>
<td>MgCaATPase</td>
<td>0.49 ± 0.03 (16)</td>
<td>2.08 ± 0.15 (7)</td>
</tr>
<tr>
<td>CaATPase</td>
<td>0.38 ± 0.03 (14)</td>
<td>0.34 ± 0.03 (5)</td>
</tr>
<tr>
<td>Mn2+</td>
<td>2.31</td>
<td>8.61</td>
</tr>
<tr>
<td>Mg2+</td>
<td>5.16</td>
<td>14.27</td>
</tr>
<tr>
<td>Mg2+ + Ca2+</td>
<td>6.74</td>
<td>39.10</td>
</tr>
<tr>
<td>Mg2+ + K+</td>
<td>7.44</td>
<td>21.81</td>
</tr>
<tr>
<td>Mg2+ + Ca2+ + K+</td>
<td>6.87</td>
<td>38.39</td>
</tr>
<tr>
<td>Mg2+ + Ca2+ + K+ + ATP</td>
<td>2.36</td>
<td>12.55</td>
</tr>
<tr>
<td>Mg2+ + K+ + ouabain</td>
<td>4.77</td>
<td></td>
</tr>
</tbody>
</table>
Mommaerts (21). It is possible that ADP hydrolysis could be accounted for by its prior conversion to ATP, if adenylate kinase were a contaminant. The concentration of each nucleotide tested (5 mM) was above saturation; the $K_m$ value for each was not determined.

**Effect of Temperature and pH—**ATPase activities of sarcosomal membranes were strongly influenced by temperature of incubation (Fig. 4). Energies of activation calculated from Arrhenius plots were in the range of 12 to 16 Cal per mole. Sarcolemmal ATPase activity possessed a pH optimum of 7.5 when assayed in the presence of Mg$^{2+}$, Ca$^{2+}$ or Ca$^{2+}$ plus Mg$^{2+}$ (Fig. 5). K$^+$ (100 mM) significantly inhibited sarcolemmal MgCa-ATPase at all pH values, but slightly stimulated this activity in sarcoplasmic reticulum (Fig. 5).

**Effect of La$^{3+}$—**Recently it was reported that La$^{3+}$ specifically inhibited CaATPase of red cell membranes (22); this cation is known to inhibit Ca$^{2+}$ transport in red blood cells and liver mitochondria (22-24). We have observed that La$^{3+}$ inhibited the release of Ca$^{2+}$ from sarcolemmal membranes at concentrations which did not affect Ca$^{2+}$ binding (15). La$^{3+}$ when added to the MgATPase assay system was found to stimulate enzyme activity (Fig. 6), in fact, maximal stimulation by this cation was equivalent to that of Ca$^{2+}$ (inset). When La$^{3+}$ and Ca$^{2+}$ were present together maximal stimulation was reduced by 50% compared with either ion alone. CaATPase was not stimulated by La$^{3+}$, nor was MgCaATPase (Fig. 6). At concentrations of

![Fig. 2. Effect of ATP concentration on sarcolemmal ATPase. Standard assay conditions were used except ATP concentrations were varied: $\bullet$, MgATPase (5 mM MgCl$_2$ + 0.1 mM EGTA); $\Delta$, CaATPase (5 mM CaCl$_2$); $\bigcirc$, MgCaATPase (5 mM MgCl$_2$, 20 $\mu$M CaCl$_2$). Inset, CaCl$_2$ concentration was varied at two fixed concentrations of ATP, 0.5 mM and 2.0 mM.](http://www.jbc.org/)

![Fig. 3. Substrate specificity of sarcolemma and sarcoplasmic reticulum. Standard assay conditions were used except that the substrate was varied as indicated, each at 5 mM. Grey bars, CaATPase; hatched bars, MgATPase; solid bars, MgCaATPase. ADP and GDP were each present at 5 mM, assay conditions were the same as for ATP.](http://www.jbc.org/)

![Fig. 4 (left). Effect of temperature on ATPase activity. Standard assay conditions were used except the temperature was varied: $\bullet$, MgATPase; $\Delta$, CaATPase; $\bigcirc$, MgCaATPase; $\square$, "extra" ATPase which is the difference between MgCaATPase and MgATPase. Inset, similar studies using sarcoplasmic reticulum.](http://www.jbc.org/)

![Fig. 5 (center). Effect of pH on sarcolemmal and sarcoplasmic reticular ATPase. Standard conditions were used except the pH was varied as indicated. Sarcolemmal ATPase (---) is displayed as ordinate A, sarcoplasmic reticular ATPase (---) as ordinate B. $\bullet$, MgATPase; $\bigcirc$, MgCaATPase; $\square$, MgCaATPase plus 100 mM K$^+$. Inset, similar studies using sarcoplasmic reticulum.](http://www.jbc.org/)

![Fig. 6 (right). Effect of La$^{3+}$ on ATPase activity. Standard conditions were used except LaCl$_3$ was present at the concentrations indicated and 0.25 mM EGTA was present. $\bullet$, MgATPase; $\Delta$, CaATPase; $\bigcirc$, MgCaATPase. Inset, standard MgATPase, with Ca$^{2+}$ (\$\Delta\$) or La$^{3+}$ (\$\Delta\$), or Ca$^{2+}$ plus La$^{3+}$ (\$\bigcirc\$), at the concentrations indicated.](http://www.jbc.org/)

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La³⁺ above 0.2 mM all ATPase activities were strongly inhibited. These observations suggest a competition between Ca²⁺ and La³⁺ to activate ATPase. We have observed that Na⁺ and K⁺ (100 mM) inhibited ATPase activity when assayed in the presence of Mg²⁺, Ca²⁺ or Mg²⁺ and Ca²⁺. Similar observations have been reported for ATPase of muscle sarcoplasm isolated by another procedure (25). In contrast, Na⁺ and K⁺ (100 mM) were found to inhibit ATPase activity when assayed in the presence of Mg²⁺, Ca²⁺ or Mg²⁺ and Ca²⁺. Similar observations have been reported for ATPase of muscle sarcoplasmic reticulum.

Formation of Phosphoprotein—When sarcolemmal membranes were incubated in the presence of [γ-³²P]ATP at 0° or 37° there was a rapid incorporation of ³²P into the trichloroacetic acid-insoluble residue (Fig. 7A). Because of high ATPase activities at 37°, it was convenient to examine the incorporation of ³²P at 0°. Transfer of the terminal phosphate of ATP to membrane protein was markedly stimulated by Ca²⁺ in the absence or presence of Mg²⁺ (Fig. 7B). Maximal incorporation of phosphate occurred with Mg²⁺ and Ca²⁺ together.

Phosphorylation of membrane protein did not display a sharp dependency on pH, but was readily measurable from pH 5.5 to 9; however, a maximum occurred at pH 8.0 with possibly a smaller maximum at pH 5.5 to 6. Martonosi (12) has reported similar findings for sarcoplasmic reticulum. Phosphorylation of the membranes was strongly dependent on ATP concentration (Fig. 8). The response to ATP seemed somewhat biphasic in the presence of Mg²⁺ and Mg²⁺ plus Ca²⁺, making it difficult to determine a precise Kₐ value. The ATP dependency seems similar to that reported by Inesi et al. (13) for sarcoplasmic reticulum, but de Meis (28) failed to observe such ATP dependency.

When denatured with trichloroacetic acid, phosphate was readily removed from the phosphoprotein with hydroxylamine (Fig. 9). The phosphoprotein was relatively stable at acidic pH but was labile at alkaline pH values (Fig. 9, inset). Relative stability to acidic pH and lability in the presence of hydroxylamine suggest the linkage of phosphate to protein may be of the acyl phosphate type. It is known that the phosphoprotein intermediate of sarcoplasmic reticulum is sensitive to hydroxylamine (12-14). These activities bear a number of similarities to those of sarcoplasmic reticulum (4). There are some differences however: (a) Na⁺ and K⁺ stimulate MgCaATPase of sarcoplasmic reticulum while they inhibited this activity in sarcolemma; (b) CaATPase of sarcolemma is greater than MgATPase while in sarcoplasmic reticulum these two activities were similar; (c) sarcoplasmic reticular ATPase hydrolyzed ADP much more rapidly (compared to ATP) than the enzyme from sarcolemma; (d) p-nitrophenylphosphatase of sarcoplasmic reticulum was greatly stimulated at Ca²⁺ and K⁺ (3- to 5-fold) while sarcosomal activities were stimulated only 1.5- to 2-fold; (e) the specific activities of sarcolemmal ATPase

![Fig. 7 (left). Effect of time and cations on phosphoprotein formation. A, membrane (134 μg) was incubated in the standard assay for the times indicated at 0° (---) and 37° (---), with 5 mM Mg²⁺ plus 0.5 mM EGTA, (O); and with no added metal ion plus 12.5 mM EGTA, (Δ). B, the time of incubation was 30 s (258 μg of protein) using Mg²⁺ (○); Ca²⁺ (△); and Mg²⁺ plus Ca²⁺ (Δ) as indicated. Values are corrected for controls carried out with no added cation and containing 12.5 mM EGTA. Temperature, 0°.](http://www.jbc.org/)

![Fig. 8 (right). Dependency of phosphoprotein formation on ATP concentration. Sarcolemmal protein (397 μg) was incubated at 0° in the standard reaction except that ATP concentration was varied. Metal ion additions were: ○, 5 mM MgCl₂ (±0.5 mM EGTA); △, 5 mM CaCl₂; Δ, 5 mM MgCl₂ plus 1 mM CaCl₂; O, difference between MgCl₂ plus CaCl₂ and MgCl₂ alone.](http://www.jbc.org/)

![Fig. 9 (left). Hydroxylamine reactivity and pH stability of phosphoprotein. Sarcolemmal membranes (6 mg of protein) were incubated in a medium containing 50 mM imidazole HCl, pH 7.5, 1 mM ATP (1250 cpm per mole), 2 mM CaCl₂ (Δ), 5 mM MgCl₂ (○), or 5 mM MgCl₂ and 2 mM CaCl₂ (O) at 0° for 30 s in a final volume of 2 ml. The reaction was stopped by the addition of 4 ml of 12% trichloroacetic acid. After centrifugation the residues were washed twice with trichloroacetic acid, then with 10 ml of H₂O. The residue was suspended in 3 ml of H₂O. Aliquots (200 μl) were incubated in 125 mM Tris-maleate, pH 5.0 in the presence of 0.4 mM (- - -), and 0.9 mM (+ +) hydroxylamine, or 0.8 mM KCl (- - -) at 23° for the times indicated (final volume, 2 ml). Trichloroacetic acid (2 ml) was added, the suspension was centrifuged and washed once with H₂O. The sediment was dissolved in 1 ml NaOH for determination of radioactivity. Additional 200-μl aliquots were added to 1.8 ml of 125 mM Tris-maleate buffer at the pH values indicated (inset), after 1 hour at 23°, the suspensions were sedimented, washed, dissolved, and counted as above.](http://www.jbc.org/)

![Fig. 10 (right). Effect of Ca²⁺ on MgATPase and phosphoprotein formation. MgATPase was measured under standard conditions (155 μg of protein) with 5 mM ATP. Phosphoprotein formation was measured at 0°. CaCl₂ was added to each assay at the concentrations indicated. Phosphoprotein, ○; MgATPase, Δ.](http://www.jbc.org/)
and p-nitrophenylphosphatase are lower than those of sarcoplasmic reticulum.

The membrane preparation used in these studies consisted of empty tubular structures devoid of visible myofibrillar contamination when examined by phase contrast microscopy (6). We have described (15) detailed experiments which eliminated sarcoplasmic reticulum as a contaminant. To examine further possible presence of myofibrillar and actomyosin ATPase, experiments were conducted in which the final KBr extraction was repeated. It was at this step that much of these proteins are removed.

In two preparations the mean activities of MgATPase MgCaATPase, and CaATPase were 0.12, 0.28, and 0.27 μmole of P1 per mg of protein per min, respectively. In one preparation the specific activity of adenylate cyclase was 1322 pmole of cyclic AMP per mg per min, a 36-fold increase over the starting homogenate with a yield of 53%. After a second extraction with 25% KBr mean MgATPase, and MgCaATPase of the membrane preparation were unchanged, 0.13 and 0.26 μmole of P1 per mg per min, respectively; CaATPase was 0.16 μmole of P1 per mg per min. Thus, we feel that remaining myofibrillar ATPase was effectively removed by one extraction with KBr.

Weiner and Lee (22) observed that La3+ inhibited CaATPase activity of red cell membranes; however, there was no effect of this cation on MgATPase. Entman et al. (29) reported that La3+ did not affect MgCaATPase of heart microsomes. In the present study, La3+ at concentrations of 0.1 to 0.2 mM strongly stimulated MgATPase of sarcosome (and sarcoplasmic reticulum). These concentrations slightly inhibited Ca2+ binding and accumulation by sarcosomal membranes (15).

Sarcolemmal membranes were phosphorylated by [γ-32P]-ATP and the reaction was significantly stimulated by Ca2+ in the presence or absence of Mg2+. Protein phosphorylation and ATPase showed a similar response to Ca2+ concentration. Similarly, ATPase and phosphoprotein formation showed a similar ATP dependency. These observations might support the view that the phosphoprotein intermediate formed by MgCaATPase may participate in the active binding of Ca2+. This idea is supported by the fact that phospholipase C treatment of minced muscle inactivated both Ca2+ binding and MgCaATPase (15).

Stability of the phosphoprotein to acid pH, lability to alkaline pH, and to hydroxylamine would be compatible with formation of an acyl phosphate. In these regards the phosphoprotein possesses properties analogous to that described by several workers for sarcoplasmic reticulum (12-14). Thus, the sarcolemmal Ca2+ binding system and ATPase may represent a common structure, or discrete proteins. Recently, MacLennan et al. (30) and Lehninger and co-workers (31) have isolated a Ca2+ binding protein from sarcoplasmic reticulum and mitochondria. These proteins are devoid of ATPase activity suggesting separate systems for Ca2+ binding and ATPase action. The significance of the CaATPase activity reported here is not clear. The presence of this activity in preparations containing MgATPase has been observed in a number of membranes from different tissues. Since ATP-dependent Ca2+ uptake requires Mg2+ (15), it is attractive to consider that it is the Ca2+-stimulated MgATPase (MgCaATPase) which might mediate this process.

The transport of Ca2+ across the muscle plasma membrane must be an active process, since a concentration difference of ionized Ca2+ of at least three orders of magnitude exists between intra- and extracellular compartments (32). An involvement of ATPase in the process could therefore be envisaged. The existence of an active calcium pump in sarcolemma has been previously considered (32). The presence of an active Ca2+ binding system (15) and ATPase in these membranes provides support for this concept.

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